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DENIS LEPAGE

Variation saisonnière du succès reproducteur chez la Grande Oie des neiges *(Chen caerulescens atlantica*)

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
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Ce 24 jour du mois de avril 19 97 , les personnes soussignées , e
leur qualité de membres du jury de la thèse de Monsieur Denis Lepage
ont assisté à la soutenance de cette thèse.

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André Desrochers	Université Laval	
Cyrille Barrette	Université Laval	
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SIGNATURE DU PRÉSIDENT DE LA SOUTENANCE

RÉSUMÉ SUCCINCT

L'objectif de cette thèse était d'examiner les variations saisonnières du succès reproducteur chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans l'arctique canadien, et d'en comprendre les causes. De façon générale, le succès reproducteur décline avec la progression de la saison, mais tous les paramètres ne sont pas affectés de la même manière. Nous avons détecté un déclin saisonnier de la taille de ponte et de la survie et de la croissance des jeunes. Il existe toutefois un coût au niveau du succès de nidification pour les parents les plus hâtifs. Nous avons également réalisé des échanges de couvées entre des parents de différente qualité de façon à déterminer la contribution relative de la qualité des parents et des conditions environnementales sur les variations de succès des jeunes. Ces expériences montrent que les variations de qualité parentale ne jouent pas un rôle important lors de l'élevage des jeunes.

Denis Lepage – Candidat

Gilles Gauthier – Directeur de recherche

RÉSUMÉ DE LA THÈSE

L'objectif de cette thèse était d'examiner les variations saisonnières du succès reproducteur chez la Grande Oie des neiges (*Chen caerulescens atlantica*) et d'en comprendre les causes. Les données ont été recueillies à l'île Bylot (T.N.-O.), dans l'arctique canadien, entre 1988 et 1995. Les fortes contraintes saisonnières de l'Arctique forcent les couples nicheurs à changer presque chaque année leur site de nidification, ce qui contraste avec la grande fidélité au site habituellement observée chez les oies. Les avantages associés à la fidélité sont possiblement moins importants que les coûts associés à un délai de la nidification. En effet, les résultats démontrent que les effets saisonniers sur les différentes composantes du succès reproducteur sont considérables et que de façon générale, le succès reproducteur décline avec la progression de la saison. Nous présentons aussi un modèle pour tenter de comprendre pourquoi la majorité des individus semblent se comporter de façon sub-optimale. Des variations saisonnières dans l'environnement ou des différences dans la qualité parentale sont deux hypothèses qui peuvent expliquer les variations saisonnières du succès reproducteur. Une analyse détaillée du taux de croissance des jeunes démontre qu'une grande partie de la variation intra- et inter-annuelle de la croissance peut être expliquée par des variations saisonnières dans la disponibilité de la nourriture. L'hypothèse que des variations de qualité parentale entre les parents hâtifs et tardifs peuvent expliquer une partie du déclin saisonnier de la survie et de la croissance des jeunes a été vérifiée en échangeant des couvées entre des parents hâtifs et tardifs. Nos résultats montrent que la survie et la croissance des jeunes n'ont pas été affectées par le changement de qualité parentale et donc que ce facteur ne contribue pas au déclin saisonnier. Nous avons aussi examiné par des manipulations de taille de couvée si la relation entre la taille de couvée et la croissance et la survie des jeunes est une conséquence de différences dans l'habileté des parents à élever les jeunes. Ces expériences démontrent que l'habileté des parents à élever des jeunes ne limite pas la taille de couvée.

Denis Lepage – Candidat

Gilles Gauthier – Directeur de recherche

ABSTRACT

The objective of this thesis was to examine the seasonal variations of reproductive success in greater snow goose (*Chen caerulescens atlantica*) and to understand their causes. The data were collected at Bylot Island (N.W.T.), in the Canadian Arctic, from 1988 to 1995. The strong seasonal constraints force breeders to modify the nest site location among years, which contrasts with the usually high nesting site fidelity in geese. The advantages of site fidelity are probably smaller than the cost associated with delayed nesting. Indeed, our results show that the seasonal effects on the various components of reproductive success are considerable and that reproductive success generally declines with nesting date. We also present a model that allows us to understand why the majority of the individuals seem to behave sub-optimally. Seasonal variations of environment or differences in parental quality are two hypotheses that could explain the seasonal variations of reproductive success. A detailed analysis of gosling growth rate shows that a large part of intra- and inter-seasonal variation in growth rate can be explained by seasonal variations of food availability. We verified the hypothesis that differences in parental quality are responsible for the seasonal decline in offspring success by exchanging broods between early and late nesters. Our results showed that variations in parental quality do not contribute to the seasonal variation of offspring success. Similarly, we examined, by manipulating brood size, the role of parental quality in the relationship between brood size and gosling growth and survival rate. Our results showed that parental ability to raise offspring does not limit brood size.

Denis Lepage – Candidat

Gilles Gauthier – Directeur de recherche

AVANT-PROPOS

Est-il vraiment possible de remercier tous les gens qui ont contribué à la réalisation de ce travail ? Tellement de gens ont participé au cours des ans au projet de l'île Bylot que je crains fort d'en oublier plusieurs. Mon premier remerciement va d'emblée à mon directeur de thèse, Gilles Gauthier, pour sa magnifique organisation du travail, sa disponibilité malgré un horaire chargé, son amitié, et surtout pour m'avoir permis de retourner toutes ces années dans l'arctique. Je veux aussi particulièrement remercier Austin Reed, le co-responsable de ce projet d'envergure, pour ses précieux conseils et sa passion de l'Arctique.

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Note: La majeure partie de la thèse (chapitres 1 à 5) est constituée d'article qui ont été soumis ou seront soumis à diverses revues scientifiques de langue anglaise. Je suis l'auteur principal de ces articles dans tous les cas. En plus de mon directeur de thèse, les coauteurs (Austin Reed aux chapitres 1 et 3, et André Desrochers aux chapitres 4 et 5) ont soit contribué lors de l'élaboration des objectifs des chapitres respectifs ou de par leurs commentaires sur les versions préliminaires des manuscrits. Le chapitre 1 a été publié en 1996 dans la revue *Canadian Journal of Zoology* (vol 74, p.1866–1875), tandis que les chapitres 2 et 5 ont respectivement été soumis aux revues *Ecology* et *Journal of Animal Ecology*.

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INTRODUCTION

Depuis longtemps, les naturalistes, et plus récemment les écologistes du comportement, essaient de comprendre les causes et les conséquences des variations du succès reproducteur chez les populations animales. Darwin fut l'un des premiers à reconnaître que le “but” ultime d'un organisme vivant est d'assurer la transmission de ses caractères dans les générations subséquentes via sa descendance. Ce concept a relativement peu évolué depuis Darwin, si ce n'est que l'on connaît maintenant beaucoup mieux les mécanismes impliqués dans la transmission des caractères, d'abord grâce aux travaux de Mendel (1866) sur l'hérédité, puis grâce à la découverte du rôle de l'ADN dans le codage génétique par Avery, MacLeod et McCarthy (1944). La théorie que Darwin a défendue dans son livre *The Origin of Species* (1859), la survie du mieux adapté via la sélection naturelle (*survival of the fittest through natural selection*), demeure le meilleur outil dont nous disposons pour comprendre et analyser les variations dans le comportement et les stratégies reproductrices chez les êtres vivants.

Tous les organismes vivants sont soumis à un grand nombre de contraintes diverses et ceux-ci doivent régulièrement faire des compromis afin de maximiser leur succès reproducteur, c'est-à-dire le nombre de descendants viables et capables de se reproduire, produits au cours de leur vie. Il existe par exemple un compromis inévitable entre le nombre de descendants produits et la qualité de ceux-ci : les espèces dites de stratégie *r* investissent la majorité de leur énergie reproductrice dans la production d'un grand nombre d'ovules et ne prodiguent pas de soins parentaux, tandis que les espèces de stratégie *K* sont des organismes qui consacrent une part importante de leur énergie aux soins parentaux et produisent relativement peu de descendants, souvent après une longue période de maturation juvénile. Les cas les plus extrêmes de cette stratégie se retrouvent chez les mammifères, qui investissent davantage dans la qualité de leurs descendants au détriment de leur nombre.

À l'intérieur d'un groupe taxinomique, parmi des individus qui partagent sensiblement les mêmes contraintes et les mêmes caractéristiques, on retrouve aussi des variations dans les stratégies reproductrices. À l'intérieur d'une même population, les comportements varient de façon individuelle, une conséquence de l'interaction entre les variations dans le bagage génétique individuel et les facteurs d'ordre environnemental. Évidemment, tous les comportements ne représentent pas nécessairement la même valeur adaptative. En fait, il n'est pas inhabituel que seule une faible proportion des individus réussissent à se reproduire avec succès, contribuant à la presque totalité des descendants produits, alors que la majorité des individus ne produisent aucun descendant viable (Newton 1989). Dans ce contexte, on définit alors la qualité d'un individu selon son efficacité à transmettre ses gènes par rapport aux autres individus de la population.

Variations saisonnières du succès reproducteur

Un phénomène universel dans les variations intra-spécifiques est celui qui relie le moment de la reproduction dans le cycle annuel avec le succès reproducteur (insectes : Ohgushi 1991, Cushman et al. 1994; poissons : Schultz 1993, Cushing 1990; mammifères : Clutton-Brock et al. 1982). Chez les oiseaux, la plupart des composantes du succès reproducteur, tel le nombre d'oeufs pondus, la viabilité des jeunes ou la probabilité qu'ils deviennent eux même des adultes reproducteurs, varient également selon le moment de la nidification. Le plus souvent, les parents qui nichent tôt obtiennent un meilleur succès reproducteur que les parents tardifs (Perrins 1970, Daan et al. 1988).

La taille de couvée est certainement l'une des composantes qui a reçu le plus d'attention dans la littérature. Le déclin saisonnier du nombre d'oeufs pondus par la femelle a été rapporté par la vaste majorité des études, chez une grande variété d'espèces (Klomp 1970). En présence d'un phénomène aussi généralisé, il est normal de tenter de lui trouver une explication unique. Plusieurs auteurs ont examiné les causes immédiates (*proximate factors*) du déclin, alors que d'autres se sont plutôt attardés aux causes fondamentales (*ultimate factors*) et il est crucial de faire la distinction entre ces deux niveaux de réponses.

Au cours de ma thèse, je ne m'attarderai pas en détail aux causes immédiates qui affectent la taille de ponte et le moment de la nidification. Toutefois, il semble que la condition physique des individus soit l'un des facteurs les plus importants : les individus en bonne condition réussissent généralement à nicher plus tôt et à pondre plus d'oeufs (Daan et al. 1988). De nombreuses expériences d'alimentation ont aussi montré qu'en augmentant la condition des individus, on pouvait aussi avancer le moment de ponte et augmenter le nombre d'oeufs dans la couvée (voir la revue dans Daan et al. 1988 et Boutin 1990). D'autres auteurs ont examiné le rôle de la disponibilité des ressources alimentaires avant la ponte et ont proposé que la taille de ponte était conditionnée par celle-ci (Perrins 1965, 1970, Lack 1967, 1968). Toutefois, si la disponibilité de la nourriture pendant ou avant la ponte peut effectivement limiter le nombre d'oeufs, il est peu probable qu'elle puisse expliquer le déclin saisonnier. En effet, durant la période de formation des oeufs, soit au début de la saison de reproduction, les ressources disponibles augmentent plutôt que de diminuer avec l'avancement de la saison. Dans la littérature, les oies arctiques ont souvent été citées comme une exception à cette règle, notamment suite aux études de Ryder (1970) et de Ankney et MacInnes (1978). Ces études, réalisée sur l'Oie de Ross (*Chen rossii*) et la Petite Oie des neiges (*Chen caerulescens caerulescens*) avaient suggéré que les femelles ne s'alimentaient pas sur les aires de reproduction et ne comptaient que sur les réserves accumulées sur les aires migratoires pour la vitellogénèse. Donc, les oies ne pouvaient tirer aucun avantage de l'augmentation des ressources alimentaires avec la saison, alors que leurs réserves s'épuisaient avec le temps. Toutefois, des études plus récentes sont venues contredire cette idée et ont montré que les oies s'alimentent parfois de façon importante avant la ponte (Budeau et al. 1991, Gauthier et Tardif 1991, Bromley et Jarvis 1993, Choinière et Gauthier 1995, Ganter et Cooke 1996, Carrière 1996).

Les effets saisonniers sur les autres composantes du succès reproducteur ne sont toutefois pas aussi bien documentés. Ceci tient en partie à la difficulté de recueillir les données nécessaires pour évaluer la survie des jeunes ayant quitté leur nid ou leurs chances de recrutement dans la population nicheuse. Malgré tout, des études ont montré que dans plusieurs populations les jeunes éclos plus tôt ont de meilleures chances de survie et de recrutement (Perrins 1965, 1966, von Haartman 1967, Cavé 1968, Nisbet et Drury 1972, Harris 1980, Dow et Fredga 1984, Harris *et al.* 1992, Newton et Marquiss 1984, Gauthier 1989, Tinbergen et Boerlijst 1990, van Noordwijk et al. 1995), alors que chez d'autres, la date a peu d'influence sur leur succès (Parsons et al. 1976, Hedgren 1981, Kersten et Brenninkmeijer 1995, De Forest et Gaston 1996). Parmi les éléments les plus importants identifiés comme cause immédiate du déclin saisonnier du succès des jeunes, on retrouve le déclin saisonnier de la disponibilité de la nourriture (Eriksson 1978, Verhulst et Tinbergen 1991). En théorie, les oiseaux devraient synchroniser le moment de la croissance des jeunes, alors que la demande en nourriture est la plus forte, avec le pic de disponibilité de nourriture. Selon ce scénario, les nicheurs tardifs auraient une éclosion qui surviendrait après le pic d'abondance de nourriture et auraient donc accès à moins de ressources que les individus hâtifs (Daan et al. 1988). Une différence saisonnière dans les risques de prédation, surtout chez les espèces coloniales, pourrait aussi expliquer une partie de la variation de survie des jeunes. Finalement, une différence entre la qualité des parents hâtifs et tardifs peut aussi être en cause (Brinkhof et al. 1993, Verhulst et al. 1995). Si les parents qui réussissent à nicher tôt sont des individus de meilleure qualité (Drent et Daan 1980), il se peut qu'ils soient aussi plus efficaces dans les soins qu'ils apportent à leurs jeunes, soit par un meilleur apport en nourriture ou une protection accrue contre les prédateurs.

Le modèle de Drent et Daan

Le déclin saisonnier du succès reproducteur soulève un paradoxe : puisque le meilleur succès est atteint par une minorité d'individus hâtifs, la majorité de la population se comporterait de façon sub-optimale, contredisant ainsi les préceptes établis par la sélection naturelle. Dans certains cas, il est possible que des changements récents dans l'environnement aient amené un déséquilibre temporaire et que la population évolue vers une nidification plus hâtive, mais on ne saurait sérieusement généraliser cette explication à toutes les populations.

Le modèle proposé par Rudolf Drent et Serge Daan (1980), qui a la qualité de savoir réconcilier le phénomène du déclin saisonnier avec la théorie de la sélection naturelle, précise que le moment optimal de nidification est une caractéristique individuelle déterminée par la condition corporelle de la femelle. À cause des coûts potentiels associés à un délai de la nidification sur le succès reproducteur, et à cause du temps requis pour produire les oeufs, leur modèle prédit une combinaison optimale de taille de couvée et de date de nidification pour chaque individu, en fonction de son habileté à recueillir des nutriments de son environnement et/ou de sa condition corporelle. À une date donnée, les coûts (le temps nécessaire pour accumuler plus de ressources, selon un taux d'accumulation spécifique à chaque individu) et les bénéfices relatifs (une augmentation du nombre de descendants potentiels) devraient déterminer si la femelle doit ou non retarder sa date de ponte pour augmenter la taille de celle-ci (Figure 1). Leur modèle prédit aussi que le déclin saisonnier devrait être moins prononcé dans les environnements où les variations saisonnières du succès des jeunes sont moins fortes, comme les milieux tropicaux, et plus prononcé chez les populations exposées à de fortes contraintes saisonnières (Klomp 1970, Briggs 1993, Young 1994).

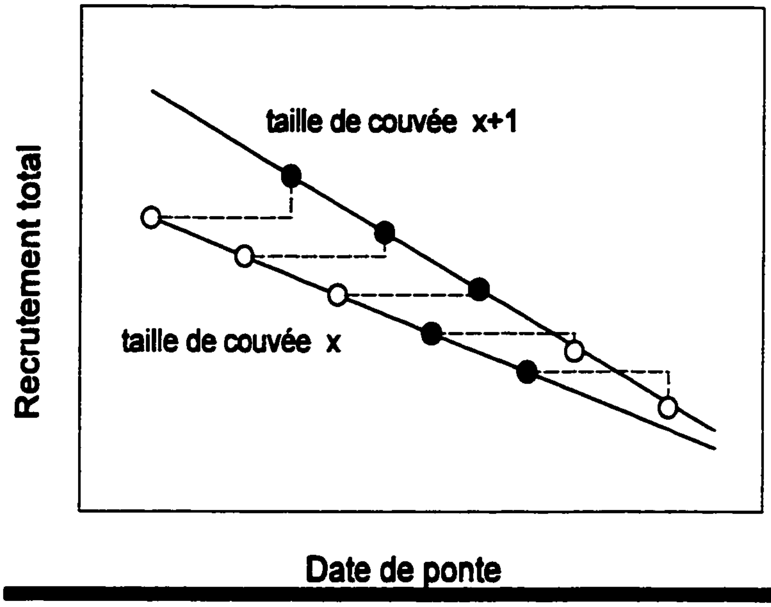

Figure 1. Modèle de Drent et Daan (1980) permettant de prédire la taille de ponte selon la date de ponte et le déclin saisonnier du succès des jeunes. Les points pleins illustrent la décision optimale. À cause du déclin saisonnier de la valeur de chaque jeune, la contribution d'un oeuf additionnel au recrutement total diminue avec la date de ponte. Si le temps nécessaire à l'accumulation des nutriments pour l'ajout d'un oeuf (couvée x + 1 illustré par le trait pointillé) est constant, les parents hâtifs devraient attendre et pondre x + 1 et les parents tardifs devraient pondre x oeufs.

Objectifs de la thèse

Mon objectif principal, au cours de cette thèse, sera donc de mesurer les conséquences de la date de nidification sur le succès reproducteur de la Grande Oie des neiges (*Chen caerulescens atlantica*) et de tenter de comprendre, avec une approche expérimentale, les mécanismes qui sont en cause. À cause de son environnement de nidification extrêmement saisonnier, de la dépendance exclusive des jeunes envers une ressource relativement peu nutritive mais facilement quantifiable (les plantes graminoïdes) et de la facilité d'obtenir de grands échantillons à cause de son mode de reproduction colonial, cette espèce est un sujet de choix pour réaliser cette étude.

Les composantes du cycle reproducteur

Le diagramme présenté à la figure 2 permet de mieux exprimer les relations entre les différentes composantes impliquées dans le succès reproducteur chez les oiseaux. Dans ce diagramme, j'ai illustré les mécanismes qui sont à mon sens les plus importants pour comprendre le succès reproducteur. Je vais utiliser ce diagramme pour expliquer le cas des oies arctiques en particulier, mais il pourrait tout aussi bien permettre d'expliquer la situation chez la plupart des autres espèces d'oiseaux. Je vais définir chaque composante de la figure et expliquer quels sont les mécanismes qui l'influencent. Ce diagramme est évidemment une simplification de la réalité et il est probable que certains facteurs ou composantes ou mécanismes n'y soient pas illustrés. De même, il est possible que certains des mécanismes illustrés n'aient pas un effet prépondérant pour expliquer les variations de succès reproducteur entre les individus. Dans le diagramme, les cases ombragées illustrent les composantes mesurables du fitness des parents. Ce sont ces composantes qui sont utilisées lorsque vient le temps d'évaluer le succès reproducteur (cf. chapitre 2). Ainsi, la taille de couvée [6] et le succès de nidification [5] par exemple, sont des composantes directes du succès reproducteur, alors que la date de nidification est un facteur qui l'influence.

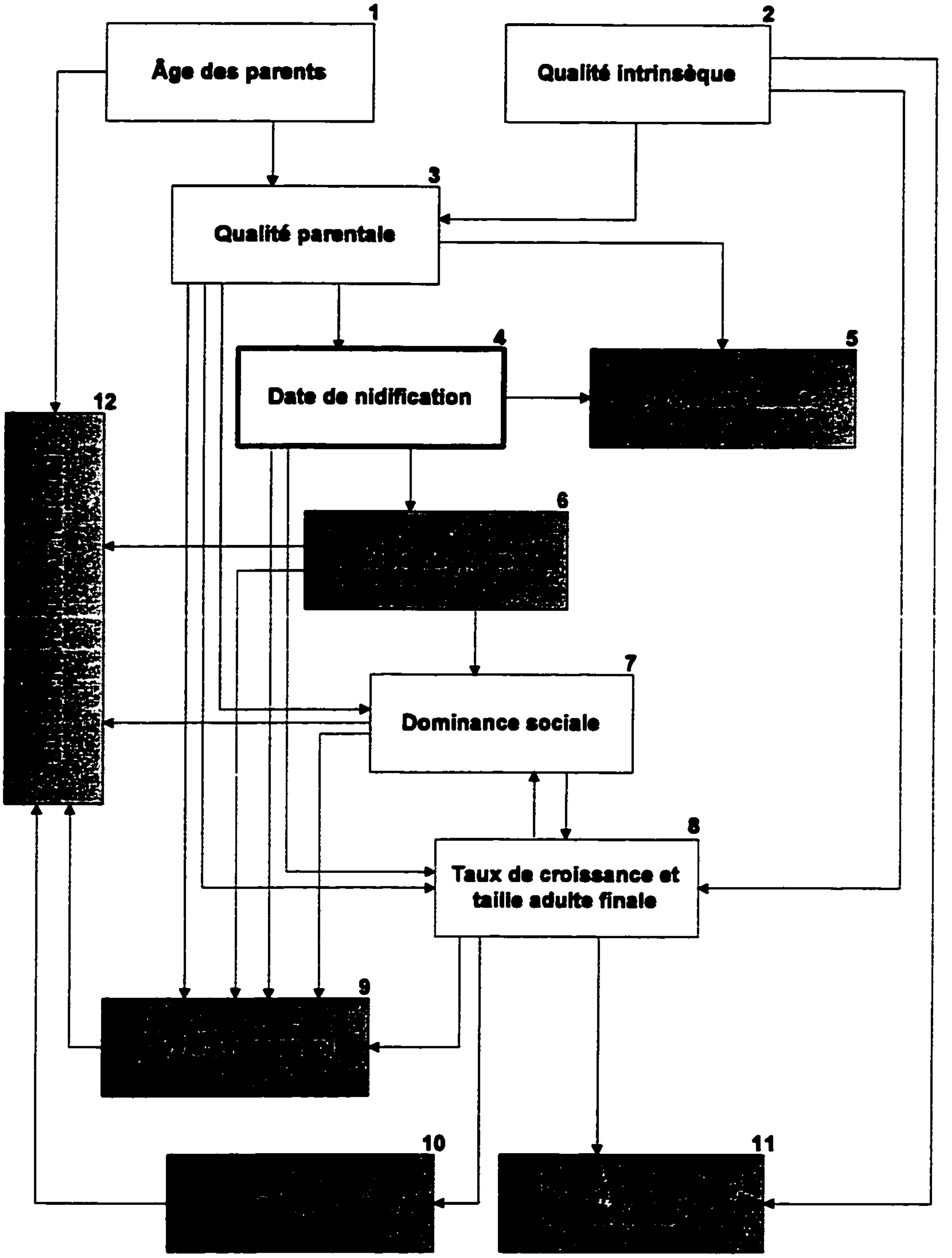

Figure 2. Diagramme illustrant les facteurs (cases blanches), les différentes composantes du succès reproducteur (cases ombragées) et les mécanismes (flèches) qui permettent de comprendre le succès reproducteur chez les oiseaux.

1. **Âge des parents.** L'expérience et la sénécence sont deux processus qui se déroulent à mesure que les adultes vieillissent. D'abord, les individus prennent de l'expérience et deviennent plus efficaces dans l'accomplissement des processus vitaux (e.g. alimentation), ce qui leur permet d'améliorer leur succès reproducteur. Il est connu chez de nombreuses populations aviaires par exemple, que les individus nichent plus tôt et que leur taille de couvée augmente à mesure qu'ils vieillissent. D'autre part, au moins une étude a aussi montré que, passé un certain âge, les capacités reproductrices déclinaient à cause de la sénécence (Cooke et al. 1995). Toutefois, ce phénomène ne devrait se manifester que chez les espèces longévives.

2. **Qualité intrinsèque** (génotypique). Ce terme est difficile à définir précisément sans faire appel à la notion de succès reproducteur, puisque c'est elle qui détermine en bout de ligne la qualité d'un individu. Cependant, bien que les études soient peu exhaustives sur le sujet, on peut facilement concevoir qu'il existe des différences génétiques qui permettent à certains individus d'atteindre un meilleur succès, indépendamment de leur expérience. Parmi les mécanismes possibles, on peut penser à une plus grande efficacité physiologique à assimiler les nutriments, une plus grande capacité d'apprentissage, une taille corporelle plus grande permettant un entreposage de réserves (graisses, protéines, etc.) supérieur, ou encore une plus grande agressivité. Contrairement à l'expérience, cette composante ne change pas avec le temps pour un individu adulte, puisqu'elle est entièrement définie dans son bagage génétique.

3. **Qualité parentale** (phénotypique). Par ce terme, j'entends "l'habileté à produire des oeufs et à donner des soins parentaux" que l'on peut effectivement observer et mesurer sur le terrain. C'est la combinaison de la qualité intrinsèque des parents [2→3] et de leur expérience [1→3].

4. **Date de nidification.** C'est le thème central de mon étude. En termes absolus, elle est déterminée par des phénomènes environnementaux comme la disponibilité de la nourriture et les conditions météorologiques (cf. chapitre 1). Il existe aussi des différences entre les individus dans la date de nidification au sein d'une même population au cours d'une même année. En termes relatifs (date de nidification d'un individu par rapport à la moyenne de la population), elle est probablement largement déterminée par la qualité relative des individus [3→4] comme il sera surtout discuté au chapitre 2.

5. **Survie des oeufs.** Dans cette expression, j'entends ici à la fois le succès de nidification tel que défini aux chapitres 1 et 2, mais aussi la proportion des oeufs pondus qui réussissent à

éclore et à produire un jeune. Puisque les oies nichent en colonie, la date relative de nidification peut avoir un impact sur les chances de survie des oeufs [4→5]. De même, tous les individus n'ont pas nécessairement la même habileté à défendre leur nid [3→5], soit à cause de leur agressivité ou parce qu'une faible condition physique peut les obliger à quitter le nid davantage pour se nourrir. Ces mécanismes sont surtout décrits au chapitre 2, mais aussi au chapitre 1.

6. **Taille de ponte**. Un des thèmes centraux des chapitres 2 et 5. Ici, je ne suis pas vraiment intéressé à comprendre les mécanismes évolutifs qui font que la taille de ponte se situe dans un intervalle donné, mais plutôt à expliquer les variations actuelles qui existent entre les individus et particulièrement le déclin saisonnier de la taille de couvée [4→6] (cf. chapitre 2).

7. **Dominance sociale** (accès aux ressources). Cette composante est importante pour des espèces grégaires comme les oies. Plusieurs faits suggèrent que l'accès aux ressources alimentaires fait l'objet d'une compétition entre les individus, aussi bien sur l'aire de nidification que sur les aires d'hivernage. Bien qu'il puisse exister une hiérarchie de dominance au sein d'une même unité familiale, c'est la dominance entre les familles qui semble la plus importante. Les parents jouent probablement un rôle important dans l'établissement de la dominance entre les familles [3→7], mais elle est aussi influencée par la taille de la famille [6→7] et peut-être même par la taille corporelle des individus [8→7]. Le rôle respectif des parents et de la taille de la famille sur la dominance est discuté au chapitre 5.

8. **Croissance des jeunes et taille adulte finale**. Les variations dans la croissance des jeunes est le thème central du chapitre 3, principalement en fonction de la date [4→8]. Le rôle de la date se fait vraisemblablement sentir surtout via des changements dans la disponibilité de la nourriture, bien que des effets reliés aux conditions climatiques ne soient pas exclus (cf. chapitre 3). La qualité des parents peut contribuer à la croissance des jeunes [3→8], via par exemple le choix des habitats d'élevage. La taille de la couvée peut aussi jouer un rôle dans la croissance, probablement par l'entremise de la dominance sociale (c.-à-d. un meilleur accès à la nourriture) [7→8]. Finalement, plusieurs études ont montré une forte héritabilité de la taille corporelle [2→8]. Toutefois, malgré certaines assertions, rien ne permet encore de séparer sans ambiguïté l'importance relative des gènes et celui de l'environnement commun sur la taille corporelle de la descendance (cf. chapitre 3).

9. **Survie avant l'envol**. Il est plus simple ici de séparer la survie des jeunes avant et après l'envol parce que les mécanismes qui l'affectent peuvent différer. Par exemple, avant l'envol, les jeunes sont probablement beaucoup plus dépendants de leurs parents [3→9] et leur survie peut dépendre de l'habileté de ces derniers à leur procurer des sites à l'abri des prédateurs. L'effet de la date sur la survie avant l'envol [4→9] semble surtout important en termes relatifs, comme pour la survie des oeufs (voir [4→5]). La taille de couvée peut aussi avoir un effet direct sur la survie [6→9] si elle affecte l'efficacité des parents à protéger tous leurs jeunes aussi efficacement. La dominance sociale [7→9] peut aussi affecter la survie si elle permet un accès différent aux sites qui offrent la meilleure protection contre les prédateurs. Finalement, il existe certains indices qui permettent de croire que la survie des jeunes avant l'envol peut être reliée à leur croissance [8→9]. Par exemple, un jeune qui ne croît pas suffisamment rapidement pourrait être plus susceptible aux maladies ou sera moins habile pour se sauver en présence des prédateurs. Les différents mécanismes qui affectent la survie avant l'envol sont discutés plus en détail au chapitre 2.

10. **Survie après l'envol**. Un des éléments apparemment les plus déterminants dans la survie des jeunes immédiatement après l'envol est leur taille [8→10]. Cela dépend entre autres de la quantité de réserves qu'ils ont été en mesure d'accumuler avant la longue migration, mais aussi du niveau de développement des muscles nécessaires au vol. Après l'envol, les jeunes sont moins susceptibles à la prédation naturelle. Par contre, la chasse peut-être un élément déterminant dans leur survie, particulièrement durant le premier automne.

11. **Succès reproducteur des jeunes**. Peu de choses sont connues sur les éléments qui affectent les chances de recrutement des jeunes qui ont réussi à survivre jusqu'à l'âge adulte. Toutefois, certaines études, en particulier chez les anatidés, ont montré que la taille corporelle [8→11] pouvait affecter leur chance de se reproduire. D'autres études ont montré une certaine héritabilité de la taille de couvée [2→11], mais l'importance relative des gènes et de l'environnement commun des parents et des jeunes reste à démontrer.

12. **Succès reproducteur résiduel des parents**. Le succès reproducteur d'un individu ne dépend pas uniquement du nombre de jeunes qu'il réussit à élever au cours d'une saison, mais aussi du nombre de saisons durant lesquelles il réussit à se reproduire. Le succès reproducteur résiduel (après la saison en cours) peut dépendre de l'âge (risques de mortalité, sénécence) et

de l'effort que les parents investissent dans la reproduction actuelle. Un effort additionnel, l'augmentation de la taille de couvée par exemple [6→12], pourrait avoir un impact négatif sur la condition des adultes et donc sur leurs chances futures de produire d'autres jeunes. Par contre, une dominance sociale accrue [7→12], en partie favorisée par une plus grande taille de couvée, pourrait aussi permettre à la femelle un meilleur accès aux ressources et donc augmenter ses chances ultérieures de reproduction. De même, la présence de jeunes, que ce soit avant [9→12] ou après l'envol [10→12], pourrait affecter la capacité des adultes à acquérir une bonne condition corporelle s'il y avait des coûts associés à l'élevage, voire même affecter les chances de survie à cause de la plus grande susceptibilité des familles à la chasse.

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CHAPITRE 1

BREEDING SITE INFIDELITY IN GREATER SNOW GEESE: A CONSEQUENCE OF CONSTRAINTS ON LAYING DATE?

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RÉSUMÉ

Nous avons étudié les variations annuelles dans la répartition spatiale des nids et des colonies de la Grande Oie des neiges (*Chen caerulescens atlantica*) sur l'île Bylot (T.N.O.), dans le Haut-Arctique canadien, entre 1988 et 1994. La répartition et la taille des colonies dans l'aire d'étude étaient très variables d'une année à l'autre. La distance entre le centre des colonies au cours d'années consécutives variait de 2.9 à 6.9 km ($\bar{x} = 3.9$) sans chevauchement dans l'aire occupée par les colonies. La fonte des neiges, et donc la disponibilité des sites de nidification, ont aussi été très variables. Certaines années, l'aire d'étude était dégagée au moment de l'arrivée des oies, tandis que d'autres, la neige a persisté plus de trois semaines après leur arrivée. Toutefois, même dans les saisons où la fonte de la neige était la plus hâtive (1988, 1993 et 1994), les oies ont utilisé des sites très différents, autant dans les terres basses que hautes. Les oies ont niché en association avec des harfangs des neiges (*Nyctea scandiaca*) les 2 années où les harfangs ont niché et leur succès de nidification a été nettement meilleur, probablement à cause de l'effet dissuasif des harfangs sur les renards arctiques (*Alopex lagopus*), le principal prédateur des nids. Ceci suggère que la protection contre les prédateurs est un critère important lors du choix du site de nidification par les oies. Cette faible fidélité au site est inhabituelle parmi les populations d'oies arctiques. Nous suggérons que la grande variabilité annuelle dans la date de fonte de la neige, l'intensité de la prédation et la disponibilité de la nourriture avant la ponte, couplée avec la nécessité de nicher à une date optimale en raison de la courte saison de nidification dans l'Arctique, expliquent probablement ce phénomène chez cette population.

ABSTRACT

We studied annual variation in the distribution of greater snow goose (*Chen caerulescens atlantica*) nests and colonies at a High Arctic breeding site (Bylot Island, N.W.T., Canada) from 1988 to 1994. Annual distribution and size of colonies within the study area were highly variable. The distance between colony centers in successive years ranged from 2.9 to 6.9 km ($\bar{x}$= 3.9), with no overlap of the areas occupied. Timing of snow melt and nest site availability were also very variable. In some years, the area was snow-free at the time the geese arrived whereas in others, snow persisted for up to three weeks after their arrival. However, even in the 3 years of earliest snow-melt (1988, 1993 and 1994), geese used markedly different nesting areas, both in lowland and upland areas. Geese nested in association with snowy owls (*Nyctea scandiaca*) in the 2 years that owls nested and their nesting success was markedly improved, probably because of the deterring effect of owls on arctic foxes (*Alopex lagopus*), the main nest predator. This suggests that protection from nest predators is an important determinant of nest site selection. The lack of fidelity to a specific nesting location is unusual in arctic-nesting geese. We suggest that large annual variability in timing of snow melt, predation pressure, and availability of feeding areas during pre-nesting, combined with the need to lay at an optimal date because of the short arctic nesting season, probably explain the low nest-site fidelity in this population.

INTRODUCTION

Breeding site fidelity has been reported in most taxa of birds and mammals (Greenwood 1980, Greenwood and Harvey 1982). In birds, site fidelity is strongest in species whose nest sites are limited, like cliffs or burrows of some seabirds (Harris and Wanless 1991, Fairweather and Coulson 1995), or cavities of passerines (Bent 1964, Harvey et al. 1979, Drilling and Thompson 1988), owls (Bent 1961) and waterfowl (Dow and Fredga 1983, Gauthier 1990, Hepp and Kennamer 1992). However, site fidelity is also common in many ground-nesting birds where nest sites are not limited (Reed 1975, Greenwood and Harvey 1982, Gratto et al. 1985, Bollinger and Gavin 1989, Schieck and Hannon 1989, Anderson et al. 1992).

Breeding site fidelity is generally regarded as an adaptive strategy that minimizes the energy costs or increased vulnerability to predators associated with moving to a new location (Gaines and McClenaghan 1980), and the acquisition of knowledge on resource availability in unfamiliar areas (Greenwood 1980, Boyd and Richerson 1985). Pairs that nest in familiar areas often initiate nests earlier, lay larger clutches, and have higher nesting success than those that nest in a new location (Harvey et al. 1979, Newton and Marquiss 1982, Dow and Fredga 1983, 1984, Gratto et al. 1985, Korpimaki 1988, MacInnes and Dunn 1988, Gauthier 1990). Reproductive success also influences site fidelity as birds are generally more likely to return to the same site after successful nesting than after a breeding failure (Newton and Marquiss 1982, Dow and Fredga 1983, Gratto et al. 1985, Weatherhead and Boak 1986, Hepp and Kennamer 1992). However, in long-lived birds site fidelity can occasionally become maladaptive if the local environment deteriorates over the lifetime of individuals (Cooch et al. 1993, Rockwell et al. 1993, Williams et al. 1993).

Early nesting is especially important in arctic-nesting birds because of severe time constraints imposed by the short breeding season. Therefore, we would expect site fidelity to be strong in these species to minimize the time spent prospecting for a nest site. Several arctic-nesting passerines have been reported to reuse the same nest-cup in consecutive years (Wynne-Edwards 1952), unlike most passerines. Several species of arctic-nesting geese also show a high degree of nest site fidelity (Johnsgard 1978). Greylag geese (*Anser anser*, Young 1972, Newton and Kerbes 1974), pink-footed geese (*Anser brachyrhynhus*, Kerbes et al. 1971, Ferns and Green 1975) and cliff-nesting barnacle geese (*Branta bernicla*, Dementiev and Gladkov

1967, Ferns and Green 1975) often use the same nest sites during several consecutive years, though not necessarily by the same individuals. In a marked population of lesser snow geese (*Chen caerulescens caerulescens*), 72% of the females were found nesting near (<500 m) their previous year's nest site, with several females reusing the same nest cup (Cooke and Abraham 1980, see also Cooch 1958).

Here, we report on a low level of site fidelity in a goose population. Between 1988 and 1994, we monitored nesting by greater snow geese (*Chen caerulescens atlantica*) in a large glacial valley (~65 km^2) used by up to 1 000 pairs. In this paper, we show the extent of breeding site infidelity in this population, and examine the factors that may explain annual changes in nesting location.

METHODS

Study area

The study was conducted on Bylot Island (73°08'N, 80°00'W), Northwest Territories, Canada. Much of the island is occupied by mountains and glaciers, except for a large plain of ca. 1 600 km^2 in its southern part (Figure 1). Rolling hills, covered by upland tundra and isolated wetland patches and cut by numerous valleys, dominate the landscape of this plain (Reed and Chagnon 1987, Reed et al. 1992). It is the most important breeding site of greater snow geese (27 000 nesting pairs were censused in 1993, Gauthier et al. 1996) which occur in several nesting colonies on the island. Wet meadows and ponds are preferred by brood-rearing geese (Hughes et al. 1994), but geese use both wetland and dry upland habitats for nesting. Dominant plants in the wetlands are *Dupontia fisheri*, *Carex aquatilis* var. stans, *Eriophorum scheuchzeri* and *E. angustifolium* (Gauthier and Tardif 1991), whereas dry lowland and upland are dominated by *Cassioppe tetragona*, *Salix arctica* and some graminoids.

Our main study area, the Base-camp valley, is a 12km-long glacial valley (Figure 1) that includes the largest concentration of wetland habitats on the island. An area of ca. 65 km^2 was searched for nests in all years (partially in 1988-1990, thoroughly in 1991-1994). Another study area (Camp-2 area) was located about 30 km south of the Base-camp valley in habitat that was a mosaic of dry upland habitat, isolated small wetlands and a narrow river valley; an area of ca. 8 km^2 was searched for nests in 1992 and 1994.

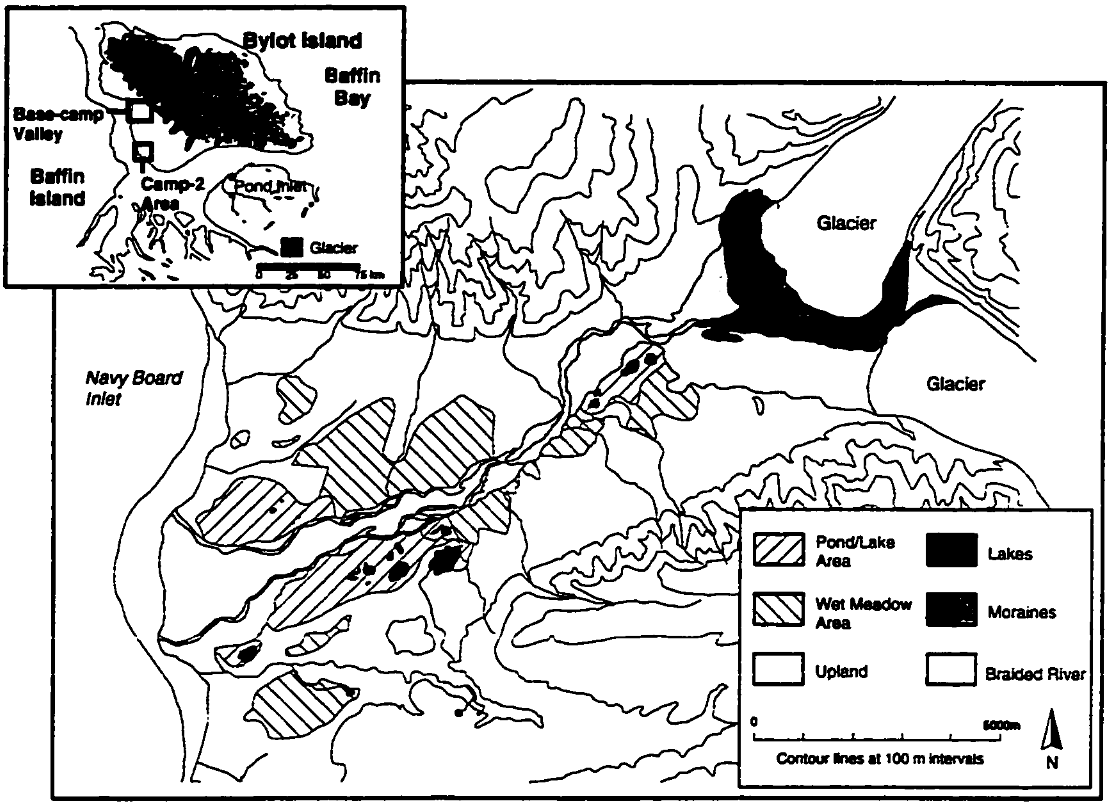

Figure 1. Location of the 2 study areas and detailed map of the main study area (Base-camp valley) showing the topography and the 2 major wetland habitats (pond/lake and wet meadows).

Field methods

Each spring, we visually evaluated the snow cover in various parts of Base-camp valley. Extensive nest searches were conducted during laying and incubation in June. Each nest was marked with a wooden stake 10 m away and its location was plotted on a large scale map (1:12 750), or determined by GPS (Global Positioning System, ±25 m) in 1993 and 1994. Eggs were marked individually and signs of predation were noted on each visit. In all years but 1988, nests were revisited at mid-incubation, during the hatching period, and after the goslings had left in order to determine their fate. Predation was the main cause of nest failure in all years. Arctic fox (*Alopex lagopus*) was the main nest predator although jaegers (*Stercorarius* *parasiticus* and *S. longicaudus*), glaucous gulls (*Larus hyperboreus*) and ravens (*Corvus corax*) also preyed on eggs.

Data analysis

Nest initiation dates were obtained by one of three different methods (listed in decreasing order of precision): 1) for nests found during egg-laying, initiation date was estimated by subtracting the number of eggs in the nest minus one to the date of discovery (if >3 eggs were present in the nest, another day was subtracted because the laying interval averages 33 hours in snow geese; Schubert and Cooke 1993); 2) for nests found during incubation but with a known hatching date, the initiation date was estimated by subtracting the clutch size (minus one if ≤3 eggs) and the incubation length (23-day; Gauthier, unpubl. data) from hatching date; 3) for nests of unknown hatching date, an egg density index (mass/length*breadth^2) was used to estimate initiation date based on the linear relationship between egg density and stage of incubation (Gauthier, unpubl. data). Methods 2 and 1 were most frequently used. Variation in median date of nest initiation among years was analyzed with a Kruskall-Wallis (K-W) analysis of variance followed by a-posteriori multiple comparisons.

A nest was considered successful when at least one egg hatched. Nesting success was calculated using the Mayfield method (Mayfield 1975, Johnson 1979). Comparisons of nesting success among years were made by applying z-tests to the daily mortality probabilities (Johnson 1979). Because this procedure is a series of pairwise comparisons, the Bonferroni correction was used to adjust the significance level ($0.05/c$ where c is the number of pairwise comparisons; α values after the Bonferroni adjustment are reported for each comparison).

Harmonic means, used to illustrate the distribution of nests and to identify areas of highest nest density, were determined with the McPAAL software (Stüwe and Blohowiak 1985). Colony center was defined as the arithmetic mean of the geographic position of each nest in the colony. Nest density was calculated for each nest based on the number of nests within a 1-ha circular area centered on the nest (minimum nest density using this method was 1 nest/ha). Mean nest density was the arithmetic mean of individual values and provided an index of nest aggregation rather than a genuine measure of nest density.

We used mean daily temperature and snow depth, from mid-May to late June, to estimate yearly variations in nest site availability. Weather data was obtained from the Pond Inlet meteorological station (65 km SSE of the study area; from 1988 to 1993) and from an automated weather station (temperature only) installed at our study site (in 1993 and 1994). Examination of the data for 1993 revealed a very close association between the two stations. We calculated correlation coefficients between median initiation date and weather variables in each year: spring temperature (average of mean daily temperature from 15 May–30 June), snow depth (on 5 June) and proportion of snow-free area in the Base-camp valley (on 5 June).

RESULTS

Annual variation in the nest distribution

Location and size of the colonies were highly variable over the 7-year study period and very few sites were used more than once (Figure 2; see also Appendix 1). In the Base-camp valley, the distance between colony centers in successive years was 2.9–6.9 ($\bar{x} = 3.9$ km) with no overlap in the area occupied by colonies. The only recurrent pattern (in 1988, 1990, 1991 and 1993) was that of a main colony (around 200-400 nests) located in the valley lowlands with single nests or small clusters of nests scattered elsewhere in the lowlands or along the hillsides. The number of isolated nests was highly variable in these years, being highest in 1991 (up to 50%; based on a visual survey during incubation).

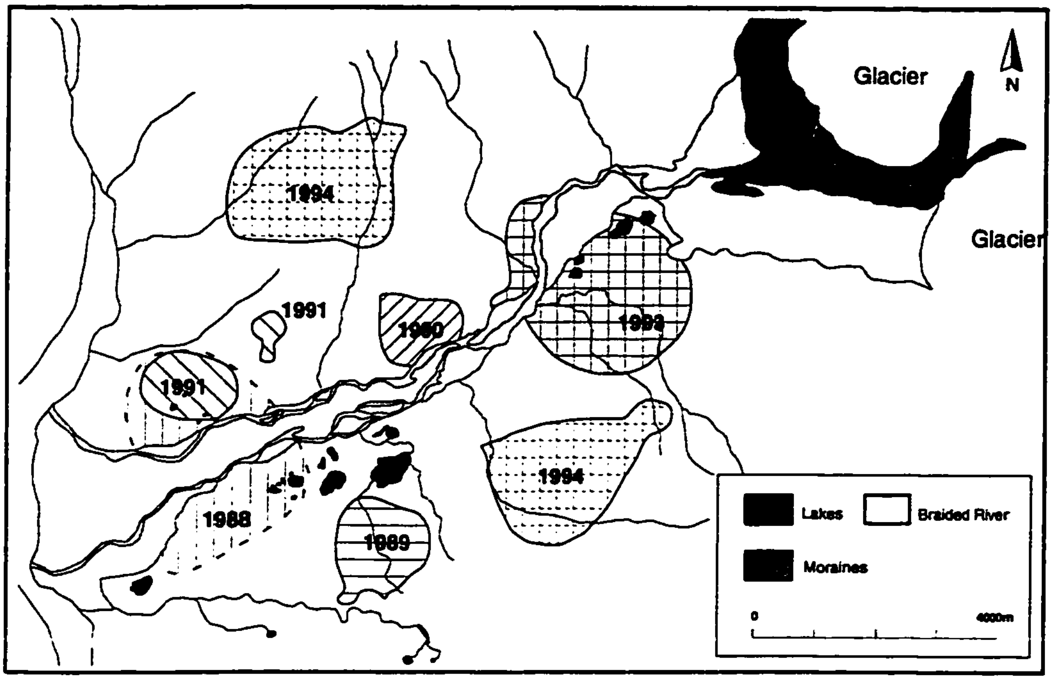

Figure 2. Location of greater snow goose colonies from 1988 to 1994 in the Base-camp valley, Bylot Island. Area occupied by colonies are contour intervals obtained with the harmonic means method based on the position of all individual nests (see methods and Figure 3 for more details). We used the contour line that best represented the extent of the main colony in each year (85% in 1989–1991 and 75% in 1993–1994), according to the dispersion of the nests. The area in 1988 was hand-drawn from field notes.

Few geese nested in the Base-camp valley in 1992 and 1994 (Table 1). In 1992, there was little breeding effort throughout the island, though a small colony of a few hundred nests was found in the Camp-2 area. A reconnaissance flight made by helicopter during incubation failed to reveal any other colonies over a large portion of the island. In contrast, in 1994, a large and dense colony (estimated ca. 5 000 nests, with a density more than twice as high as previous years; Table 1) was located in Camp-2 area. In these two years, we monitored a sample of nests at the Camp-2 area.

Table 1. Nesting conditions and nesting parameters of greater snow goose nests monitored on Bylot Island from 1988–1994.

	1988	1989	1990	1991	1992	1993	1994
Number of nests monitored	32	87	168	289	14 (200)	368	51 (346)
Snow-melt[b]	E	A	A	E–A	L	E–A	E
Snow-free area in Base-camp valley on 5 June (%)	>90	20	15	40	5	75	>90
Median laying date in June[b]	8	11 *ab*	13 *a*	11 *b*	(20) *c*	6 *d*	(11) *b*
Nesting success (%)	—	70	79	72	0 (70)	89	23 (43)
Mean nest density (nests/ha)	—	1.55	2.18	2.64	(2.78)	2.94	(5.91)
Habitat[c]	Low	Up	Low	Low	Low (up)	Low + up	Up (up)
Snowy owl (no. of nests found)	0	1	0	0	0	12	0

Note: Values in parenthesis are for the Camp-2 area.

[a] E=Early, A=Average, L=Late.

[b] Date with the same letter do not differ significantly ($P > 0.05$, multiple comparisons); 1988 was excluded because data were incomplete.

[c] Dominant nesting habitat used: Low=Lowland, Up=Upland.

Snowy owls (*Nyctea scandiaca*) were found nesting in the study area in 1989 and 1993 (Table 1). In both years, the largest concentration of goose nests was centered on owls nests. In 1993, almost all goose nests found were located within 500 m of a pair of nesting owls, and conversely, most owl nests were surrounded by nesting geese (Figure 3). Snowy owls initiated their nests ≥ 2 weeks before the geese, suggesting that geese chose to settle near owls rather than the reverse. A similar phenomenon was observed in 1994 when, in the absence of owls, 13 pairs of geese nested close to a rough-legged hawk (*Buteo lagopus*) nest (Figure 4).

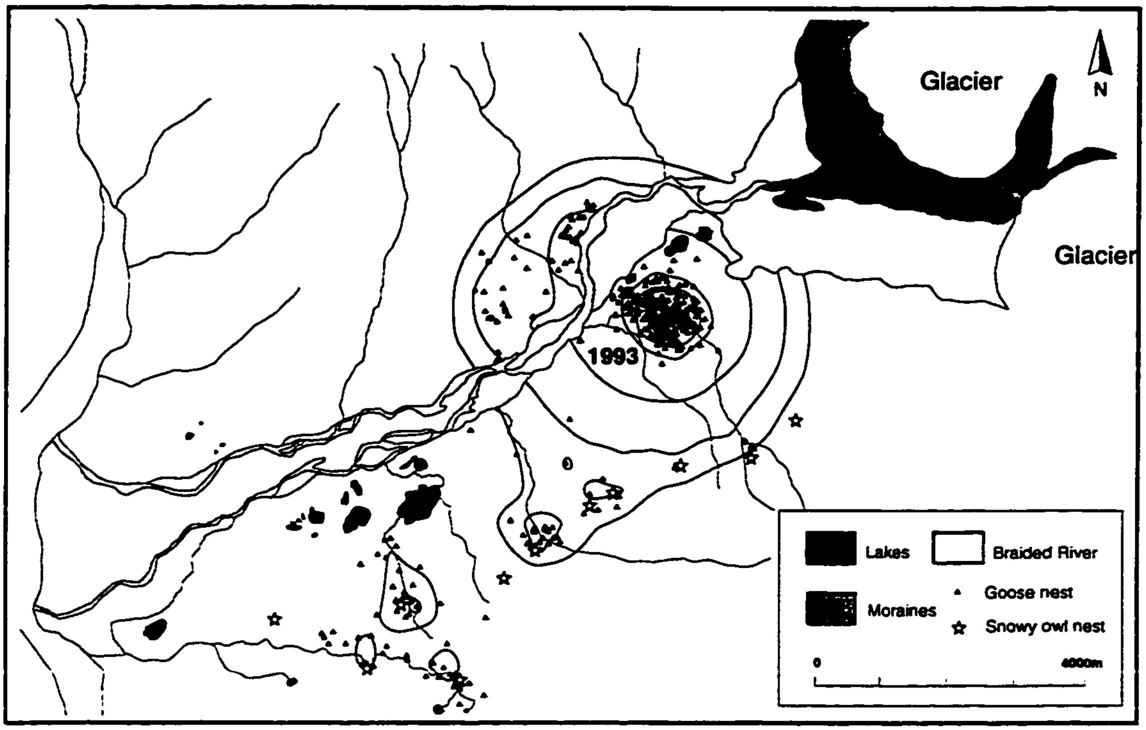

Figure 3. Greater snow goose nest distribution in the Base-camp valley in 1993. Contour lines were generated with the harmonic means method and illustrate the surface occupied by 55%, 65%, 75%, 85% and 95% of the nests, starting from the center of the colony.

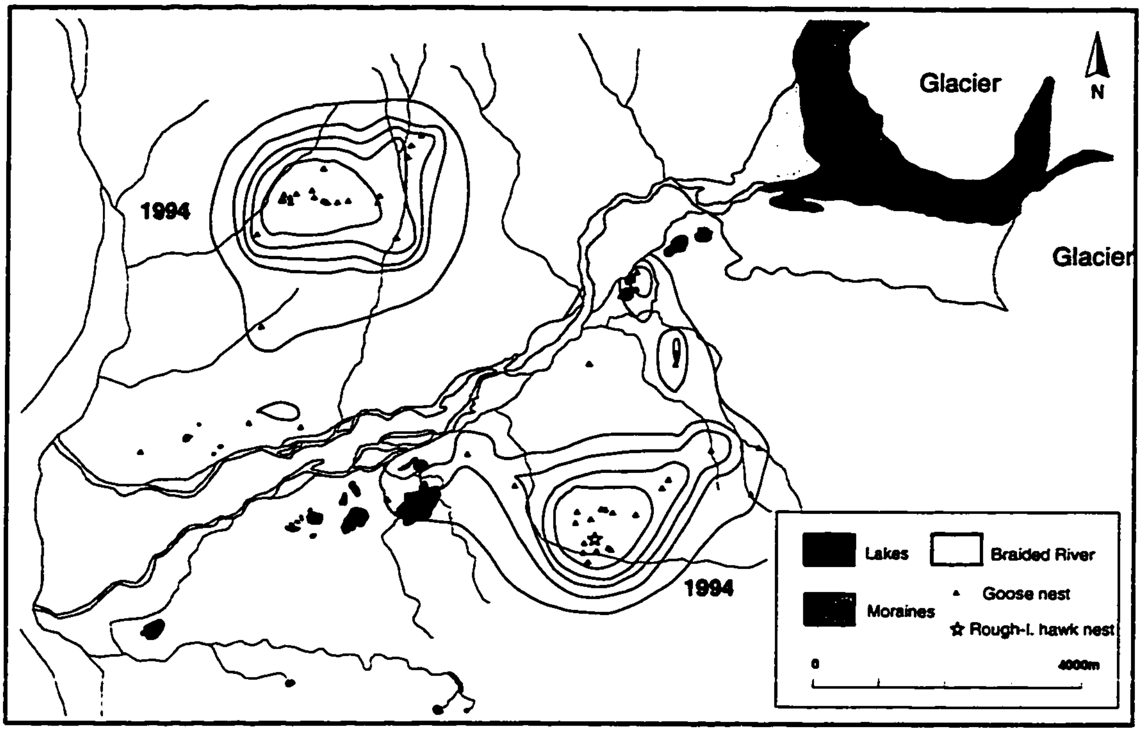

Figure 4. Greater snow goose nest distribution in the Base-camp valley in 1994. Contour lines were generated with the harmonic means methods and illustrate the surface occupied by 55%, 65%, 75%, 85% and 95% of the nests, starting from the center of the colony.

Annual variation in site availability and timing of nest initiation

There was considerable annual variability in timing of snow-melt, hence nest site availability, from 1988 to 1994 (Table 1). In both 1988 and 1994, snow-melt was almost completed (90% of the area snow-free) at the time of goose arrival in late May and snow should not have limited nest site availability. Snow melt was moderately early in 1991 and 1993, moderately late in 1989 and 1990 and very late in 1992 when it was at least 2 weeks later than in other years.

Nesting was very synchronized in all years with ≥ 83% of the nests initiated within 1 week (Figure 5). Nest initiation varied significantly among years (K-W $H = 893$, $P < 0.001$). In the near average snow-melt years of 1989, 1990 and 1991, median date of nest initiation was similar (11–13 June; Table 1). In early melt years, initiation was earlier in 1988 (8 June), but not in 1994 (11 June; Table 1). Nest initiation was earliest in 1993 (6 June) even though snow melt was only slightly earlier than average (Figure 5). Peak of nest initiation was severely delayed in 1992 (20 June) due to the very late snow-melt (Figure 5).

Median initiation date was correlated with mean spring temperature ($r = 0.91$, $n = 6$, $P = 0.011$). Correlations were not significant between median initiation date and snow depth ($r = 0.78$, $n = 6$, $P = 0.067$) or proportion of snow-free area in the Base-camp valley ($r = 0.73$, $n = 7$, $P = 0.061$). There was also less annual variation in median nest initiation date (range = 14 d) than in timing of snow-melt (range > 30 d; Figure 5).

Habitat use

Goose nests were predominantly located in wet meadow habitat in 1988 and 1991 and to a lesser extent in 1990 and 1993. The 14 nests found in 1992 in the Base-camp valley were also located in the valley lowland, near the site of the 1990 colony. In wet meadows, geese typically nested on elevated rims separating low-centered polygons. Nesting in dry upland habitat was predominant in 1989, when geese nested around a snowy owl nest, and in 1994. Some geese also used upland habitat in 1990, and in 1993 when several snowy owls nested in upland (Figure 3). At the Camp-2 area, the habitat used by nesting geese was predominantly dry upland habitat in both years.

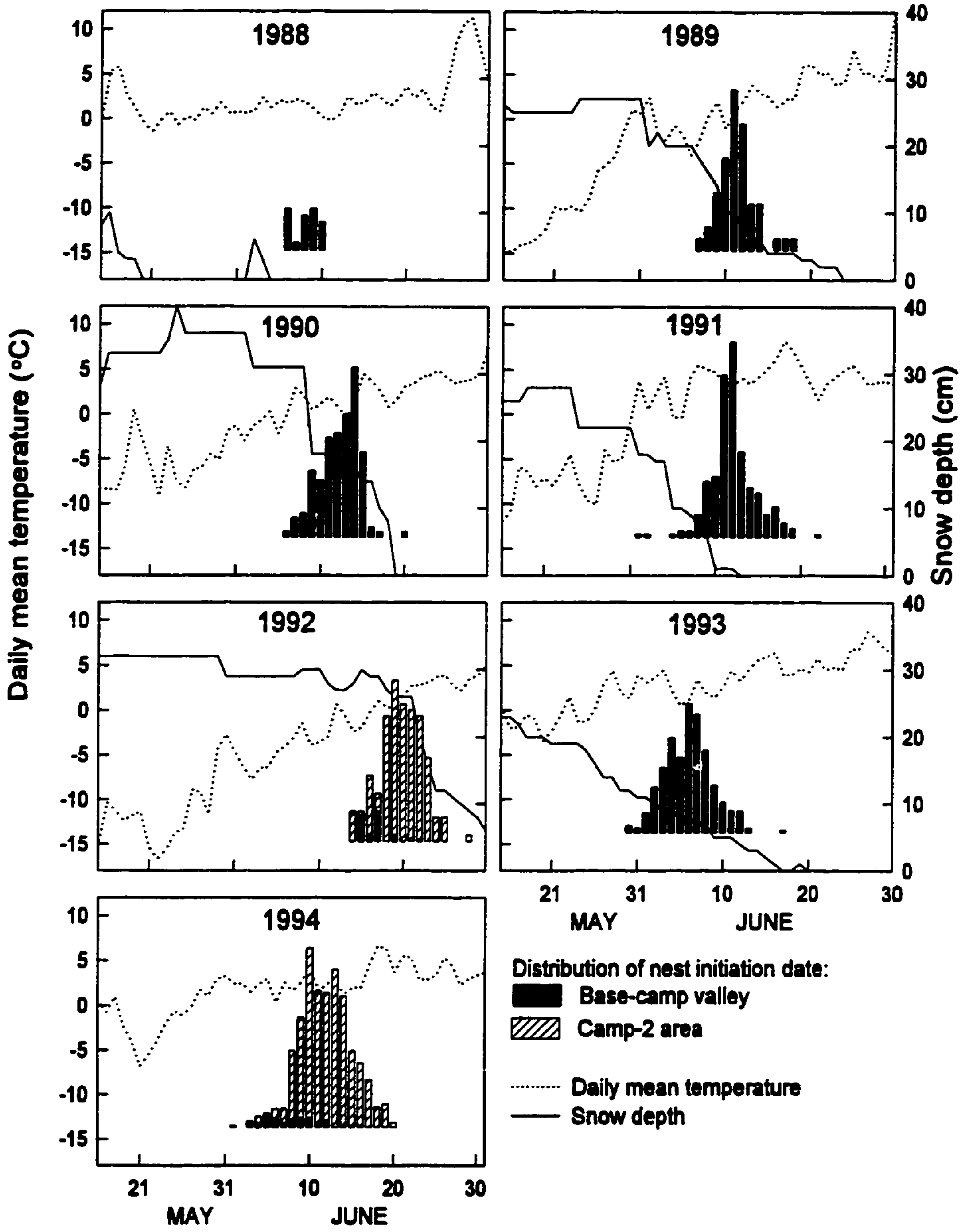

Figure 5. Frequency distribution of nest initiation dates (1989–1994) in the Base-camp valley and the Camp-2 area, and weather data for the spring period. Mean daily temperatures (°C) were recorded at the Base-camp valley, Bylot Island (1993–1994), and at the Pond Inlet weather station (1989–1992), and snow depth (cm) was recorded at the Pond Inlet weather station (no data available from the Pond Inlet weather station in 1994).

Nest predation

The abundance of nest predators (arctic foxes and to a lesser extent jaegers, gulls and ravens) is largely controlled by fluctuations in lemming (*Lemmus sibericus* and *Dicrostonyx torquatus*) populations. Although we did not quantify lemming abundance (except in 1994), casual observations suggested that their numbers were relatively low between 1989 and 1991, low to moderate in 1992, very high in 1993 and again low in 1994 (0.87 lemmings/100 trap-night, Gauthier unpubl. data). The pattern of lemming abundance was associated with variations in goose nesting success (Table 1). Annual nest success was between 70 and 79% from 1989 to 1992, possibly a consequence of low predator numbers. In 1993, the peak of lemming abundance and the aggregation of geese around the snowy owl nests were associated with high nesting success (Table 1). Nesting success was indeed higher in 1993 than in other years ($P < 0.01$ for all years except 1991 when $P = 0.02$; $\alpha = 0.01$). The crash in the lemming population between 1993 and 1994 was followed by very low nesting success of geese in 1994 (Table 1) although the five nests closest to the rough-legged hawk nest were all successful. In 1989, geese also nested close to a pair of owls but this apparently did not enhance their nesting success. However, lemming numbers were low that year, and the owls deserted their nest while the geese were incubating.

In the two years where the number of nesting geese in the Base-camp valley was very small (1992, 1994), the nesting success of the few nests initiated there was very low (Table 1). The poor nesting success of 1992 was associated with a very late snow-melt and a low breeding effort by geese over much of Bylot Island. This was not the case in 1994 as snow-melt was very early and the breeding effort at Camp-2 area was considerable. High predation pressure in the Base-camp valley in 1994 may have been the cause of the early cessation of nesting attempts there by geese (Figure 5). Nesting success, although better at the Camp-2 area than at the Base-camp valley, was still low (43%), mostly because of predation.

DISCUSSION

The lack of fidelity to a specific nesting location that we reported here is unusual in arctic-nesting geese. Lemieux (1959) also mentioned that locations of greater snow goose colonies on Bylot Island changed in successive years based on reports from local Inuit. The recapture of several marked birds on the brood-rearing area during banding operations in late summer suggests that some breeding geese do return to nest on Bylot Island (Gauthier and Reed, unpubl. data) but not to a specific nest site or colony location. Given the advantages associated with fidelity to a specific nesting site, the absence of site fidelity in this population suggests that other factors are involved.

Influence of timing of snow melt

Snow cover may limit site availability in spring and influence nest site selection (Abraham 1980, Petersen 1990). Although there is evidence that snow conditions in spring may affect micro-habitat selection within a locality (Cooke and Abraham 1980, Ely and Raveling 1984, Jackson et al. 1988, Petersen 1990), there are few cases where the location of whole colonies was affected. In lesser snow geese, Geramita and Cooke (1982) reported that an unusual number of unmarked geese nested at La Pérouse Bay in one year and attributed that to an influx of individuals that probably met unfavourable nesting conditions in their usual nesting range. In contrast, Ganter (1994) showed that geese nesting in La Pérouse Bay were generally highly faithful to their nesting location, even when the habitat was considerably degraded. Barry (1962) also stated that "Brant have a strong inclination to return to the same nesting grounds regardless of habitat conditions".

If snow limits nest site availability and is responsible for the displacement of geese, we would expect locations of colonies to be most similar in years of early snow melt. However, in the 3 earliest snow-melt years (1988, 1993 and 1994), geese used markedly different areas. Thus, although snow may restrict the choice of specific nesting areas in late years, other factors must affect colony location in years of normal or early snow melt.

Feeding opportunities during incubation

Feeding habitat during incubation could also influence colony location. Feeding is important for breeding adults during pre-laying and laying (Choinière and Gauthier 1995), as well as during incubation (Reed et al. 1995). To maximize protection of the nest from predators, feeding should take place close to the nest. This can be achieved by nesting near wet meadows or ponds that provide better feeding and drinking opportunities than dry upland. Moreover, geese nesting along hillsides incur an additional cost because they have to travel farther to preferred brood-rearing areas in wet lowlands (Hughes et al. 1994) with their newly hatched goslings. Although geese often nested in wet lowlands (1988, 1990, 1991 and 1993), in some years colonies were located in upland areas (1989, 1992 and 1994). As wetlands are more abundant toward the sea where snow-melt occurs latest (Figure 1), geese could be prevented from nesting there in late snow melt years (e.g. 1992). However, even in average or early snow melt years (e.g. 1989 and 1994) geese sometimes nested predominantly on hillsides suggesting that timing of snow melt and quality of feeding habitat around the nest are not the only factors involved in nest site selection.

Predation

Protection from predators afforded by a site is probably another important determinant of nest site selection. In the 2 years where snowy owl nests were found, almost all nesting geese in our study area settled close to an owl. Nesting in association with snowy owls is probably an anti-predator strategy against foxes (Boyd 1989, Dorogoi 1990, Syroechkovskiy et al. 1991, Summers et al. 1994) and similar associations have been documented in many other bird taxa (Erwin 1979, Burger 1984, Young and Titman 1986, Blomqvist and Elander 1988, Groom 1992, Ueta 1994, Norrdahl et al. 1995, Robertson 1995). Owls rarely prey on goslings (only one carcass was found at an owl nest during regular visits). We suggest that the high nesting success of geese in 1993 was a consequence of the presence of snowy owls which chased off foxes from around their nest. Snowy owls nested in abundance on the study area in the only year that their main prey, lemmings, reached a peak in abundance. In the absence of snowy owls, hillside habitats may offer more concealment for nests due to the more rugged microtopography (Tremblay et al. 1997). Thus, in years of high predation pressure (e.g. in 1994, the year after the lemming peak), upland nesting may be an advantageous strategy even though feeding opportunities are less favourable there.

Site fidelity and nest initiation date

Annual variation in spring snow cover has often been identified as a factor influencing the timing of nest initiation in geese, and we found that date of nest initiation was weakly related to timing of snow-melt. Delayed nest initiation can reduce reproductive success in arctic geese (Barry 1962, Owen and Black 1989, Cooch et al. 1991, Sedinger and Flint 1991). Time constraints are more severe in greater snow geese than in many other goose populations because they nest further north and have a shorter breeding season. Thus, any delay in the timing of nest initiation will have a negative impact on their fitness (Lindholm et al. 1994, chapter 2 and 3). We suggest that, because of these severe time constraints, greater snow geese are limited in their ability to delay nest initiation when snow-melt is late, which forces them to be more flexible in their choice of nest site and hence display less site faithfulness.

Even though geese are flexible in their choice of nest site, snow-melt may also influence timing of nest initiation by decreasing feeding opportunities. As most of the nutrients invested in eggs comes from local food intake in greater snow geese (Gauthier and Tardif 1991, Gauthier 1993, Choinière and Gauthier 1995), late snow melt could reduce food intake by preventing access to lowland feeding areas and thus delay the onset of laying. This means that availability of feeding sites could have a greater influence on laying date than nest site availability.

In addition to timing of snow-melt and feeding opportunities before and during incubation, other environmental factors also vary considerably among years. Presence of snowy owls had a strong effect on the location of goose colonies but owls only nested in years of lemming abundance. Furthermore, variations in lemming abundance influence the abundance of foxes and other nest predators, and this may also affect nest site selection.

The unpredictability of nesting conditions in the High Arctic from year to year combined with the need to lay at an optimal date because of the extreme seasonality of the environment probably explain the low nest site fidelity of greater snow geese. The long interval between arriving on the breeding ground and egg-laying (Gauthier and Tardif 1991) is presumably used by greater snow geese to prospect for potential nest sites and to assess their quality in terms of feeding opportunity and safety from predators.

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CHAPITRE 2

TIMING OF REPRODUCTION AND REPRODUCTIVE SUCCESS IN GREATER SNOW GEESE

RÉSUMÉ

Nous avons étudié les variations saisonnières du succès reproducteur chez la Grande Oie des neiges (*Chen caerulescens atlantica*) nichant dans l'arctique canadien. Leur environnement est caractérisé par des étés courts et des conditions de reproduction imprévisibles. La nidification fut très synchronisée à l'intérieur d'une année, avec habituellement plus de 90% des nids initiés en 8 jours. Les parents tardifs ont généralement obtenu un succès reproducteur plus faible que les parents hâtifs, et ce, pour la majorité des composantes précédant l'envol des jeunes. Le déclin saisonnier de la taille de couvée que nous avons observé (-0.18 oeuf par jour) est comparable à celui rapporté chez d'autres populations d'oies arctiques. Entre les années, la taille de ponte annuelle moyenne était aussi reliée à la date médiane de ponte, les femelles pondant moins d'oeufs en moyenne lors des années tardives. Nous avons détecté un déclin saisonnier de la survie des oeufs et des oisons, mais le succès d'éclosion n'était pas relié à la date de ponte. La relation entre la date de ponte et le succès de nidification était curvilinéaire, les nids hâtifs et tardifs étant plus souvent prédatés que les nids initiés près de la date médiane. L'indice qui intègre les différentes composantes du succès reproducteur a décliné de façon linéaire au cours de la saison de reproduction. Le succès reproducteur attendu a décliné de 0.75 à 0.25 jeunes par couple au cours de la saison. L'examen des paramètres de survie révèle que leur relation avec la date de nidification est curvilinéaire, et qu'il existe un coût associé à une nidification hâtive.

ABSTRACT

We studied the seasonal variation of reproductive success in arctic-nesting greater snow geese (*Chen caerulescens atlantica*). Their environment is characterized by short summer and unpredictable breeding conditions. Nesting was very synchronized within a year, with usually more than 90% of the nests being initiated in about 8 days. Late parents tended to perform more poorly than early parents in most pre-fledging components of reproductive success. The seasonal decline in clutch size that we observed (-0.18 egg per day) was comparable to values observed in other Arctic goose populations. Between years, mean annual total clutch laid was also related to median laying date, females laying less eggs on average in late years. There was a seasonal decline of egg survival and gosling survival, but hatchability was not related to laying date. The relationship between laying date and nesting success was curvilinear, early and late nests being more predated than nests initiated near the median. The resulting, integrating value of reproductive success showed that there was a continuous decline of reproductive success over the nesting season. Expected reproductive success declined from about 0.75 to 0.25 offspring per pair over the season. When examining only the survival components, the relationship with nesting date was curvilinear, indicating that there is a potential cost associated with early nesting.

INTRODUCTION

Virtually all organisms live in seasonal environments where fitness costs and benefits associated with survival and reproduction vary over time. Because life-history theory predicts that any heritable trait or behavior in a population evolves on average to maximize fitness, we expect that parents should time their reproductive effort to maximize the number of viable offspring produced. Within a population, there are variations in the timing of reproduction which in turn may have consequences on reproductive success. More than a century ago, Darwin (1871) proposed that early-nesting birds were favored by natural selection because they produced more offspring of higher quality. Subsequent studies confirmed that several components of reproductive success decline during the breeding season (Daan et al. 1988). As a rule, early-nesting birds lay larger clutch size than late-nesting ones (Klomp 1970, Briggs 1993). Early hatched offspring can also experience a higher growth (Birkhead and Nettleship 1982, Cooch et al. 1991a, Sedinger and Flint 1991), survival (Perrins 1965, Harris 1969, Lloyd 1979, Dow and Fredga 1984, Daan et al. 1988, Perrins and McCleery 1989, Grand and Flint 1996) and recruitment rate (Cooke et al. 1984, Harris et al. 1994) than late-hatched ones.

A paradox emerged from the frequent observation that the majority of individuals in a population were not nesting at the time nor laying the clutch size that maximized reproductive success, and thus seemed to behave sub-optimally (Lack 1968, Perrins 1970, Perrins and Moss 1975). Some authors argued that such populations had not yet reached equilibrium and were still under directional selection (Nur 1984, Boyce and Perrins 1987, Rockwell et al. 1987, Gibbs 1988). However, many long-term studies failed to document changes in timing of nesting with time (Boyce and Perrins 1987, Rockwell et al. 1987, Gibbs 1988; see also Price et al. (1988) and Cooke et al. (1990) for a different perspective). Others proposed that clutch size and timing of laying were constrained by physiological or environmental factors that prevented most individuals from performing the optimal behavior (Lack 1968, Mountford 1968, Ryder 1970, Ankney and MacInnes 1978, Boyce and Perrins 1987).

This apparent contradiction was reconciled with life-history theory when Drent and Daan (1980) proposed a model where timing of reproduction and clutch size were dependent on the individual quality of the female. Because of the fitness costs associated with delayed nesting and the time required to gather enough nutrients for egg production, their model predict an optimal combination of clutch size and timing for every individual based on its ability to collect nutrients from the environment. At any given date, the relative costs (the time required to accumulate more nutrients, given a specific rate of accumulation for each individual) and benefits (the addition of one potential offspring) should determine whether the female should start laying now or wait to lay a larger clutch later. This is generally referred to as the *cost-of-delay* hypothesis. To adequately test this model, one should precisely know what is the fitness value of each offspring produced at different dates in the season.

Evaluating reproductive success

If everyone readily accepts that individual fitness is the propensity to perpetuate one's genes over the next generations, few agree on how we should measure it in practice (McGraw and Caswell 1996). The total number of offspring recruiting into the breeding population, produced over the lifetime of an individual, is generally considered one of the best measures of reproductive success. However, this is complex to adequately measure in large animals and few studies are sufficiently detailed to do so. One alternative is to use a composite measure of reproductive success that incorporates several individual components (clutch size, nesting success, offspring growth, survival and recruitment rate, etc.), each evaluated over a different sample of the population (Prout 1969, Bundgaard and Christiansen 1972, Hedrick and Murray 1983, Cooke et al. 1985, Rockwell et al. 1987, 1993). This circumvents the difficulty of measuring all these variables on the same individuals, a task that would require a large number of marked individuals or very peculiar conditions (e.g., sedentary populations). The components model thus allows examination of the desired effects on any of the individual variables of the model or on the composite values that integrate all the variables.

Greater snow geese (*Chen caerulescens atlantica*) are the most northerly arctic-nesting geese in North-America. They nest in a highly seasonal environment characterized by short summers and unpredictable breeding conditions. This extreme seasonality provided a unique opportunity to study the relationships between timing of reproduction and reproductive success. Our objective is thus to evaluate the effect of intra- and inter-annual variation in the timing of nesting on different pre-fledging components of reproductive success and on a composite value that integrates these components. This is a first step toward a test of the *cost-of-delay* hypothesis.

METHODS

Study area

The study was conducted on Bylot Island (73°08'N, 80°00'W), Northwest Territories, Canada. Much of the island is occupied by mountains and glaciers, except for a large plain of ca. 1 600 km^2 in its southern part. About 27 000 nesting pairs (1993 census, Gauthier et al. 1996) are distributed over the island in several sub-colonies which size and location vary in time and space (Lepage et al. 1996). Our main study area, the Base-camp valley, is a 12 km-long glacial valley that extends to the sea. Another study area (Camp-2 area) was located about 30 km south of the Base-camp valley. A more detailed description of the study area is found in Gauthier et al. (1995) and Lepage et al. (1996).

Field methods

From 1991 to 1995, extensive nest searches were conducted during the laying and incubation periods in June. The Base-camp valley (65 km^2) was searched thoroughly in all years, whereas at the Camp-2 area, an area of ca. 8 km^2 was searched for nests in 1992, 1994 and 1995. Nests were revisited in the first half of incubation, during the hatching period and after the goslings had left in order to determine the final outcome. Eggs were marked individually in nests and signs of predation were noted on each visit. Arctic fox (*Alopex lagopus*) is the main nest predator, usually accounting for more egg loss than all other predators combined (jaegers [*Stercorarius parasiticus* and *S. longicaudus*], glaucous gull [*Larus hyperboreus*] and raven [*Corvus corax*]; Tremblay et al. 1997). At hatch, we marked goslings before they left the nest with numbered web-tags, either in piped eggs (Alliston 1975) or after hatching.

Parents with their young were captured about 5 weeks after hatching, shortly before fledging, in mass-banding drives. At that time, molting adults are unable to fly due to the loss of their flight feathers. On Bylot Island, goose families are very mobile and movements occurred between the two study areas: in all years that families were marked at the Camp-2 area, several were recaptured in the Base-camp valley, 30 km to the north. The latter area is a major brood-rearing site on Bylot Island (Reed et al. 1992) because it includes a high concentration of wet meadow habitats which attract many families hatched elsewhere on the island. Thus, all marked geese were part of the same population, regardless of where we marked them (Base-camp valley or Camp-2 area). All goslings were checked for the presence of web-tags and all captured birds were marked with US Fish & Wildlife metal bands. A second recapture event for web-tagged birds occurred in the fall with tags recovered from birds killed by hunters and birds captured alive in cannon-nets during banding operations held on the fall staging area in southern Québec (see Maisonneuve and Bédard 1992 for a description of the migratory habits of this species).

Data analysis

Egg laying date

Date of first egg laid (laying date) was estimated by one of three different methods (methods are listed in decreasing order of precision): 1) for nests found during egg-laying, laying date was estimated by subtracting the number of eggs in the nest minus one to the date of the discovery (if > 3 eggs were present in the nest, another day was subtracted since laying interval averages 33 h in snow geese; Schubert and Cooke 1993); 2) for nests found during incubation but with a known hatching date, the laying date was estimated by subtracting the clutch size (minus one if ≤ 3 eggs) and the incubation length (23-day; Gauthier, unpubl. data) from hatching date; 3) for nests without known hatching date, egg density (mass/[length*breadth^2]) was used to estimate laying date based on a linear relation between density and stage of incubation (Gauthier, unpubl. data). Methods 2 and 1 were most frequently used. Laying dates were transformed as deviation from the median laying date in each year (relative laying date).

Survival estimates using capture-recapture data

We used SURGE4 program (Lebreton et al. 1992) to obtain estimates of survival using the capture-recapture data of web-tagged goslings. Each year, we had one marking event (webtagging at hatching) and two recapture events (fledging period and fall staging in Québec), making four possible capture-recapture histories each year (Table 1). The terminal recapture event did not differentiate between birds killed by hunters and reported to us or birds captured alive by cannon-netting (Morez 1997). We tested the effect of year (y), laying date (d), and time (t; pre- and post fledging periods) on the probabilities of survival (ϕ) and recapture (p). However, since we did not have sufficient data to estimate the parameters in a general models that included all three effects (e.g. $\phi_{y*d*t}\, p_{y*d*t}$), we tested separately the effect of year and laying date in two series of models.

To evaluate the effect of laying date, we first estimated survival and recapture probabilities with the model $\phi_{d*t}\, p_{d*t}$, where ϕ and p were specific to both time (t) and laying date (d, divided in 7 groups according to the relative laying date of individuals: -6 to -4, -3 and -2, -1, 0, 1, 2 and 3, and from 4 to 6, all years combined). We then tested reduced models where either ϕ or p were constrained to be equal over time or laying date. We also tested if ϕ could be related through either a linear or a quadratic regression with laying date using SURGE4. The difference in deviance between two models (likelihood-ratio test) and the Akaike Index Criterion (A.I.C.) were used to choose the best model. For example, when constraining survival to be equal over laying date (e.g., from model $\phi_{d*t}\ p$ to model $\phi_t\, p$), a significant increase of deviance would indicate that date-specific values for survival provide a better fit to the data and that survival is thus dependant on laying date (see Lebreton et al. 1992 and Burnham et al. 1995 for more details on model selection). The same type of analysis was realized to test the effect of year on ϕ and p using $\phi_{y*t}\ p_{y*t}$ as the most general model.

Table 1. Number of goslings captured each year for each combination of capture-recapture (CR) history. The three capture occasions are hatching, fledging and fall staging (see text) and birds were only marked on the first occasion each year. For a CR history, a captured gosling (either previously marked or not) is showed by a 1, while a gosling not captured (either missed or deceased) by a 0 (e.g., CR history 1 0 1 means a bird captured and marked at hatching, missed at fledging, but recaptured during fall staging).

CR history	1991	1992	1993	1994	1995	total
1 0 0	296	240	979	1941	1374	4830
1 1 0	17	45	93	62	72	289
1 0 1	4	2	18	11	17	52
1 1 1	0	2	9	0	2	13
total	317	289	1099	2014	1465	5184

Composite measure of pre-fledging reproductive success

We used a composite measure of pre-fledging reproductive success similar to the one used by Rockwell et al. (1993) in lesser snow geese (*Chen c. caerulescens*). The various components of pre-fledging reproductive success were defined as follow. *TCL* (total clutch laid) is the number of eggs laid in a nest and was defined as the maximum number of eggs found in a nest (parasitism is low in this population as <2% of the nests contained >6 eggs; nests with a *TCL* of only 1 egg (4%) were removed from the sample as they are assumed to result from partial predation). *CSH* (clutch size at hatch) is the number of eggs in nests where at least one egg hatched. Finally, *GLN* is the number of goslings leaving the nest.

We also calculated three transition probabilities: egg survival ($P1 = CSH/TCL$) is the proportion of eggs surviving to hatch in successful nests; hatchability ($P2 = GLN/CSH$) is the proportion of surviving eggs that hatched; gosling survival ($P3$) is the proportion of hatched goslings that survived to fledging and was estimated with capture-recapture models as described above. Nest success (*NS*) is the proportion of nests where at least one egg hatched successfully, and was calculated with the Mayfield method (Johnson 1979, Lepage et al. 1996). The different components of reproductive success were estimated for each date over the range of laying date using the maximum sample available for each component (we sometimes had to group nests with different laying dates when sample sizes were too low). Expected reproductive success (*RS*) was estimated with the following formula, for each laying date d:

$$E(RS)_d = \overline{TCL}_d \times \overline{NS}_d \times \overline{P1}_d \times \overline{P2}_d \times \overline{P3}_d \qquad \text{eqn 1}$$

We also calculated expected survival of individual offspring (*S*), which gave the survival probability of an individual offspring from the moment of laying up to the time of fledging, defined as the product of the successive probabilities of survival, again calculated for each laying date d:

$$E(S)_d = \overline{NS}_d \times \overline{P1}_d \times \overline{P2}_d \times \overline{P3}_d \qquad \text{eqn 2}$$

We generated 95% confidence intervals for the *RS* and *S* estimates with Monte-Carlo simulations (see Appendix 2 in Rockwell et al. 1993). We used the method of Rockwell et al. (1993) to evaluate seasonal effects on egg survival (*P1*) and hatchability (*P2*): *DevP1* and *DevP2* were calculated as deviations from the expected value of *CSH* and *GLN* under the null hypothesis that *P1* and *P2* did not depend on laying date but only on year. We calculated expected clutch size at hatch, *E(CSH)*, and *DevP1* for each individual *i* in year *y* as:

$$E(CSH)_{iy} = TCL_{iy} \times \overline{P1_y} \qquad \text{eqn 3}$$

$$DevP1_{iy} = CSH_{iy} - E(CSH)_{iy} \qquad \text{eqn 4}$$

We used similar equations to estimate *E(GLN)* and *DevP2*. We used general models to test the effect of laying date, laying date^2 and year on individual values of *DevP1*, *DevP2* and *TCL* and on average values of *NS*.

We tested the effect of laying date on *P3* by comparing models with or without the constraint of laying date on survival by using deviance values obtained with SURGE4. Finally, the effect of laying date on *E(RS)* and on *E(S)* was evaluated with an ordered series of polynomial regressions. All analyses, except capture-recapture, were performed with the Statistical Analysis Software (SAS Institute inc. 1990).

RESULTS

Laying date

Median laying dates varied from 6 to 20 June between 1991 and 1995, whereas median dates of hatching were between 3 and 15 July. Laying was earliest in 1993, latest in 1992, and similar in the other three years (Figure 1). Nesting was very synchronized within a year, with usually more than 90% of the nests being initiated in about 8 days (Figure 1). There was no confirmed renest.

Clutch size

Mean clutch size (*TCL*) was 3.79 ± 0.03 [SE] ($n = 1598$). As expected, late-nesting female laid fewer eggs than early nesting female (Figure 2a). The seasonal decline varied from -0.11 to -0.26 egg per day of delay (significant in all years, Table 2) although the rate of decline differed among years as shown by the significant interaction between year and laying date ($P < 0.001$). In late nesting years, females also laid fewer eggs on average than in early years and the relationship between mean clutch size and median laying date was curvilinear (Figure 3a). There was a reduction in mean *TCL* of about 1 egg between the earliest and the latest year.

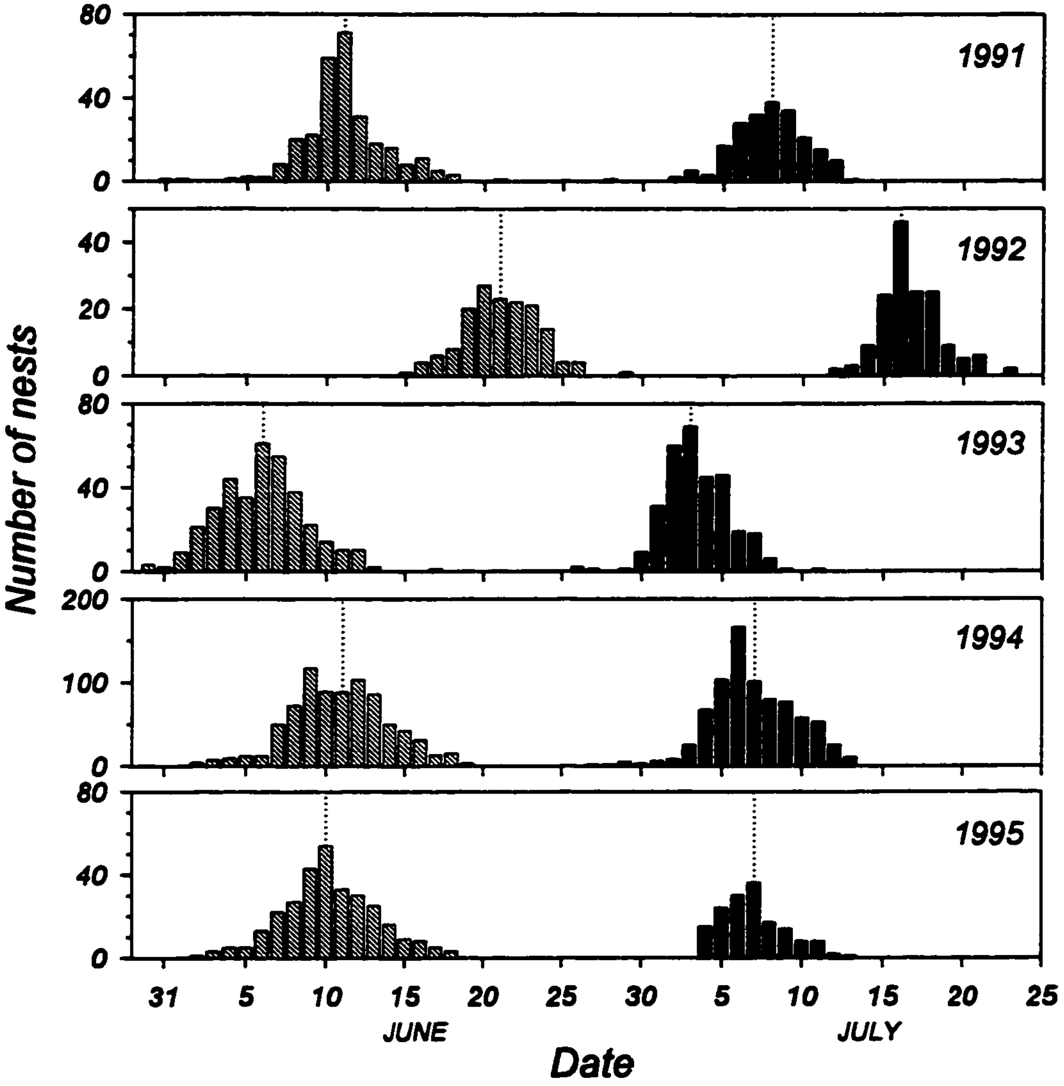

Figure 1. Distribution of laying date of the first egg (hatched bars) and hatching date (filled bars) in Greater Snow Goose at Bylot Island from 1991 to 1995. Stippled line is the median for each variable.

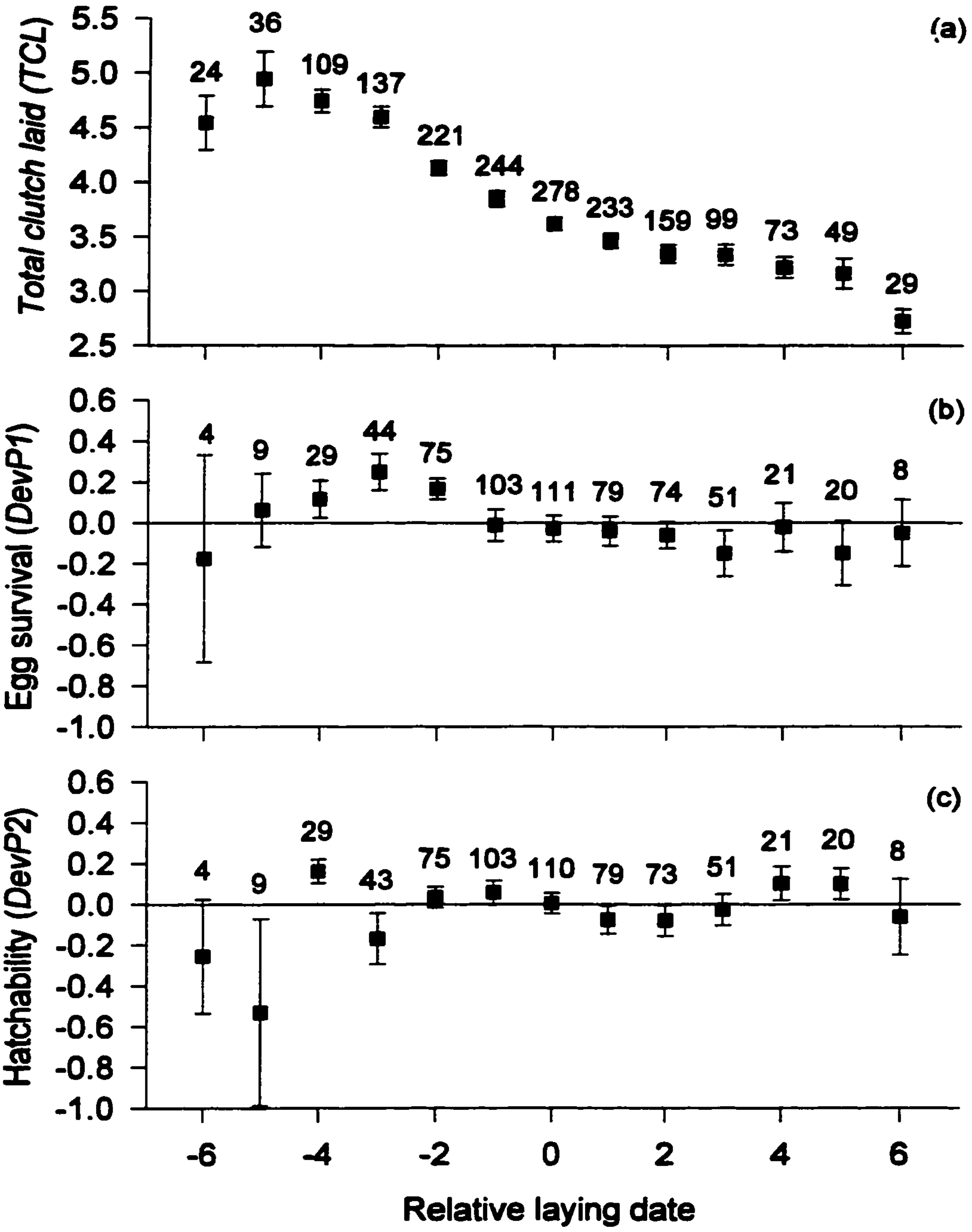

Figure 2. Seasonal effect on (a) total clutch laid, (b) egg survival and (c) hatchability (means with standard errors), all years combined (1991-1995). Egg survival and hatchability are illustrated as deviation from null expected values for a given year (see text for more details). Laying date is standardized relative to the median (0 = median laying date in each year). Sample size is shown above each point.

Egg survival

Mean egg survival (*P1*) was 91.4 ± 0.7 % [SE] ($n = 637$). When all years were pooled, *DevP1* was inversely related to laying date (Figure 2b), but the decline was slight (0.03 egg lost per day of delay, Table 2). When year effects were included in the model, the overall effect of laying date was no longer significant ($P = 0.086$), although the slope of the relationship was negative in all years and significant in 1991 (0.10 egg lost per day of delay) (Table 2). The mean annual egg survival was not related to median laying date (Figure 3b).

Hatchability

Mean hatchability (*P2*) was 92.9 ± 0.6 % [SE] ($n = 634$). When years were pooled, *DevP2* was not related to laying date (Figure 2c, Table 2). When the variable year was included in the model, the overall effect of laying date was at the limit of significance ($P = 0.056$) and laying date had a significant effect in 1991 (a seasonal increase in hatchability) and 1993 (a slight seasonal decrease; Table 2). Thus, effects of laying date on hatchability were very small and inconsistent among years. There was no relationship between mean annual hatchability and median laying date (Figure 3c).

Nesting success

Overall nesting success (*NS*) averaged 56.7 ± 1.7 % [SE] ($n = 1301$) although it was quite variable among years. Mayfield estimates of nesting success (*NS*) showed a tendency for higher failure in early and late nests compared to average ones in all years but 1991 (Figure 4). These trends were significant in 1995, and almost ($P = 0.06$) in 1992. The relationship between *NS* averaged over the 5 years and relative laying date showed a similar trend and approached significance ($P = 0.07$). The earliest (from date -6 to -4) and the latest (from date 4 to 6) nests were about 10 % less successful on average than nests initiated closer to the median date.

Table 2. The effect of laying date and year on total clutch laid (*TCL*), egg survival (*DevP1*) and hatchability (*DevP2*). Slopes (*P* values in parentheses) of the linear models are shown for all years combined and each individual year.

	Year	Total clutch laid	Egg survival	Hatchability
R^2		0.207	0.012	< 0.001
slope	all years	-0.182 (<0.001) *n* = 1598	-0.028 (0.006) *n* = 637	0.002 (0.827) *n* = 634
R^2		0.302	0.024	0.026
slopes	1991	-0.230 (<0.001) *n* = 219	-0.101 (0.006) *n* = 80	0.097 (0.003) *n* = 78
	1992	-0.255 (<0.001) *n* = 179	-0.044 (0.088) *n* = 108	0.008 (0.722) *n* = 108
	1993	-0.248 (<0.001) *n* = 283	-0.025 (0.166) *n* = 168	-0.034 (0.035) *n* = 168
	1994	-0.172 (<0.001) *n* = 670	-0.029 (0.150) *n* = 128	-0.004 (0.807) *n* = 127
	1995	-0.111 (<0.001) *n* = 247	0.013 (0.573) *n* = 153	0.027 (0.195) *n* = 153

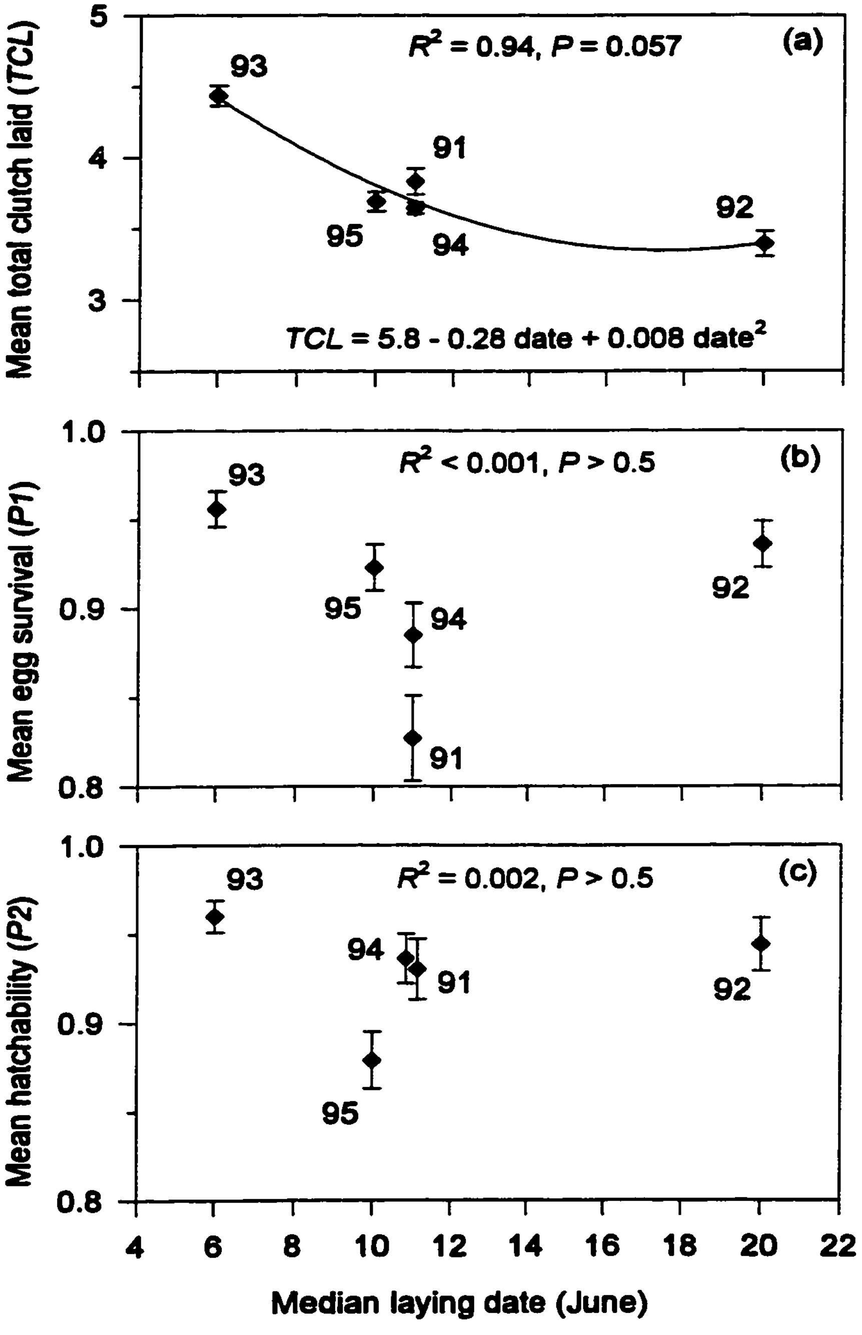

Figure 3. Relationship between median laying date and mean annual (a) total clutch laid, (b) egg survival and (c) hatchability (± SE; $n = 5$). Curve and R^2 were obtained with second (*TCL*) or first order (*P1* and *P2*) regressions.

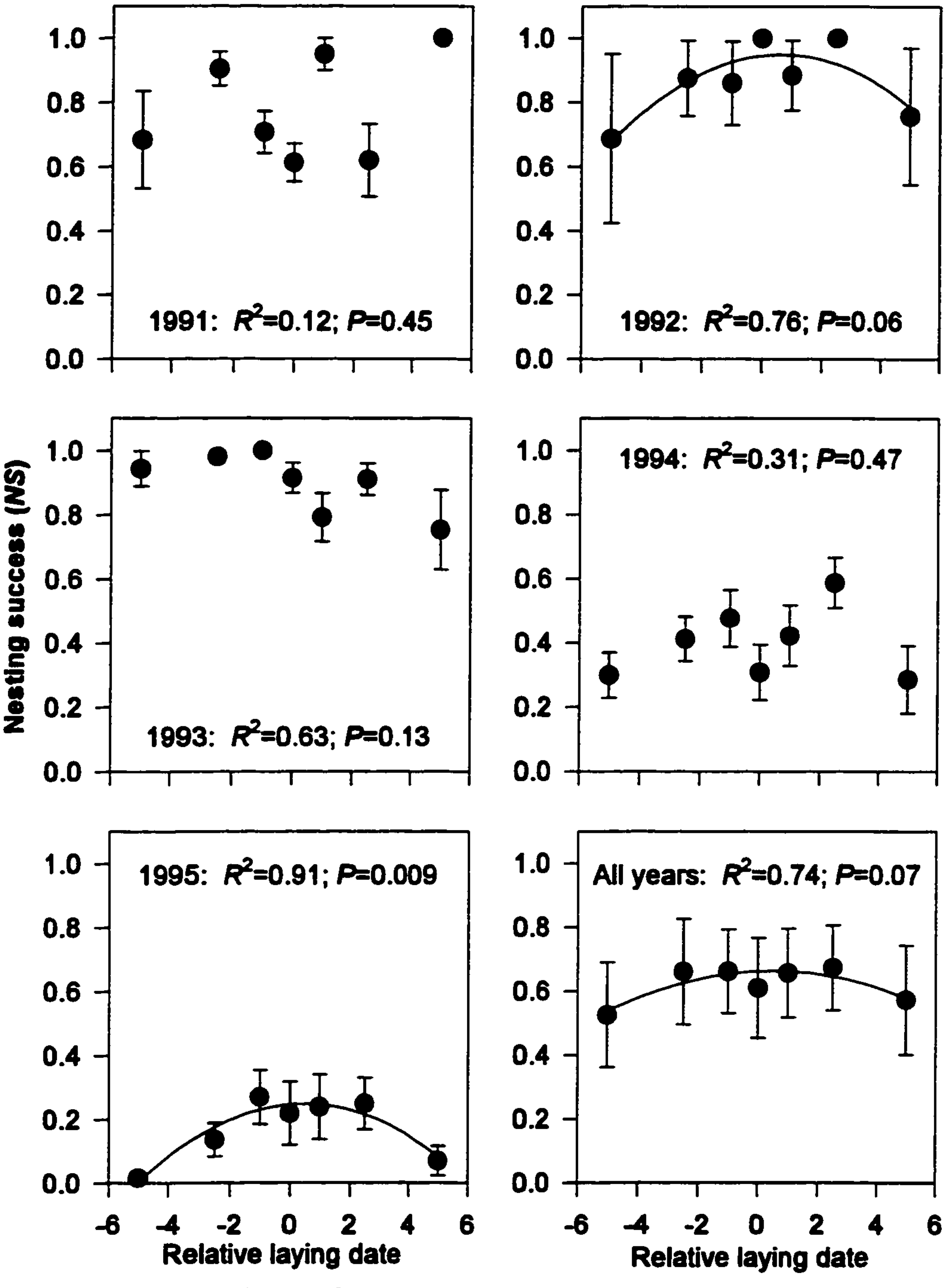

Figure 4. Relationship between mean nesting success (± SE) and relative laying date from 1991 to 1995 and for all years combined ($n = 7$). Curves and R^2 were obtained with second order regressions, except in 1991 (first order).

Gosling survival

In the first series of models testing the effect of laying date on the probability of survival and recapture, the model where survival was specific to laying date and time, and capture rate constant ($\phi_{d*t}\,p$) fitted best the data (Table 3). Removal of the laying date effect on the survival estimates (model $\phi_t p$ compared to model $\phi_{d*t}\,p$) caused a significant increase of the deviance, thus indicating that survival differed among goslings hatched from nests initiated at different dates. Although there was a tendency for goslings hatched from early nests to survive better than goslings from late nests (Figure 5), replacing the survival estimates by either a quadratic (cnstr (d^2) $\phi_{d*t}\,p$) or a linear regression with laying date (cnstr (d) $\phi_{d*t}\,p$) did not improve the fit of the model (Table 3).

In the second series of models which tested the effect of year, the model that best fitted the data ($\phi_t\,p_{yt}$) indicates that survival probabilities did not differed among years but that capture probabilities did, and that both parameters were specific to time. Summer capture rates ranged from 9 to 46% among years.

Composite measure of reproductive success and offspring survival

There was a linear decline of expected *RS* (number of young produced at fledging) along the season, the earliest laying birds producing twice as many offspring at fledging than the latest birds (Figure 6). The linear regression explained 64% of the variation in the data and higher order of regression did not improve the fit of the model. On average, each pair fledged 0.61 young per breeding attempt.

The relationship between survival offspring survival (*S*) and relative laying date was curvilinear (Figure 7). Maximum chance of survival for offspring was around laying date -2 and declined for offspring hatched in nests initiated earlier and later. The earliest offspring (day -6) had about equal chances of survival than average ones (day 0), but the survival probability for the latest offspring was less than half the value at day -2. The ordered series of polynomial regressions showed a significant improvement of the fit up to order 2, the model explaining 52% of the variation.

Table 3. Model selection with SURGE4. A significant change in deviance between two models (likelihood-ratio test) indicates that additional constraints on the model significantly reduce the fit of the model, and hence should be rejected. The Akaike index criterion (AIC = Deviance + 2 × number of parameters estimated) with the lowest value indicates the model that best fits the data (shown in bold).

no.	model [a]	# parameters	deviance	vs.[b]	Δ deviance	*P*	AIC
1	$\phi_{d*t}\,p_{d*t}$	21	2929.1	–	–	–	2971.1
2	$\phi_{d*t}\,p_t$	16	2935.5	1	6.4	0.269	2967.5
3	$\boldsymbol{\phi_{d*t}\,p}$	**15**	**2935.5**	**2**	**0**	**1.000**	**2965.5**
4	cnstr (d^2) $\phi_{d*t}\,p$	11	2955.1	3	19.6	< 0.001	2977.1
5	cnstr (d)$\phi_{d*t}\,p$	10	2957.1	3	21.6	< 0.001	2977.1
6	$\phi_t\,p$	3	2986.0	3	50.5	< 0.001	2992.0
7	$\phi_{yt}\,p_{yt}$	15	2870.0	–	–	–	2900.0
8	$\boldsymbol{\phi_t\,p_{yt}}$	**12**	**2873.3**	**7**	**3.3**	**0.069**	**2897.3**
9	$\phi_{yt}\,p_t$	12	2881.4	7	11.4	0.001	2905.4
10	$\phi_t\,p_t$	3	2986.0	8	112.7	0.001	2992.0
11	$\phi_{yt}\,p$	11	2881.4	9	0.0	1.000	2903.4
12	$\phi_t\,p$	3	2986.0	10	0.0	1.000	2992.0
13	$\phi\,p$	2	2987.5	12	1.5	0.221	2991.5

[a] Indices for the parameters ϕ and p were used as follow. d: the parameter was estimated for 7 classes of laying date (see methods); y: the parameter was estimated for each year; t: the parameter was estimated for each time period. Cnstr (d)ϕ_{d*t} indicates that the survival parameters were assigned to a linear (or quadratic for d^2) regression with laying date.

[b] the model to which the current model is compared to.

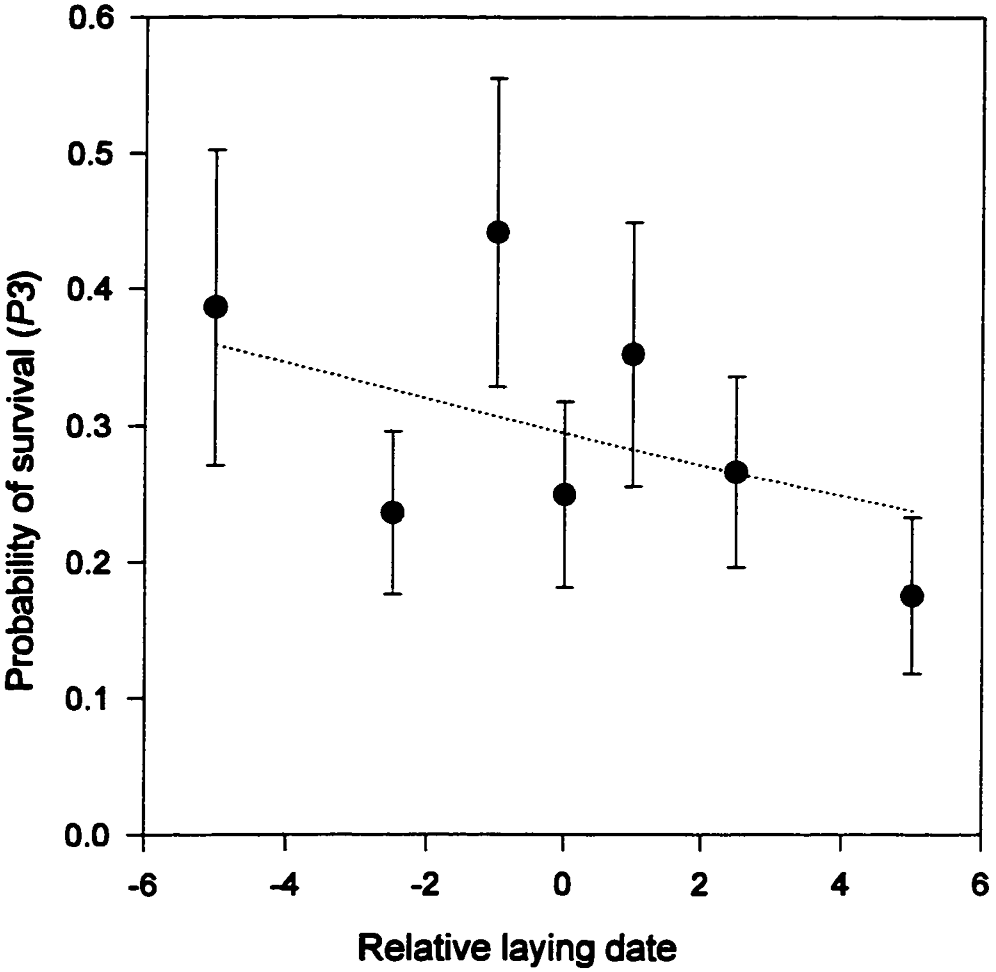

Figure 5. Pre-fledging probability of gosling survival (*ϕ* ± SE) in relation the the relative laying date of nests where they hatched (0 = median laying date). Regression line obtained with a linear constraint of laying date on survival with SURGE4 (see text).

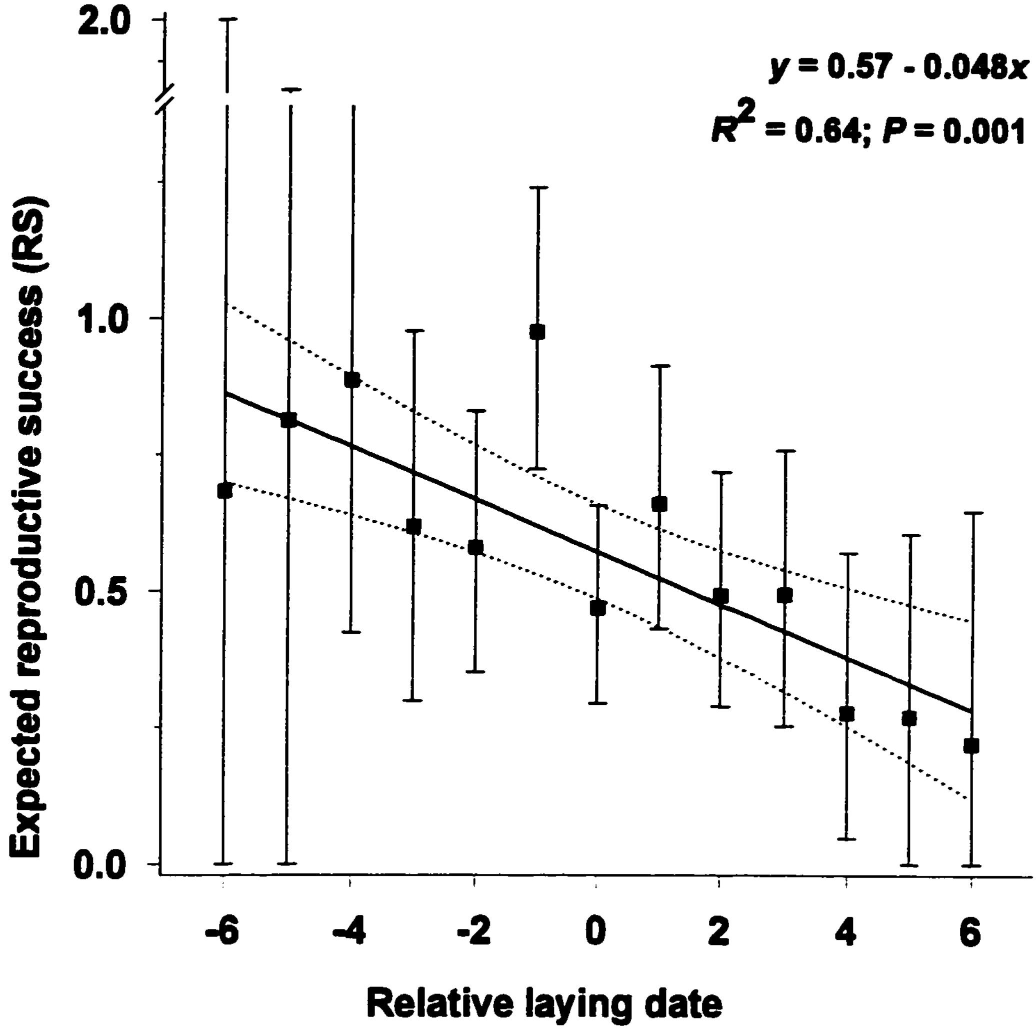

Figure 6. Composite measure of reproductive success (number of young produced at fledging) calculated for each date over the range of relative laying date. The 95% confidence intervals for each parameter were generated with Monte-Carlo simulation. The regression curve (solid line) corresponds to the equation given (n = 13). Dotted lines illustrate 95% confidence limits for the regression.

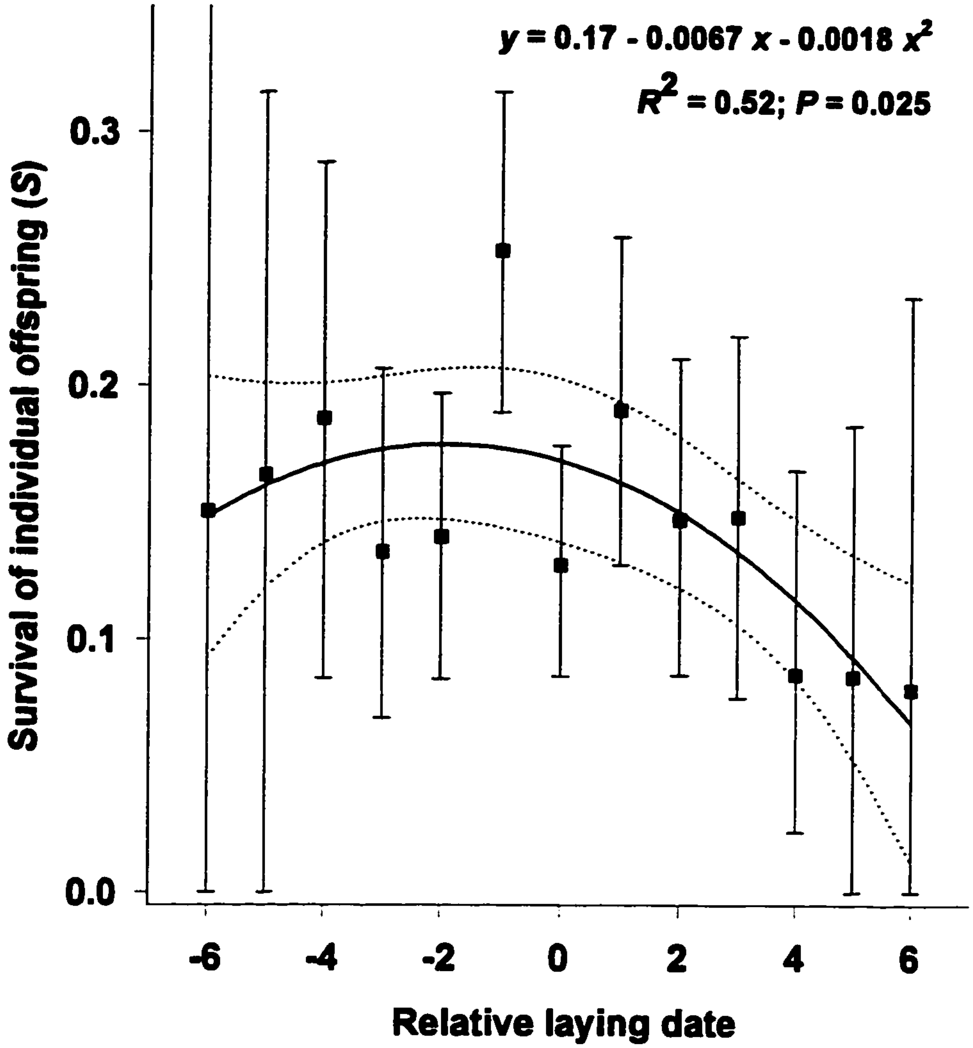

Figure 7. Survival probability of individual offspring from laying to fledging calculated for each date over the range of relative laying date. The 95% confidence intervals for each parameter were generated with Monte-Carlo simulation. The regression curve (solid line) corresponds to the equation given (n = 13). Dotted lines illustrate 95% confidence limits for the regression.

DISCUSSION

Although there was some variation, late parents tended to perform more poorly than early parents in most pre-fledging components of reproductive success, and the resulting, integrating value of reproductive success showed a continuous decline of reproductive success during the season. Reproductive success declined from 0.75 to 0.25 offspring per pair on average over the season.

The seasonal decline in clutch size that we observed (-0.18 egg per day) was similar to values observed in other Arctic goose populations (average of -0.21; Briggs 1993). Some factors like predation of early nests (in years where most of the nests were found after the start of incubation) and nest parasitism may bias our estimates of *TCL*. In the case of predation, this would tend to reduce the seasonal decline because earlier nests, which tend to have largest clutches, suffer more predation. However, early predation and nest parasitism generally explain only a small part of the seasonal variation in clutch size (Cooke et al. 1995). Among years, mean annual *TCL* was also related to median laying date: in late years, females laid less eggs in average, as was found by most authors.

When examining only the survival parameters (*S*), the relationship with nesting date was curvilinear, indicating that there is a potential cost associated with nesting too early. Among individual components of reproductive success, this cost was only observed for the nesting success as other parameters were either not related or simply inversely related to nesting date. This seasonal pattern of nesting success was also observed in lesser snow geese by Findlay and Cooke (1982) and other species where some authors showed that there are reproductive costs associated with nesting too early (Brinkhof et al. 1993, Norris 1993, Nilsson 1994). Differential susceptibility to predation is a commonly cited explanation for the seasonal variation in reproductive success. This is especially true for colonial species which success may depend on a predator swamping effect, leaving early and late nesters more vulnerable to predation.

Body condition of both parents and goslings during brood-rearing may explain some of the seasonal variation in gosling survival. In chapter 3, we showed that growth rate was negatively affected by the date of hatching, as in other Arctic goose populations (Cooch et al. 1991, Sedinger and Flint 1991), mostly because of the diminution in food availability for late nesters. Smaller goslings of lower body condition may be easier prey for the predators. Moreover, as late nesting parents are also experiencing lower quality food than early nesting birds during brood-rearing, they may have to devote more time to feeding at the expense of vigilance for predators (Sedinger et al. 1995a). There may be a relationship between gosling body condition and mortality from sources other than predation. In an experiment where captive goslings were raised with or without supplement food, those raised only on natural vegetation had the lowest growth rate and the highest mortality rate (Lindholm et al. 1994). Higher susceptibility of late hatching birds to bad climatic conditions, diseases and parasites could also be involved, but this would require further investigations.

Among years, the survival components (egg survival, hatchability, nesting success and gosling survival) were not affected by median laying date, contrary to findings of other authors (Prop et al. 1984). We believe that factors other than absolute nesting date are probably more important in annual variation of survival components. The number of predators and the availability of alternative preys (mostly lemmings) for them are certainly some of the main sources of variation, but climatic conditions may also play a role.

Age of parents

As older parents tend to start laying earlier than younger ones (Perrins and McCleery 1985, Nol and Smith 1987, Finney and Cooke 1978), some of the observed seasonal trend may be caused by different parental ability to provide adequate care for their offspring. For instance, Rockwell et al. (1993) showed that pre-fledging components of reproductive success in lesser snow geese, including clutch size, nesting success and gosling survival improved from age 2 to 6 and that laying date was advanced with age. However, their result could also partly be an artefact of the correlation between age and timing of nesting, and age may not necessarily be a causal factor independent of nesting date. Support for this comes from a manipulation experiment where we exchanged goslings between parents that nested at different dates (Chapter 4). In that study, we detected no effect of parental quality on gosling growth rate or pre-fledging survival. Thus, although age may directly affect the timing of nesting and clutch size (though maybe not independently of timing either), other apparent age effects on egg or gosling success may be a consequence of timing only.

Are timing of nesting and clutch size optimal?

Arctic-nesting geese have traditionally been viewed as capital breeders (*sensu* Drent and Daan 1980, Thomas 1988) that relied solely on nutrients accumulated before the arrival on the nesting grounds to produce their eggs (Ryder 1970, Ankney and MacInnes 1978), which was an exception among birds. Because it was thought that laying females did not feed on the breeding grounds, Ryder (1970) proposed that the seasonal decline in clutch size was caused by the reallocation of the reserves to body maintenance when the females had to delay nesting (*nutrient-reallocation hypothesis* or *NRH*). For these birds, timing of nesting could not be viewed as a tradeoff between the costs and benefits of delaying, but only as a constraint imposed by the lack of suitable nesting sites (Ankney and MacInnes 1978). However, recent studies showed that, in most populations, Arctic geese are feeding intensively after their arrival on the breeding grounds and that their overall condition increases over that period instead of decreasing (Budeau et al. 1991, Gauthier and Tardif 1991, Bromley and Jarvis 1993, Choinière and Gauthier 1995, Ganter and Cooke 1996, Carrière 1996). Moreover, Arctic geese may be more flexible in the choice of their nesting site than it is often believed (Lepage et al. 1996, chapter 1). Without denying the importance of the nutritional state of the female in affecting clutch size, there is a growing body of evidence that *NRH* cannot explain the seasonal decline in clutch size in Arctic geese (Ganter 1994, Carrière 1996).

The *cost-of-delay* hypothesis, as proposed by Drent and Daan (1980), can provide an alternative explanation for the seasonal decline in clutch size in Arctic nesting geese. In order to establish the optimality of individual decisions related to timing of nesting, one should know exactly what are the fitness costs and benefits associated with these decisions. Few studies so far were able to provide such information to test the applicability of the *cost-of delay* hypothesis (Perrins and McCleery 1989, Daan et al. 1990, Cooke et al. 1995). Perrins and McCleery (1989) concluded that their data did not support completely the *cost-of-delay* in great tits (*Parus major*), and proposed that other factors could be involved. For instance, Pettifor et al. (1988) showed that parents were producing the optimal number of offspring that they were able to fledge: experimentally adding or removing young both resulted in a lower number of viable offspring produced. Thus, the costs and benefits associated with timing of reproduction will not be always the same for all individuals, depending on their ability to raise young, and this component should be included as a part of the models, especially for species that provide large amount of parental care.

In their long-term study of lesser snow geese, Cooke et al. (1995) proposed that the fitness costs of delayed nesting for the earliest females were approximately equivalent to the gain caused by the addition of one egg, but they made no further treatment of their data. They assumed that the time required to gather the nutrients for one egg was between 5 and 20 days, which seems exaggerated, especially the latter value. In greater snow geese, the delay between arrival and laying of the first egg is about 14 days, a period during which a female collects most fat and protein required for the production of 4 eggs on average (Choinière and Gauthier 1995). Although we do not have information on post-fledging components of reproductive success and our calculation of reproductive success was not made independently for every clutch size, a preliminary interpretation indicates that the earliest birds would produce more offspring by delaying nesting, because of the curvilinear relationship between date and offspring survival (Figure 7). However, the faster growth rate and larger body size at fledging for early hatched goslings (Chapter 3, Cooch et al. 1991, Sedinger and Flint 1991) will likely result in a higher post-fledging survival and recruitment rates for these birds (Francis et al. 1992, Sedinger et al. 1995b) and may well compensate for the initial costs of early breeding.

CONCLUSIONS

We believe that the *cost-of-delay* hypothesis is potentially a valuable tool to understand the individual reproductive decisions of timing of nesting and clutch size in Arctic-nesting geese. We believe that former arguments for the seasonal decline in clutch in arctic geese, namely the *Nutrient-reallocation* hypothesis, do not apply. Although our evaluation of reproductive success is still incomplete, our data generally supported the trend of declining reproductive success with time of the season, although there is also a cost associated with breeding too early. Further evaluation of the applicability of the *cost-of-delay* hypothesis will require, in addition to a detailed evaluation of the seasonal effect on post-fledging events, a better understanding of the proximate mechanisms of egg formation: the time required to collect nutrient to form an egg (fat, proteins, calcium, etc.), the origin of these nutrients (from accumulated reserves or directly from the environment), and the individual variations between early and late nesters in their ability to collect nutrients.

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CHAPITRE 3

SEASONAL VARIATION IN GROWTH OF GREATER SNOW GOOSE GOSLINGS: THE ROLE OF FOOD SUPPLY

RÉSUMÉ

Bien que le taux croissance est une composante importante du fitness, la mesure dans laquelle les parents ajustent le moment de l'éclosion aux variations naturelles dans la disponibilité de nourriture pour maximiser la croissance des jeunes est toujours controversée. Nous avons étudié le rôle de la disponibilité de la nourriture dans les variations inter- et intra-annuelle du taux de croissance des jeunes de la Grande Oie des neiges pendant 5 ans. Nous avons trouvé que le pic d'éclosion des oeufs coïncidait avec le pic de disponibilité de nourriture, sauf dans une année. Toutefois, les jeunes éclos avant le pic de nourriture ont grandi plus rapidement que les jeunes éclos au moment du pic, qui ont à leur tour grandi plus rapidement que les jeunes éclos après, mais ce phénomène ne s'est pas produit à tous les ans. Nous avons aussi détecté des variations considérables du taux de croissance entre les cinq années, les plus petits oisons de la meilleure année (1991) étant plus grands que les plus grands oisons de la mauvaise saison (1994). Nous avons calculé 3 indices de disponibilité de nourriture, basé sur la disponibilité cumulée de la biomasse végétale et du taux d'azote contenu dans les plantes durant la période de croissance des jeunes. Nos résultats montrent que l'exposition cumulée à la biomasse d'azote permet d'expliquer jusqu'à 44 % des variations inter- et intra-annuelle de croissance des oisons. Durant les années avec beaucoup de nourriture, les oisons hâtifs ont eu plus d'azote à leur disposition que les oisons éclos durant le pic ou après, et ils ont connu un meilleur taux de croissance. Durant les années avec peu de nourriture, les oisons éclos plus tôt n'ont pas eu d'avantage d'azote et nous n'avons observé aucun effet saisonnier sur la croissance des jeunes. Ce résultat confirme le rôle critique de la disponibilité de nourriture dans les variations saisonnières du taux de croissance des jeunes oisons en milieu arctique.

ABSTRACT

Even though growth rate is an important fitness component, it is still controversial to what extent parents adjust the timing of hatch to natural variations in food supply to maximize offspring growth. We studied the role of food availability in explaining inter- and intra-seasonal variation of growth rate in goslings of greater snow geese over five years. The peak of hatching coincided with the peak of food availability in all years but one. However, early-hatched goslings grew faster than birds hatched at the peak, which in turn grew faster than late-hatched goslings, but this phenomenon was not observed in all years. There was also considerable variation in growth rate among the five years, the smallest goslings produced in the best year (1991) being larger than the largest goslings of the poorest year (1994). We developed 3 indices of food availability, based on the cumulative availability of plant biomass and nitrogen content during the growth period, and showed that the cumulative exposure to nitrogen biomass explained up to 44 % of the intra- and inter-annual variations in body size just before fledging. In years with good feeding conditions, early-hatched goslings had access to more nitrogen than peak and late-hatched ones during their growing period and they grew faster. In years of lower food availability, early-hatched goslings had no advantage over peak or late-hatched birds for access to protein-rich food and no seasonal decline in growth rate was then observed. These results confirmed the critical role of food supply in the seasonal variation of growth rate in Arctic-nesting geese.

INTRODUCTION

All animals live in seasonal environments where periods of high food abundance alternate with periods of low abundance. Because nutrient requirements are highest during early growth, animals should time their reproduction to provide newly hatched offspring with optimum feeding conditions (Drent and Prins 1987, Daan et al. 1988, Cushing 1990, Blondel et al. 1993, Fortier et al. 1995). According to this hypothesis, peak of hatch should thus coincide with or occur shortly before the peak in food availability, and individuals that breed too early or too late with respect to the period of highest food availability should have lower success, both in terms of lower number of surviving offspring and of reduced growth (Lack 1968, Perrins 1970). However, in contrast to this prediction, most studies in birds have shown that offspring of birds that breed early grow and survive better (Perrins 1970, Daan et al. 1988, Sedinger and Flint 1991, Cooch et al. 1991a, but see van Noordwijk et al. 1995). A first explanation of this paradox could be that growth in birds is relatively insensitive to natural variation in food supply (Konarzewski et al. 1989, 1990). However, there is experimental evidence that the intake of protein and energy during the nestling period, affects growth rate and final adult size (Johnson 1971, Ricklefs 1983, Jørgensen and Blix 1985, Boag 1987, Lindholm et al. 1994).

A second explanation could be that peak of hatch does not coincide with peak food availability but occurs after, so that only the earliest nesting birds can benefit from it. This could occur if conditions such as food availability at laying time prevents parents from nesting early enough for their clutch to hatch in synchrony with the peak of food availability (Daan et al. 1988). Alternatively, cues that could be used by parents to anticipate the timing of peak in food availability may be lacking during the laying period (van Noordwijk et al. 1995). Finally, measures of food availability in the field may not adequately reflect what birds actually perceive from their environment in all situations.

Few studies have related seasonal variation in timing of hatch and growth rate with food supply in wild birds (Larsson and Forslund 1991) although many studies have inferred such relationships (Birkhead and Nettleship 1982, Cooch et al. 1991a, Sedinger and Flint 1991, Cooch et al. 1996). This is surprising given the fitness consequence of early growth in birds. Young that grow slowly and fledge with below average body mass often have relatively low survival (Hunt and Hunt 1976, Owen and Black 1989, Tinbergen and Boerlijst 1990, Magrath

1991, Sedinger et al. 1995), low recruitment (Cooke et al. 1984, Alatalo and Lundberg 1986, Sedinger et al. 1995) and perhaps even low fecundity (Sedinger et al. 1995).

In this paper, we tested the hypothesis that the timing of hatch with respect to the peak of food availability can explain seasonal variation in growth rate in birds. We examined this hypothesis in arctic-nesting greater snow geese (*Chen caerulescens atlantica*). This species lives in highly seasonal environment, with a short growth season and large inter- and intra-annual variability in environmental conditions. Moreover, geese are strict herbivores (Owen 1980, Manseau and Gauthier 1993) and feed on a few plant species, the abundance of which is relatively easy to quantify. Some authors reported large seasonal variation in growth rate of arctic geese even though hatching is fairly synchronized among individuals (Cooch et al. 1991a, Sedinger and Flint 1991). The seasonal decline of growth rate has been attributed to declining food quality and availability during the summer, although little direct empirical evidence was provided for this. Thus, our objectives were to 1) examine seasonal variation in growth rate of goslings over several years, 2) test the relationship between peak in hatch date and food availability, and 3) examine how natural variations in food supply can explain inter- and intra-annual variation in growth.

METHODS

Study site

The study was conducted on Bylot Island (73°08'N, 80°00'W), Northwest Territories, Canada. Rolling hills covered by upland tundra and isolated wetland patches, and cut by numerous valleys dominate the landscape of the southern part of the island. 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), but the location of individual goose colonies in that area is variable among years (Lepage et al. 1996, Chapter 1). Dry upland areas and wetland habitats are used for nesting (Lepage et al. 1996), while wetland habitats (wet meadows and ponds) are preferred by brood-rearing geese (Hughes et al. 1994a). Dominant plants in wetlands are *Dupontia fisheri*, *Eriophorum scheuchzeri*, *E. angustifolium* and *Carex aquatilis* var. *stans* (Gauthier et al. 1995), whereas moist lowland and upland are dominated by *Cassiope tetragona*, *Salix arctica* and some graminoids. Our main study area, the Base-camp valley, is a 12km-long valley (65 km^2) that extends from an active glacier to the sea. Another study area of ca. 8 km^2 (Camp-2 area) was located about 30 km south of the Base-camp valley.

Growth data

The Base-camp valley was searched for nests in all years (1991–1995) but geese nested there in large numbers only in 1991, 1993 and to a lesser extent in 1995. In 1992, 1994 and 1995, most successful goose nests were monitored in the Camp-2 area. During the hatching period, we visited nests daily and tagged 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 over a 1-week period. Captures were made in or close (< 5 km) to the Base-camp valley except in 1992 when we captured about half of the families 5–20 km further south toward the Camp-2 area. On Bylot Island, goose families are very mobile and movements occurred between the two study areas: in all years that goslings were web-tagged at the Camp-2 area, several were recaptured in the Base-camp valley. This latter area is a major brood-rearing site on Bylot Island (Reed et al. 1992) because it includes a high concentration of wet meadow habitats which attract many families hatched elsewhere on the island. Thus, all geese captured during mass banding drives were part of the same population, regardless of where they were initially marked (Base-camp valley or Camp-2 area). Captured goslings were sexed by cloacal examination, measured (culmen, head, tarsus and ninth primary length), weighed to the nearest 25g (nearest g in 1995) and carefully checked for the presence of web-tags.

Plant biomass data

We estimated food availability by measuring the above-ground biomass (i.e. standing crop) in grazed and ungrazed wetlands in the Base-camp valley from mid-June to mid-August (1991–1995). Data for ungrazed areas were obtained from 12 annual exclosures (1x1 m) erected in wet meadow habitats dominated by *Dupontia fisheri* and *Eriophorum scheuchzeri*, the preferred feeding habitat of broods (Hughes et al. 1994a). Exclosures were installed in mid-June before any significant grazing by geese had occurred. Every 2 weeks, plant biomass was sampled inside and outside each exclosure until mid-August. Graminoid vegetation (> 97%

of biomass) was clipped at a standard height (1 cm below the moss surface) in 20×20 cm quadrats, sorted and dried (see Gauthier et al. 1995 for details of the method). Total nitrogen concentration of *Dupontia* and *Eriophorum* collected in grazed plots was determined with an automated macro-Kjeldahl analyzer (Kjell-Foss, model 16210) following the AOAC (1984:154) method. Nitrogen concentration was not available for 1992 because of missing samples.

We estimated the intensity of use by geese near each exclosure by counting goose feces in permanent 1×10 m transects marked with small pegs. We removed all feces already present when exclosures were built in mid-June and feces were counted and removed every 2 weeks thereafter. No feces count was made in 1992.

Data analysis

We used two different samples to test the effects of year, age and hatch date on gosling size and mass near fledging. The first sample included all goslings captured during mass banding drives (*n* = 8 206), whereas the second included only those originally marked at hatch (*n* = 302), i.e., those of known age at capture. We estimated the age of unmarked goslings from annual linear relationships between age of marked goslings captured near fledging and length of their 9th primary. To be a good predicator of age, primary length should be relatively insensitive to environmental conditions and hatch date, and vary only with age. We tested this assumption with a general linear model, using the sample of marked goslings.

In both samples, we transformed hatch date into relative date with respect to the median annual hatch date, to test for inter- and intra-annual variations. The first axis (PC1) of a principal component analysis combining measures of tarsus, head and culmen length was used as a measure of body size (Lesage 1995). A first general linear model was used to test for the effects of year, age, sex and relative hatch date on gosling size and mass. As the effect of sex was not significant, this variable was not retained in the final analysis.

Comparisons of plant biomass in ungrazed vs. grazed plots were made with paired t-test (one-tailed) on a yearly basis, and Anova were used to compare plant biomass among years in ungrazed and grazed plots. We used plant biomass and nitrogen concentration data to build indices of the quantity and quality of food available to goslings hatched at different dates. The first index, the cumulative exposure to plant biomass (*CEB*), was defined as the summation of the daily plant biomass (g/m^2) to which goslings were exposed during growth:

$$(CEB_{35})_{yh}=\sum_{d=1}^{35} biomass \qquad \text{eqn 1}$$

where *biomass* was the daily plant biomass obtained from a linear interpolation of average plant biomass sampled in grazed areas every two weeks. This index was calculated for every combination of year (*y*) and hatch date (*h*) and represents the sum of the biomass from day (*d*) 1 to 35, starting on the hatch date. We calculated the index over three periods, in order to detect the most critical period of food requirements: CEB_{35}, CEB_{25} and CEB_{15} were, respectively, the sum of daily plant biomass from hatch to 35 d of age (the mean age at capture), from hatch to 25 d and from age 11 to 25.

The second index was the cumulative exposure to nitrogen concentration (*CEC*), an index of *food quality*. It was calculated like the first index, but used daily plant nitrogen concentration instead of biomass:

$$(CEC_{35})_{yh}=\sum_{d=1}^{35} nitrogen \qquad \text{eqn 2}$$

where *nitrogen* was the daily nitrogen concentration (average between *Dupontia* and *Eriophorum*) interpolated from values obtained at 2-week intervals. We calculated *CEC* for the three same periods as *CEB* (CEC_{35}, CEC_{25} and CEC_{15}).

Finally, we combined data on biomass and nitrogen concentration into a third index, the cumulative exposure to nitrogen biomass (*CEN*), which integrates information about food quantity and quality:

$$(CEN_{35})_{yh}=\sum_{d=1}^{35} (biomass \times nitrogen) \qquad \text{eqn 3}$$

Daily plant biomass was multiplied by its corresponding nitrogen concentration value and the index was calculated similarly for the three periods (CEN_{35}, CEN_{25} and CEN_{15}).

Regression analysis was used to test the relationship between body size or mass near fledging and the indices (*CEB*, *CEC* or *CEN*) of food quantity and quality corresponding to the hatch date of each gosling. Size and mass values of goslings were corrected for age at the time of capture, standardizing all birds to 35 d of age.

RESULTS

The number of young web-tagged at hatch varied annually from 315 to 1 977 (Table 1), and between 17 and 102 marked goslings were recaptured near fledging (Table 2). We calculated five year-specific linear models relating gosling age to 9th primary length in the samples of marked goslings. Mean errors (root MSE) on estimated age varied between 1 and 2 d (Table 2). In the two years (1991 and 1993) that goslings were marked only in the Base-camp valley, the mean estimated age of all goslings captured at the end of the summer suggested that these goslings were 2 to 3 d younger than marked goslings, whereas in the three years that goslings were marked at the Camp-2 area (1992, 1994 and 1995), the difference between the two groups was < 1 d (Table 2). This suggests slight differences in the timing of hatch between different nesting areas. There was also little difference in all years between the age predicted by the median hatch date of all marked goslings and the mean age of those recaptured, indicating that the sample of recaptured goslings was an unbiased sample of all marked goslings.

Table 1. Number of goslings marked at hatch in the two study areas, 1991–1995.

Study area	1991	1992	1993	1994	1995
Base-Camp	315	–	1099	34	43
Camp-2	–	289	–	1943	1422

Table 2. Model[a] for age estimation based on 9th primary length (mm) of captured goslings, mean age of captured goslings (± SE), mean estimated age at capture (all young; ± SE), and predicted age (capture date – median hatch date of all marked goslings)

	Marked young						All young			Difference	
Year	Intercept	Slope	√MSE[b]	R^2	*n*	Age at capture (A)	*n*	Estimated age (B)	Predicted age (C)	B–A	C–A
1991	18.98	0.111	1.80	0.73	17	39.4 ± 3.3	1118	36.3 ± 3.1	39	-3.1	-0.4
1992	19.52	0.099	1.15	0.84	47	29.6 ± 1.6	894	28.9 ± 2.4	30	-0.7	0.4
1993	22.81	0.099	1.75	0.63	102	40.2 ± 2.8	2015	38.3 ± 2.9	40	-1.9	-0.2
1994	27.62	0.071	1.69	0.72	62	36.1 ± 3.2	1851	35.8 ± 2.4	36	-0.3	0.1
1995	22.50	0.098	1.19	0.75	74	36.0 ± 2.4	2281	35.2 ± 2.3	36	-0.8	0.0

[a] model : age = intercept + 9th primary * slope

[b] MSE = Mean Square Error

Variation in gosling growth

There was considerable intra and inter-annual variation in gosling growth. All three variables (*Year*, *Age* and *Hatch date*) significantly affected both size and mass when all goslings were included in the general linear models, and most interactions among these 3 variables were significant (Table 3). When controlling for the age at capture, there was a decline in gosling size and mass near fledging with hatch date in the first three years (1991, 1992 and 1993), but not in 1994 (slight increase) and partially in 1995 (no effect on size and a slight decrease for mass) (Table 4). The magnitude (slope) of the seasonal effect differed among years (Figure 1) and these differences were generally consistent for mass and size each year. The seasonal effect was strongest in 1992 and 1993 as shown by the steeper slopes compared to other years (Table 4).

The size and mass of goslings near fledging differed significantly among years, once the effects of age and hatch date were controlled for (Table 4): goslings were largest in 1991 and 1992 and heaviest in 1991, and their size and mass decreased in each subsequent year (about 5 % per year for mass) until 1994. However, both mass and size increased in 1995.

The seasonal variations in size and mass were similar in the smaller sample of marked goslings ($n = 302$). All variables (*Year*, *Age* and *Hatch date*) and most of their interactions had a significant effect on size and mass (Table 3). Again, the seasonal decline was observed in 1991, 1992 and 1993 for the mass and size, but not in 1994 or 1995 (Table 4). The trend for a decline in size and mass between 1991 and 1994 was less clear in marked than in all goslings. Although marked birds were heaviest and largest in 1991 and lightest and smallest in 1994, they were larger and heavier in 1993 than in 1992 (Table 4).

The effect of hatch date on the 9th primary length of marked goslings was not significant ($P > 0.45$), but the effects of age ($P = 0.003$), year ($P < 0.001$) and their interaction ($P = 0.010$) were all significant, indicating that 9th primary grew at the same rate for all goslings of each cohort, independently of their hatch date.

Table 3. Factors affecting the size and mass of all goslings and marked ones near fledging. *F* and *P* values are shown for the complete model and for each independant variables in the model.

	All goslings (n = 8206)					Marked Goslings only (n = 302)				
		PC1 (R^2 = 0.661)		Mass (R^2 = 0.602)			PC1 (R^2 = 0.641)		Mass (R^2 = 0.537)	
	df	*F*	*P*	*F*	*P*	df	*F*	*P*	*F*	*P*
Model	19	835.1	< 0.001	644.0	< 0.001	15	33.9	< 0.001	22.1	< 0.001
Year	4	118.3	< 0.001	165.7	< 0.001	4	4.4	0.002	5.7	< 0.001
Age	1	3119.6	< 0.001	1861.5	< 0.001	1	31.8	< 0.001	15.4	< 0.001
Year × Age	4	106.7	< 0.001	154.4	< 0.001	4	4.0	0.004	5.3	< 0.001
Hatch Date	1	45.7	< 0.001	71.7	< 0.001	1	7.7	0.006	2.3	0.133
Hatch Date × Year	4	5.8	< 0.001	4.9	< 0.001	4	5.9	< 0.001	5.2	< 0.001
Age × Hatch Date	1	26.5	< 0.001	28.5	< 0.001	1	4.9	0.028	1.0	0.317
Age × Hatch Date × Year[a]	4	9.0	< 0.001	1.9	0.114	–	–	–	–	–

[a] This parameter was not retained in the models using marked goslings only, because it was not significant ($P > 0.8$)

Table 4. Mean size (PC1) and mass of goslings near fledging (age standardized at 35 d; ± SE), slopes (± SE) of the relationship between size or mass and hatch date, and probability (*P*) that the slope is equal to zero (SAS estimate statements, proc GLM). Analyses were performed separately on two distinct samples (all or marked goslings). Maximum *n* values are given for each year. Values with the same letter within a line were not significantly different ($P > 0.05$; SAS contrast statements, proc GLM).

Table 4. (continued)

		1991	1992	1993	1994	1995
All goslings						
	n	1121	895	2014	1873	2288
	Mean	0.42 ± 0.03^{A}	0.48 ± 0.03^{A}	0.14 ± 0.03^{B}	-0.95 ± 0.02^{D}	-0.21 ± 0.02^{C}
PC1	Slope (d^{-1})	-0.04 ± 0.01^{C}	-0.11 ± 0.01^{D}	-0.19 ± 0.01^{E}	0.04 ± 0.01^{A}	0.00 ± 0.01^{B}
	P	< 0.001	< 0.001	< 0.001	< 0.001	0.961
	Mean	1726 ± 4.4^{A}	1665 ± 6.2^{B}	1583 ± 4.6^{D}	1457 ± 3.4^{E}	1651 ± 2.7^{C}
Mass (g)	Slope ($g \cdot d^{-1}$)	-15.5 ± 1.6^{C}	-58.2 ± 2.1^{E}	-39.3 ± 1.1^{D}	5.2 ± 1.4^{A}	-4.1 ± 1.4^{B}
	P	< 0.001	< 0.001	< 0.001	< 0.001	0.005
Marked goslings						
	n	17	47	102	62	74
	Mean	1.19 ± 0.37^{A}	-0.15 ± 0.12^{B}	1.00 ± 0.13^{A}	-1.06 ± 0.12^{C}	-0.33 ± 0.11^{B}
PC1	Slope (d^{-1})	-0.63 ± 0.16^{A}	-0.17 ± 0.09^{B}	-0.46 ± 0.07^{A}	0.02 ± 0.05^{B}	0.04 ± 0.07^{B}
	P	< 0.001	0.052	< 0.001	0.744	0.566
	Mean	1761 ± 49^{A}	1575 ± 22^{B}	1735 ± 21^{A}	1420 ± 18^{C}	1629 ± 16^{B}
Mass (g)	Slope ($g \cdot d^{-1}$)	-29.5 ± 24.8^{AB}	-62.5 ± 13.8^{B}	-70.1 ± 10.5^{B}	-8.9 ± 7.8^{A}	2.3 ± 11.7^{A}
	P	0.236	< 0.001	< 0.001	0.258	0.842

PC1: first axis of a principal component analysis (head, culmen and tarsus length)

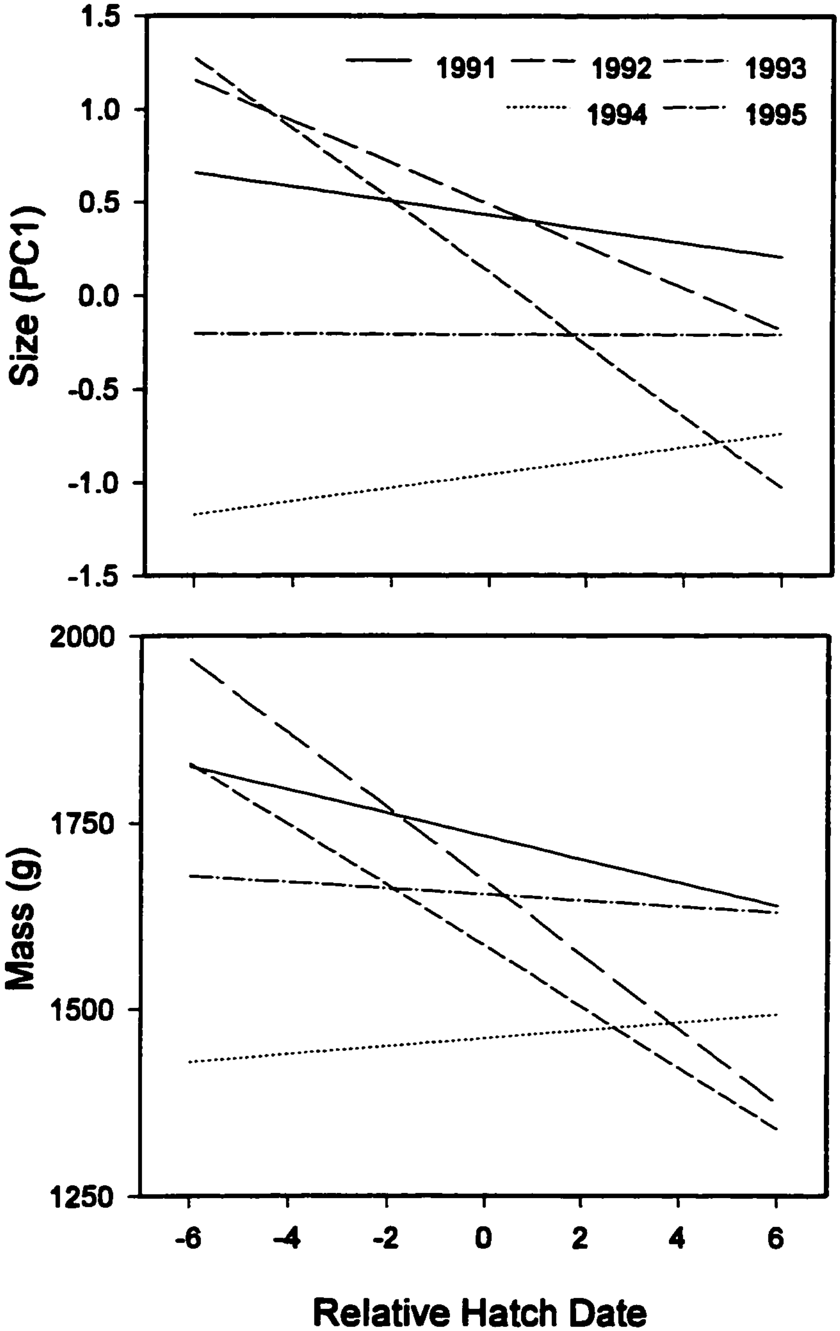

Figure 1: The effect of relative hatch date on gosling size (PC1) and mass (corrected for age at 35 days). Curves were generated from the general linear models testing for the effect of year, age and hatch date on the size and mass of all goslings (*n* = 8 206).

Seasonal variation in food availability and timing of hatch

Natural (eg. climate induced) variations in plant production and the impact of goslings themselves on the vegetation are two factors that can affect food availability and they varied considerably among years. Biomass in ungrazed plots at the end of the summer was highest in 1991 and lowest in 1994 (Table 5). There was also a negative, but variable, effect of grazing on plant biomass in all years. Annual variation in grazing impact can be partly explained by variations in brood density on the study area as suggested by feces counts (Table 5). As a result of the combined effect of variations in plant production and grazing impact, food availability in grazed areas at the end of the summer was about twice as high in 1991 and 1992 than from 1993 to 1995.

Table 5. Biomass (g/m^2) in ungrazed and grazed plots in mid-August (mean ± SE, $n = 12$ each year). Comparisons of biomass in grazed vs. ungrazed plots were made with paired t-test (one-tailed P values are shown) on a yearly basis. Values with the same letter within rows did not differ ($P > 0.05$; Duncan posteriori). Feces count is the cumulative number of feces/m^2 (mean ± SE) up to mid-August in grazed areas ($n = 12$ each year).

	1991	1992	1993	1994	1995
Ungrazed plots (U)	35.8 ± 5.3^{A}	n/a	29.3 ± 1.5^{AB}	17.7 ± 2.3^{C}	23.3 ± 3.4^{BC}
Grazed plots (G)	23.2 ± 5.0^{A}	25.6 ± 4.8^{A}	11.7 ± 1.4^{B}	12.9 ± 1.3^{B}	12.8 ± 1.3^{B}
P (U > G)	0.048	n/a	< 0.001	0.041	0.004
Feces count	60.9 ± 7.3^{B}	n/a	99.3 ± 11.5^{A}	60.5 ± 6.9^{B}	36.2 ± 4.3^{C}

The timing of hatch in relation to plant biomass in grazed areas varied among years. Biomass continued to increase after the peak of hatch in 1991, 1992 and 1995, but decreased in 1993, the year with the highest brood density, and in 1994, the year with very low plant production (Figure 2a). Nitrogen concentration in grazed plants generally decreased during the summer, but the magnitude and timing of the decline were highly variable among years. Peak nitrogen concentration was synchronized with peak of hatch only in 1993. In 1995, hatching was about a week before the peak in nitrogen concentration, but it was a week after in 1991, and up to 3 weeks after in 1994, which resulted in very low plant quality at the time of hatching that year (Figure 2b). In contrast to the previous two measurements, there was a remarkable synchrony between the peak of hatch and the peak in nitrogen availability (plant biomass × nitrogen concentration) in all years but 1995 (Figure 2c). In the first three years, nitrogen availability declined by about 40% over the 25 days that followed the peak of hatch, which again contrasted with 1995 when there was virtually no decline.

Variation in food availability and gosling growth

The pattern of seasonal variation for the three indices of food availability (cumulative exposure to biomass, nitrogen concentration and nitrogen biomass) was similar, whether the calculations were made over the period 1 and 35 d, 1 and 25 d or 11 and 25 d. Hence, only details of the indices calculated from 11 to 25 d (CEB_{15}, CEC_{15} and CEN_{15}) will be presented. The biomass to which goslings were exposed (CEB_{15}) declined steadily between 1991 and 1995 (Figure 3a). Within years, early-hatched goslings were exposed to more biomass than late-hatched goslings in all years except in 1995. Annual variations in gosling exposure to nitrogen concentration (CEC_{15}) were opposite to biomass: CEC_{15} was highest in 1995 and lowest in 1991 (Figure 3b). As with biomass, there was a seasonal decline in CEC_{15} in all years. Finally, exposure to nitrogen biomass (CEN_{15}) was highest and similar in 1991 and 1993, intermediate in 1995 and lowest in 1994. Again, there was a seasonal decline of CEN_{15} in all years but 1995 and the slope was steeper than for the other indices (Figure 3c).

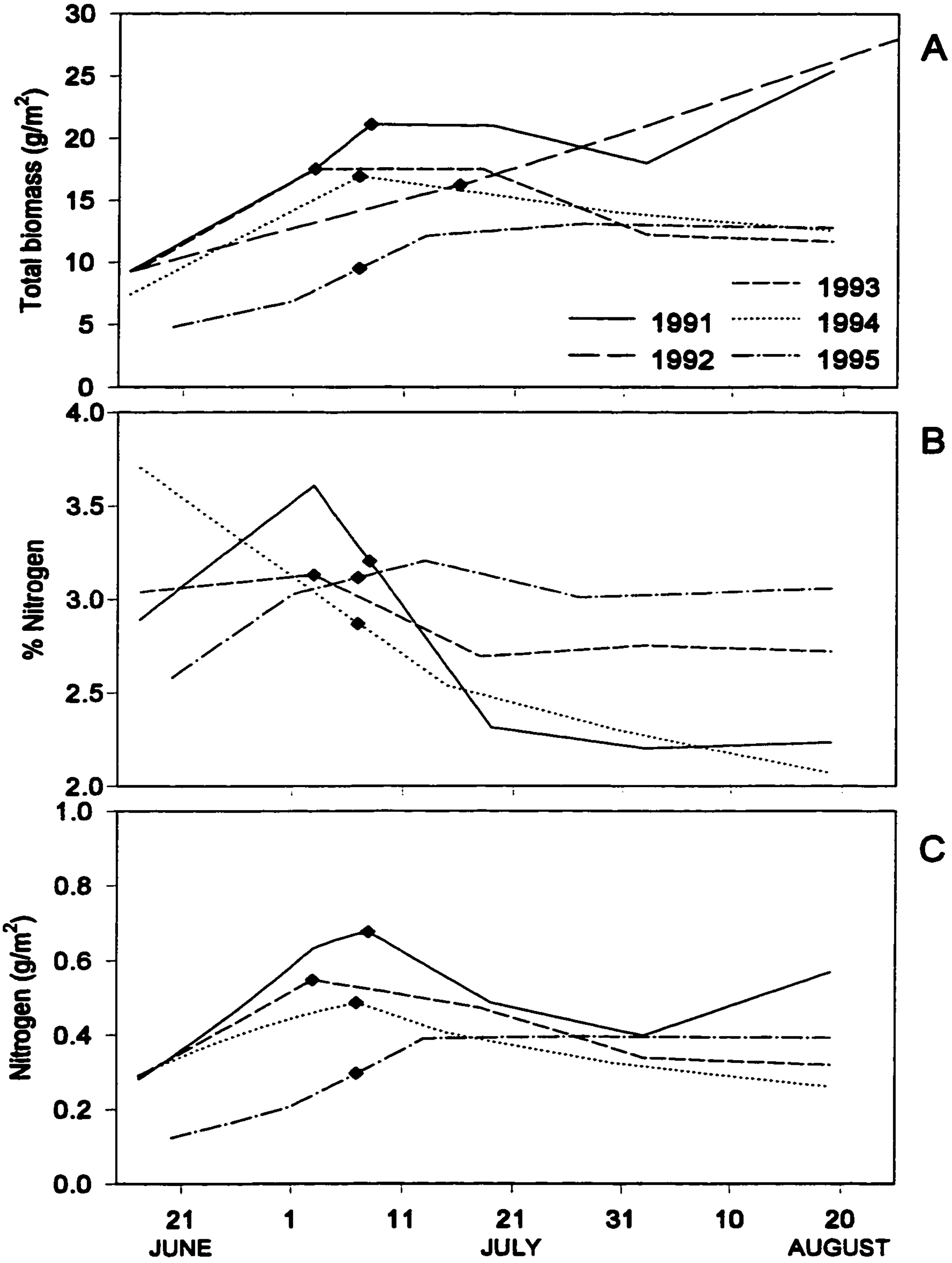

Figure 2. Seasonal change in (A) plant total biomass, (B) nitrogen concentration and (C) nitrogen biomass in grazed plots. The diamond (♦) represents the median hatch date of snow goose nests in each year.

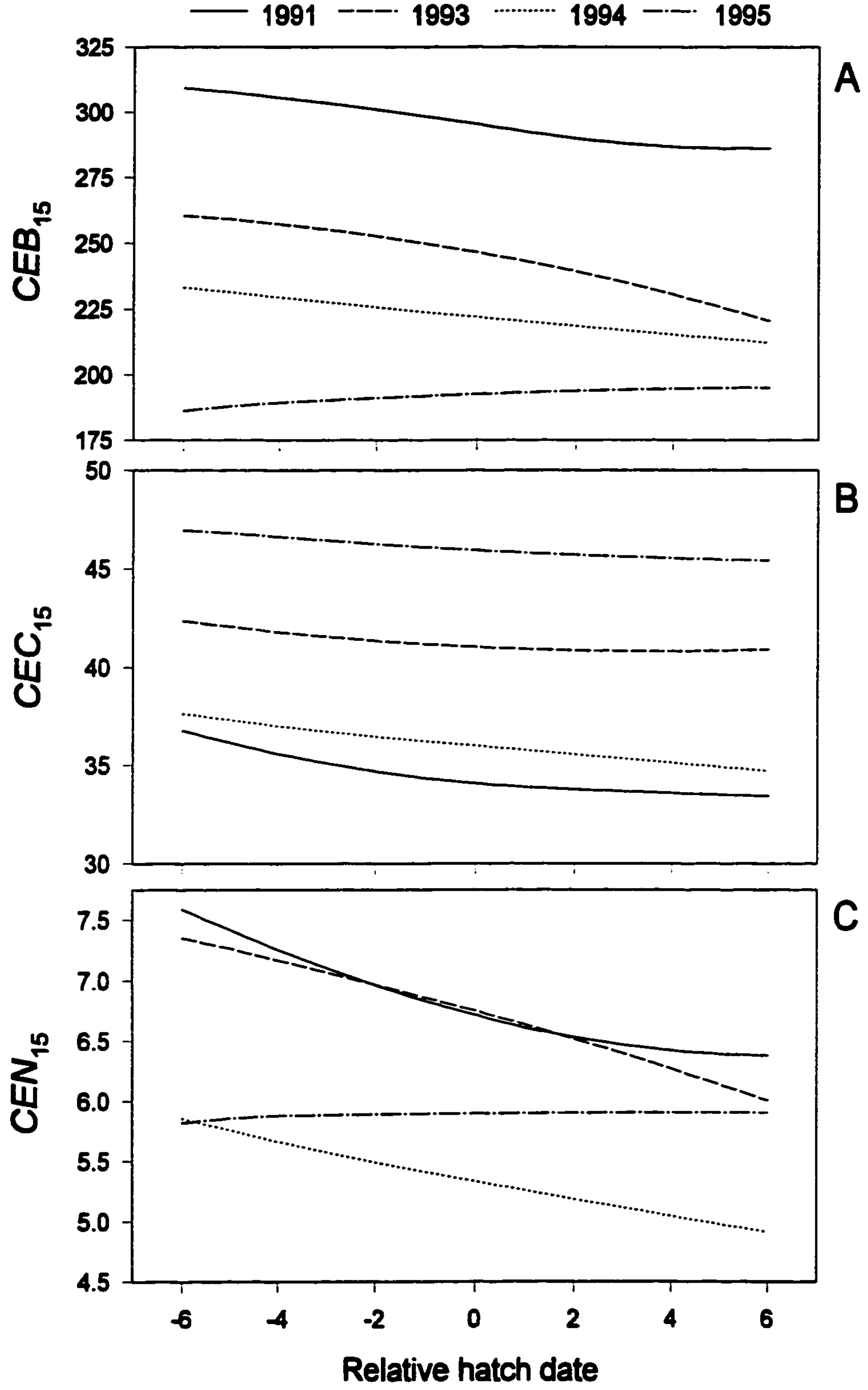

Figure 3. Seasonal change in the indices of cumulative exposure to (A) plant biomass (CEB_{15}), (B) nitrogen concentration (CEC_{15}), and (C) nitrogen biomass (CEN_{15}).

Our indices of food availability were all significantly related to the size and mass of individual goslings at 35 d, regardless of the period for which availability was estimated (1–35 d, 1–25 d or 11–25 d; Table 6). Results obtained with all goslings or only marked ones were similar. However, the first two indices explained only a small variation in gosling growth: cumulative exposure to plant biomass (*CEB*) explained less than 11% and 4% of the variation, and cumulative exposure to nitrogen concentration (*CEC*) explained less than 4% and 12% of the variation in gosling size and mass respectively (Table 6). In contrast, cumulative exposure to nitrogen biomass (*CEN*) performed much better than the other two indices: this variable could explain respectively up to 21% and 15% of the variation in size and mass of all goslings, and up to 44% and 35% of the variation in marked goslings. Overall, the cumulative exposure to nitrogen biomass over the period 11–25 d (CEN_{15}) explained more variation than any other indices.

On a yearly basis, we found a positive relationship between CEN_{15} and gosling size or mass in 1991 and 1993 (Figure 4, Table 7). There was an inverse relationship in 1994 (only significant with all goslings) and no relationship in 1995, a year where both the size of the goslings and the food availability index (CEN_{15}) did not vary seasonally (Figures 2 and 3).

Table 6. Regression between the size and mass of goslings at 35 d and various indices of food availability (see methods; 1991–1995). R^2 with P values in parenthesis are shown.

	All goslings (n = 8206)[a]		Marked goslings (n = 302)	
	Size (PC1)	Mass	Size (PC1)	Mass
CEB_{35}	0.084 (<0.001)	0.030 (<0.001)	0.030 (0.003)	0.002 (0.403)
CEB_{25}	0.071 (<0.001)	0.013 (<0.001)	0.074 (<0.001)	0.012 (0.058)
CEB_{15}	0.105 (<0.001)	0.037 (<0.001)	0.063 (<0.001)	0.015 (0.036)
CEC_{35}	0.016 (<0.001)	0.047 (<0.001)	0.030 (0.006)	0.109 (<0.001)
CEC_{25}	0.017 (<0.001)	0.053 (<0.001)	0.033 (0.004)	0.115 (<0.001)
CEC_{15}	0.006 (<0.001)	0.027 (<0.001)	0.008 (0.152)	0.066 (<0.001)
CEN_{35}	0.182 (<0.001)	0.137 (<0.001)	0.385 (<0.001)	0.284 (<0.001)
CEN_{25}	0.137 (<0.001)	0.064 (<0.001)	0.346 (<0.001)	0.210 (<0.001)
CEN_{15}	0.214 (<0.001)	0.154 (<0.001)	0.435 (<0.001)	0.354 (<0.001)

[a] n = 7122 and 254 for all and marked goslings respectively for *CEC* and *CEN* because of missing values of nitrogen concentration in 1992.

Table 7. Slopes of the regressions between the size and mass of the goslings at 35 d and an index of food availability (CEN_{15}). P values are given in parenthesis.

		All goslings			Marked goslings	
	n	Size (PC1)	Mass	n	Size (PC1)	Mass
1991	1082	0.356 (0.004)	160.4 (<0.001)	17	4.71 (0.005)	223.0 (0.355)
1993	1940	1.690 (<0.001)	352.0 (<0.001)	102	4.22 (<0.001)	646.2 (<0.001)
1994	1834	-0.483 (<0.001)	-73.2 (<0.001)	62	-0.19 (0.759)	119.3 (0.204)
1995	2266	1.637 (0.517)	-894.8 (0.025)	74	11.35 (0.602)	259.3 (0.936)

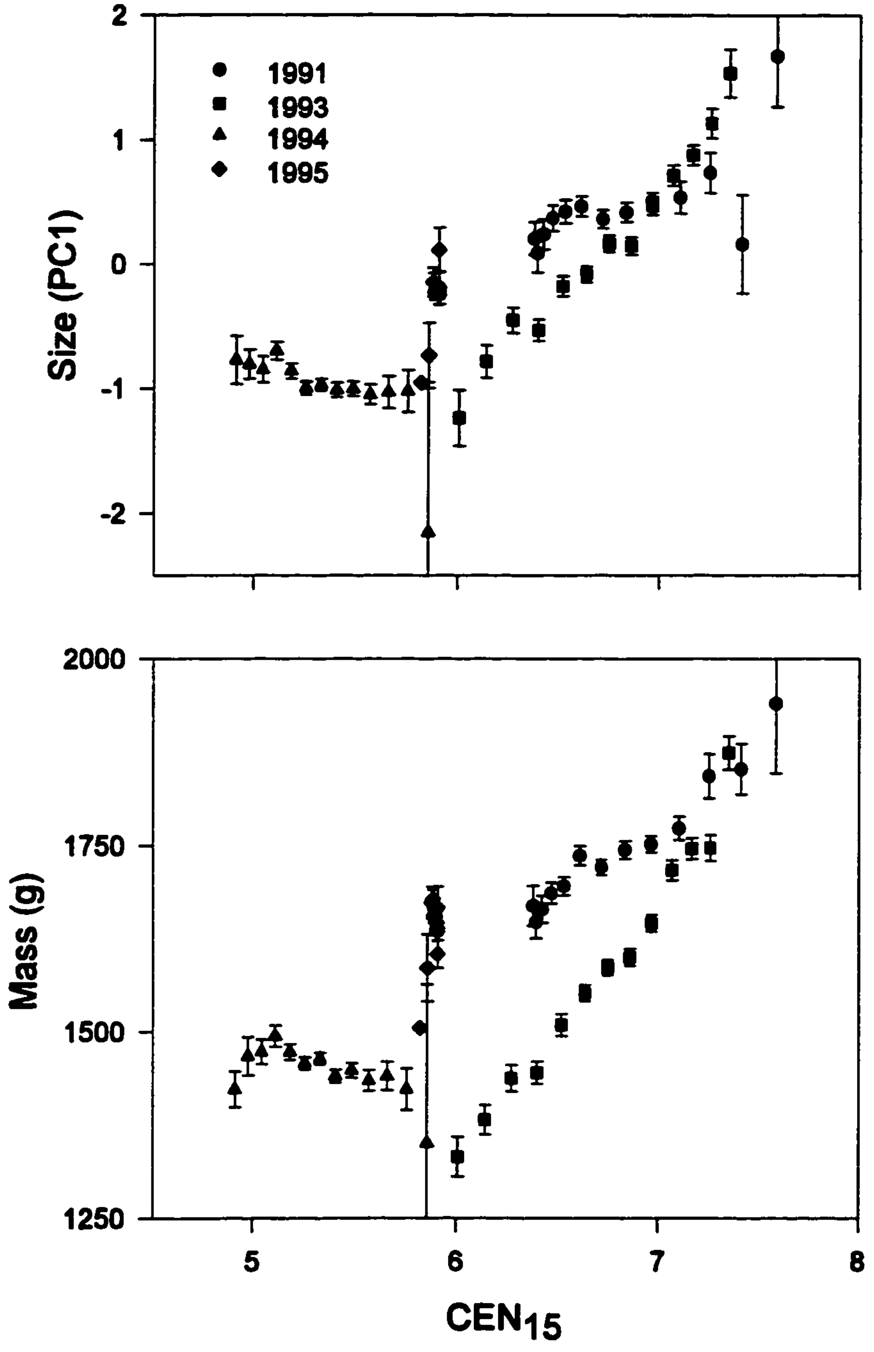

Figure 4. Relationship between gosling size (PC1) and mass at 35 d and an index of food availability during growth (*CEN*$_{15}$) using the sample of all goslings (*n* = 8 206). Each point represents the average body size or mass (± SE) calculated for each relative hatch date (from -6 to 6) in each year.

DISCUSSION

Variation in gosling growth

The larger size and heavier mass of early-hatched goslings at the end of the summer suggest that they grew faster than late-hatched goslings, but this phenomenon was not observed in all years. In lesser snow geese (*Ch. c. caerulescens*), Cooch et al. (1991a) reported a seasonal decline of growth rate in most years of their study period, but not all. Seasonal decline of growth rate have also been reported in black brant *Branta bernicla nigricans* (Sedinger and Flint 1991), barnacle goose *Branta leucopsis* (Larsson and Forslund 1991, M. Loonen, pers. comm.), pied oystercatcher *Haematopus ostralegus* (Kersten and Brenninkmeijer 1995) and various seabirds (Harris 1980, Birkhead and Nettleship 1982, Gaston et al. 1983, Weimerskirch 1990). In addition to intra-seasonal variations, there was considerable variation in growth among the five years, the smallest goslings in the best year (1991) being larger at the same age than the largest goslings in the worst year (1994). Similar inter-annual variations have also been found in other studies (Cooch et al. 1991b, Aubin et al. 1993, Reed and Plante 1997).

These variations may have major fitness consequences as several studies have shown that body size at fledging affects post-fledging survival and recruitment rate into the breeding population (Perrins 1965, Garnett 1981, Cooke et al. 1984, Owen and Black 1989, Magrath 1991, Sedinger et al. 1995). In arctic-nesting geese, the early onset of the fall migration may force late-hatched birds to allocate resources to fat accumulation at an earlier stage of development than early-hatched ones at the expense of body size (Lesage 1995). Individuals that grow slowly cannot fully compensate later, and thus become smaller adults (Cooch et al. 1991a, Larsson and Forslund 1991, Sedinger et al. 1995) and may have lower fecundity (Sedinger et al. 1995).

An important assumption in this study is that gosling age was correctly estimated with primary length. Lindholm et al. (1994) showed that the age of emergence of the 9th primary was delayed in hand-reared, late-hatched goslings facing poor feeding conditions, though growth rate after emergence was not affected. If date of emergence of 9th primary is also delayed in wild, late-hatched goslings, this would underestimate their age and hence would attenuate seasonal effects on growth. However, we believe that the 9th primary length provided a reasonable estimate for age of unmarked goslings for several reasons. First, we used year-specific models which controlled for inter-annual differences in growth of the 9th primary. Second, our analysis with marked goslings showed that the 9th primary length, unlike other body components, was not affected by intra-annual variations in hatch date. Finally, seasonal effects on growth detected in this study were very similar in all years between goslings whose age was estimated and those with known age. In the two years (1991 and 1993) that estimated age differed the most from observed age, goslings were mostly tagged in the brood-rearing area (Base-camp). This difference may reflect a genuine difference in the timing of nesting in the different parts of the island (see also Lepage et al. 1996, chapter 1), rather than a bias of our method.

Timing of hatch and food availability

Our results generally support the hypothesis that birds synchronize hatching with the peak of food supply (Lack 1968, Sedinger and Raveling 1986, Daan et al. 1988). In 1991, 1993 and 1994, we showed a good synchrony between the median hatch date and the peak in nitrogen availability, presumably one of the best index of food supply. There was no such peak in 1995, and peak of hatch was about 5 days before a plateau in food availability was reached. Although geese may not be able to perfectly synchronize hatch with food availability in all years, our results show that some adjustment is likely occurring. Food availability during egg formation early in the season may provide some cue to the geese on the timing of food availability later in the summer. Moreover, as plants are usually more predictable than other sources of food, it may be easier for herbivores to adjust the timing of their reproduction with the food supply.

However, our results also showed that goslings hatched before the peak of food availability generally grew faster than birds hatched at the peak, suggesting that the best strategy is to hatch before the peak of nutrients, rather than being synchronized with it. A simple model (Figure 5) based on hypothetical data shows that the index of cumulative exposure to food is never at its maximum value for birds hatched directly at the peak of food availability, but rather for birds hatched earlier, and that optimum hatching date varies with the period used to compute the index. Our index of nitrogen availability explained the greatest amount of variation in gosling size and mass when computed over the period 11–25 d. This may occur because the most critical period for nutritional demand in growing goslings is not immediately after hatch but later, during the most rapid phase of growth. During the period 11–25 d, goslings increase from 15% to 50% of their mass at fledging (Lesage and Gauthier 1997) and any variation in food supply at that time may have more influence on growth than at any other period. In great tits (*Parus major*) the greatest food requirement occurs about 10 days after hatching (Perrins 1991), and maximum fitness is achieved by parents that synchronize nesting accordingly (Dias and Blondel 1996).

If the best time to hatch is before the peak of food availability, then why the majority of the population apparently behaved sub-optimally by hatching in synchrony with the peak? Rockwell et al. (1987) already noted that the mean clutch size in lesser snow geese was not the one that maximized fitness and proposed that a directional selection could still be acting on a population that was formerly at a different fitness equilibrium. The same argument may potentially be applied to laying date (Cooke et al. 1995). Since growth rate is related to fitness, there could be a directional selection for earlier nesting. However, there is a growing body of literature that shows a discrepancy between optimal and observed clutch size or laying date (Perrins 1988), and many long-term studies failed to document an evolution in nesting behavior with time (Rockwell et al. 1987, Boyce and Perrins 1987, Gibbs 1988). To explain this phenomenon, Cooke et al. (1990, 1995) showed that clutch size and laying date exhibited little genetic heritability and proposed that both were mostly determined by environmental conditions. For instance, laying date may be constrained by the need to acquire nutrients for laying (Ankney and MacInnes 1978) or by site availability early in the season (but see Lepage et al. 1996 and Chapter 1). In greater snow geese, females must feed intensively during the pre-laying period (Choinière and Gauthier 1995) and may thus be very sensible to variation in environmental conditions at that time. Alternatively, Price et al. (1988) proposed a model to explain how directional selection may be observed for a trait that shows genetic heritability, but not result in a change in the mean value of this trait in the population. Both models may help to understand why laying date would not evolve despite an apparent directional selection for earlier breeding.

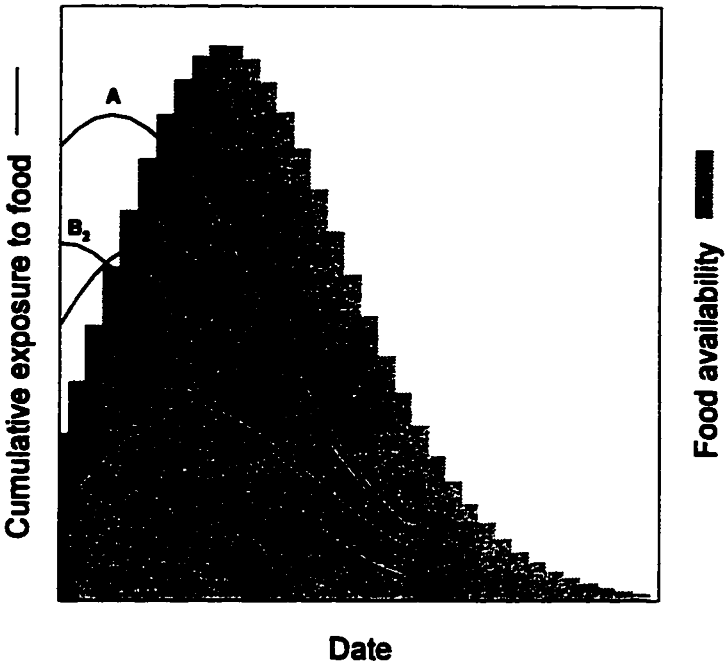

Figure 5. Indices of cumulative exposure to food during growth according to hatching date. Curves were generated from hypothetical data of food availability (gray area) for the following periods of exposure: (A) 1–35 d; (B$_1$) 1–25 d; (B$_2$) 11–35 d; and (C) 1–15 d. The hatching date which corresponds to the maximum exposure to food is always before the peak of food availability when food declines steadily after the peak. The shortest period of calculation leads to the smallest difference between peak exposure and peak of food availability. Changing only the starting date, but not the period of exposure (as with B$_1$ and B$_2$), results in a shift of the curve, but does not affect its shape.

The interaction between food supply and growth rate

Variations in food supply have often been inferred as a major cause of variations in growth rate of young (Lack 1968, Martin 1987), but this relationship has rarely been tested under natural conditions. One of the main reasons is the difficulty to correctly identify the food sources and to evaluate their respective nutritive value. Thus, a controversy exists about how much variability in growth rate can be explained by variation in food. Some authors have argued that growth rate is largely constrained by physiological factors rather than by food availability (Ricklefs 1983, Konarzewski et al. 1989, 1990). However, most of these studies were on altricial birds which are fed by their parents with protein-rich food such as insects. In contrast, herbivores that must rely on plants, a food source with a low concentration of nutrients, may be more sensitive to variations in food availability during growth.

In geese, several authors have proposed that the seasonal decline in growth is a consequence of declining plant quality and of density-dependent food depletion (Cooch et al. 1991a, Sedinger and Flint 1991). Our results support this hypothesis: early-hatched birds experienced a higher level of nitrogen biomass than late-hatched birds in all years but 1995, and had a faster growth. In 1995, the absence of seasonal variation in food availability also resulted in an absence of seasonal variation in gosling growth, thus supporting our conclusion. Growth in herbivores like geese appears to be very sensitive to slight variation in food quality because these birds may be unable to increase food intake to compensate a decline in quality (Sedinger and Raveling 1988, Manseau and Gauthier 1993, Piedboeuf 1996).

Among years, food availability also explained some of the observed variations in growth rate. In the years where food availability was highest, 1991 and 1993, average body size and mass were larger than in the two years, 1994 and 1995, with lower food availability. It is interesting that the seasonal decline in growth only occurred in the years where food availability was high. This suggests that early-hatched birds are having an advantage over late-hatched birds only if feeding conditions are good.

Although nitrogen is probably the most important nutrient for goslings, nitrogen content in itself does not describe plant quality completely. Food metabolizability may differ between different plant species and different moments in the season in response to variations in plant constituents such as fiber or water (Manseau and Gauthier 1993, Piedboeuf 1996). The method we used to combine the nitrogen concentration of *Dupontia* and *Eriophorum* (the average between the two species), was also arbitrary and may not always represent what goslings actually consumed: although *Eriophorum* is usually less abundant than *Dupontia*, goslings actively select the former. Despite these potential problems, our index of nitrogen availability appeared to be a good predictor of gosling size and mass. This index always explained a greater variation in size or mass than plant biomass or nitrogen concentration alone.

Other factors involved in seasonal variation of gosling growth

The relationship between growth and date could also be explained by differential parental quality between early and late nesters if date of nesting is correlated with parents' ability to provide suitable feeding conditions for goslings (e.g. choice of the best feeding patches; Hughes et al. 1994b). However, in an experiment where we exchanged clutches between early and late-nesting parents, difference in parental ability failed to explain any seasonal variation in gosling growth (chapter 4). Cooch et al. (1991a) showed that growth of goslings raised by the same parents at different dates in different years also differed, indicating that factors other than parental quality were responsible for the variation in growth.

Brood size in itself may affect growth rate, independently of parental quality. Several studies have shown that families with large brood size were dominant over smaller families (Boyd 1953, Raveling 1970, Black and Owen 1987, 1989). Thus, early hatched goslings, which tend to be associated with larger families, 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). However, Cooch et al. (1991a) demonstrated that hatch date had an effect on growth rate, independently of brood size. The larger body size of early-hatched goslings (both because of their age and their faster growth) compared to late-hatched ones may also confer a social advantage to their family (Black and Owen 1987).

Fortin (1995) showed that weather conditions experienced by late-hatched goslings during the summer force them to allocate up to 22% more energy to thermoregulation than early-hatched birds. Thus, within- and between-year climatic variations may well contribute to a part of the observed variation in gosling growth.

Finally, there could be a genetic component of growth associated with date. If early-nesting parents are larger birds, they may transmit that character to their offspring, which would then grow faster and attain larger final body size. Heritability of morphological characters in birds (i.e. size of the various parts of the body) is generally estimated at 60–70% (Boag and van Noordwijk, 1987). However, the heritability component is a very difficult measure to obtain in the field and most of these studies may have underestimated the effect of the common environment between parents and offsprings. For example, large parents may have a better access to local food supply, thus enhancing the growth of their offsprings (Boag and van Noordwijk 1987, Larsson and Forslund 1992).

CONCLUSIONS

Our study provides direct evidence of the critical role of food supply in the intra- and inter-annual variations of growth rate in a herbivorous bird. We showed that while parents apparently synchronized hatching of their eggs with peak food availability, goslings hatched before the peak usually grew faster. Our results suggest that goslings hatched before the peak have more food available on a cumulative basis and that the period of highest energetic demand may best coincide with the period of maximum food availability for early hatched birds. This finding may have important implications for understanding optimal reproductive strategies and timing of reproduction in relation to food.

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CHAPITRE 4

SEASONAL DECLINE OF GROWTH AND FLEDGING SUCCESS IN GREATER SNOW GEESE: AN EFFECT OF DATE OR QUALITY?

RÉSUMÉ

Les oiseaux nichant tard en saison obtiennent souvent un moins bon succès reproducteur que ceux qui nichent tôt. Ceci peut être une conséquence des variations saisonnières dans les conditions environnementales, ou des différences dans la qualité des parents hâtifs et tardifs. Nous avons testé l'hypothèse qu'une différence entre les parents hâtifs et tardifs dans leur habileté à élever leurs jeunes avec succès explique le déclin saisonnier de la survie et de la croissance des jeunes chez la grande oie des neiges (*Chen caerulescens atlantica*), une espèce nidifuge. Nous avons échangé, au cours de deux années de reproduction, les jeunes entre des parents hâtifs et des parents tardifs, de façon à modifier la qualité des soins parentaux que les jeunes recevaient. Les échanges ont été faits entre 164 nids expérimentaux dont la date d'éclosion différait de 0 à 9 jours ($\bar{x}$ = ± 3 jours). Dans la population, les jeunes éclos hâtivement ont eu un taux de croissance supérieur aux jeunes tardifs, mais nous n'avons pas détecté d'effet de la date d'éclosion sur la survie dans l'échantillon des nids expérimentaux. La croissance des jeunes provenant des nids expérimentaux n'a pas été affectée par la qualité des parents adoptifs et ne différait pas de la croissance de jeunes non-expérimentaux éclos à la même date. Nos résultats suggèrent donc que la variation saisonnière du succès reproducteur n'est pas causée par une différence dans la qualité des parents, mais principalement par des facteurs environnementaux reliés à la date de la saison.

ABSTRACT

Late-nesting birds frequently have a lower reproductive success than early-nesting ones. This could be a consequence of seasonal variations in environmental conditions or because late-nesting parents are of low quality. We tested the hypothesis that a difference between early and late parents in their ability to raise viable offspring could explain the seasonal decline in offspring growth and survival in the greater snow goose (*Chen caerulescens atlantica*), a precocial species. Over two years, we exchanged complete broods between early and late parents, to change the quality of the parental care received by goslings. We exchanged eggs between 164 experimental nests, which hatching date differed from 0 to 9 days ($\bar{x} = \pm 3$ days). Early-hatched young grew more rapidly than late hatched young, but we did not detect a seasonal effect on survival rate in the sample of experimental nests. Growth of experimental goslings was not affected by the experimental change in parental quality and was not different from that of non-experimental goslings hatched at the same date. Our results suggest that the seasonal variation in reproductive success is not caused by a difference of parental quality between early and late nesters, but mostly by environmental factors directly related to the date of the season.

INTRODUCTION

Seasonal variation in reproductive success is a general feature in living organisms. One of the most common patterns of variation in birds is a seasonal decline of reproductive success during the nesting season (Perrins 1970, Daan et al. 1988). Late nesting birds often lay smaller clutches (Klomp 1970, Drent and Daan 1980), and their offspring grow more slowly (Birkhead and Nettleship 1982, Cooch et al. 1991; Sedinger and Flint 1991) and have a lower chance of survival and recruitment into the breeding population than early-nesting birds (Perrins 1970, Daan et al. 1988).

The seasonal decline in offspring value is often viewed as a consequence of declining environmental conditions, like colder weather or reduced food availability later in the season. However, this relationship could also be explained by differential quality between early and late nesters if nesting date is correlated with parents' ability to provide adequate conditions for their growing offspring (Verhulst and Tinbergen 1991, Brinkhof et al. 1993). For instance, in many species older parents tend to nest earlier and they achieve a higher reproductive success than younger parents (Finney and Cooke 1978, Dow and Fredga 1984, Perrins and McCleery 1985, Nol and Smith 1987). Some studies have tried to determine if seasonal effects are caused by environmental or parental quality by exchanging clutches between early and late-nesting pairs in altricial bird (Hunt and Hunt 1976, Norris 1993, Brinkhof et al. 1993, Brouwer et al. 1995), or by delaying nesting by inducing replacement clutches through removal of the first clutch (Parsons 1975, Hatchwell 1991, Verhulst and Tinbergen 1991, Wiggins et al. 1994, Verhulst et al. 1995, De Forest and Gaston 1996), with mixed results.

The importance of parents in offspring success is far from clear in precocial birds. In species like shorebirds, waterfowl and grouse, precocial young are apt to feed by themselves immediately after hatch and do not directly depend on their parents for their food. The young, however, still follow their parents for a variable period of time during which they receive some parental care (Saffriel 1975, Lazarus and Inglis 1978, Winkler and Walters 1983, Schindler and Lamprecht 1987). This includes vigilance and defense against predators, brooding, leading to good feeding sites and gaining access to these sites in presence of competitors (Winkler and Walters 1983). A difference in the ability of parents to adequately supply care could thus also explain differences in reproductive success between early and late-nesting precocial birds. For example, Hughes et al. (1994b) showed that families of greater snow geese (*Chen caerulescens atlantica*) that hatched early moved less and used more high quality feeding habitats than late-hatched families, which suggests a seasonal difference in parental behavior. However, Cooch et al. (1991a) showed that parental quality was probably not the sole factor involved in seasonal variation of gosling growth as goslings raised by the same female in different years experienced a slower growth in late years. The only way to unambiguously separate the parental quality component from the environmental component in offspring success is through a manipulation such as an exchange of offspring between parents with different nesting dates.

In this paper, we present the results of such a clutch manipulation experiment realized with the greater snow goose, a large precocial bird nesting in the Arctic. In arctic-nesting geese, nest initiation is typically very synchronized and about 90% of the nests are initiated within 8 days in this population (see chapter 2). Strong seasonal effects on several components of reproductive success are nonetheless present (chapters 2 and 3, Cooch et al. 1991, Lindholm et al. 1994, Cooke et al. 1995, Sedinger et al. 1995). Our aim was to assess the role of parental quality in the seasonal variation of reproductive success in this species.

METHODS

The experiments were conducted at the Bylot Island snow goose colony, in the Canadian High-Arctic (73°N 80°W; see Gauthier et al. 1995 , Lepage et al. 1996 and Chapter 1 for details of the study area). 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. 1994b).

We monitored 209 and 240 nests from laying to hatching in 1993 and 1994, respectively. Nest initiation dates were obtained by one of three different methods (listed in decreasing order of precision): 1) for nests found during egg-laying, initiation date was estimated by subtracting the number of eggs in the nest minus one to the date of discovery (if >3 eggs were present in the nest, another day was subtracted because the laying interval averages 33 hours in snow geese; Schubert and Cooke 1993); 2) for nests found during incubation but with a known hatching date, the initiation date was estimated by subtracting the clutch size (minus one if ≤3 eggs) and the incubation length (23-day; Gauthier, unpubl. data) from hatching date; 3) for nests of unknown hatching date, an egg density index (mass/length*breadth2) was used to estimate initiation date based on the linear relationship between egg density and stage of incubation (Gauthier, unpubl. data). Methods 2 and 1 were most frequently used.

Shortly before hatching, we selected pairs of nests with equal clutch size but with different laying dates and swapped the complete clutches between the paired nests. The variable *Change in parental quality* (*CPQ*) was calculated for each offspring as its hatching date minus the hatching date of the eggs laid by the foster parents *(CPQ* from 0 to ± 9 days). A negative value was associated with a lower parental quality for the young, and a positive value with an increase in quality (Figure 1). We also exchanged eggs between control pairs with the same hatch date to test the impact of egg transfer. All goslings, either in experimental, control or unmanipulated nests, were marked at hatch with individually numbered web-tags. Daily survival rate of nests was calculated with the Mayfield method (1975), and values were compared using the pairwise test recommended by Johnson (1979).

Shortly before fledging, about 5 weeks after hatch, large family groups were captured in mass banding drives, at a time when adults are unable to fly due to the molt of their flight feathers. Each gosling caught was sexed by cloacal examination, measured (head, culmen, tarsus, and 9th primary length), weighed (nearest 25 g) and checked for the presence of a web-tag.

Pre-fledging survival of goslings was estimated by recapture of marked individuals. Probability of recapture is the product of survival rate and capture rate (i.e. probability of capturing a bird if alive). Differences in probability of recapture reflect differences in survival, assuming that capture rate is constant among experimental groups. Goose families were captured over a wide area at our study site and we have no evidence of differential dispersal among our experimental groups. We tested the effect of Year, Hatch date, *CPQ* and CPQ^2 on the proportion of gosling recaptured per brood near fledging with log-linear models (Proc Catmod of SAS Institute inc. 1988). The analysis was restricted to manipulated nests (experimental and control), and only variables that approached significance ($P < 0.10$) were retained in the final model. Because of small sample size, we could not test more than two independent variables simultaneously. We thus tested all possible two-variable combinations before removing a variable from the model.

Body measurements of goslings caught were used as indices of growth. Body size was defined as the first component of a principal component analysis combining measurements of tarsus, head and culmen. Age of unmarked goslings was estimated by the linear relationship between age of marked goslings (from both manipulated and unmanipulated nests) and length of their ninth primary feather (1993: $n = 102$, $R^2 = 0.63$; 1994: $n = 62$, $R^2 = 0.72$; see chapter 3). Age of goslings at recapture ranged from 28 to 45 d (mean = 37.1, n = 3 899 young). An initial generalized linear model was first used to test the effects of Year, Age and Hatch date on gosling size and mass using all goslings captured. To control for the effects of these variables, residuals from the first model were used to test the effect of the manipulation (CPQ and CPQ^2) on marked goslings from manipulated nests only (see Figure 1).

RESULTS

We exchanged eggs between 45 and 37 pairs of nests (CPQ from 0 to ± 9 days) in 1993 and 1994 respectively. On average, our manipulations changed by ±3.2 days the timing of hatching of experimental nests in 1993 and by ±3.3 days in 1994. Daily survival rate of manipulated nests after the manipulation was slightly higher (0.986 ± 0.003 [SE]) than that of unmanipulated nests (0.974 ± 0.003; $P = 0.002$) when all the data were combined. When survival rate was calculated for each group of nests with the same relative laying date (laying dates transformed as deviation from median laying date in each year), unmanipulated and manipulated nests did not differ, except for nests initiated one day after the median date (experimental nests had a higher survival rate) (Figure 2). Thus, manipulation of the incubation period did not have a negative impact on nest survival.

A total of 2 416 and 511 young were tagged at hatch in 999 unmanipulated and 135 manipulated nests (including controls) respectively. Near fledging, 3 899 goslings were captured, including 126 marked birds from unmanipulated nests and 38 marked birds from manipulated nests. None of the variables tested (Year, Hatch date, CPQ and CPQ^2) had a significant effect on the proportion of goslings recaptured from manipulated nests ($P > 0.13$, n = 135 nests), thus indicating that survival was similar for all birds. There was no difference in the average proportion of goslings recaptured between manipulated (6.6%, n = 135) and unmanipulated broods (5.3%, n = 148; $\chi^2 = 0.34$, $P > 0.5$, df = 1).

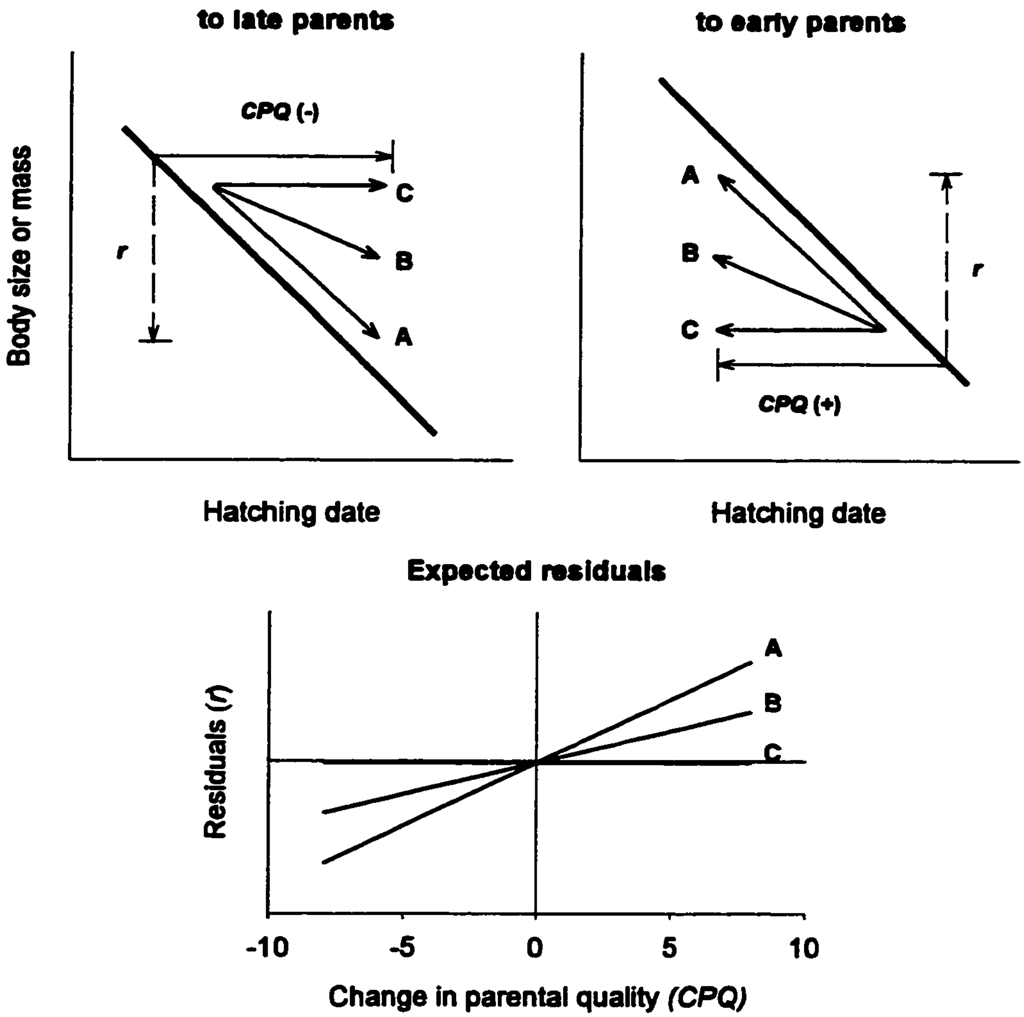

Figure 1. Possible outcomes of the experimental change in parental quality. TOP: The thick line represent the decline of body size and mass over the nesting season. On the left, giving goslings to late-nesting parents (a negative *CPQ*) should either result in line A if only parental quality is involved, in line C if only the environment is involved, or in line B if a combination of parental quality and environment explains the seasonal variation in body size or mass. The same applies to the right figure when giving goslings to early-nesting parents (a positive *CPQ*). To test the effect of the experimental manipulation (*CPQ*), we used the residual (*r*) between the observed value and the value expected under the hypothesis that only the environment explains the seasonal decline. BELOW: Expected residuals under the different hypotheses A, B or C presented above. A significant relationship between *CPQ* and the residuals would indicate that parental quality contributes to the seasonal decline.

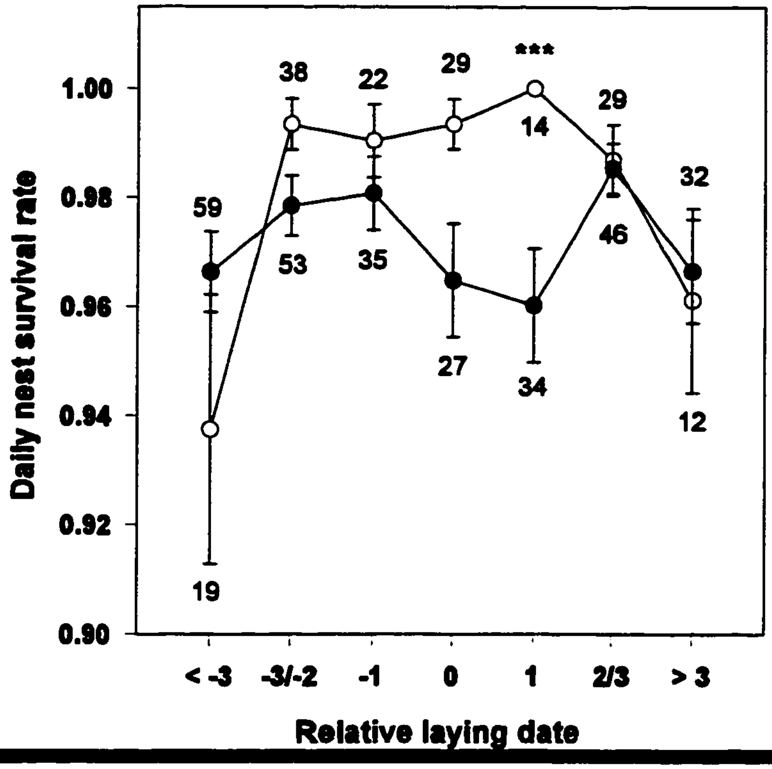

Figure 2. Daily survival (± SE) of manipulated (○) and unmanipulated (●) nests in the days following the manipulation, according to the relative laying date (laying dates transformed as deviation from median laying date in each year). We used laying date of the newly transfered eggs in the case of experimental nests, rather than the original laying date of the foster parents. Pairwise comparisons between the two groups for each laying date (*** $P < 0.001$; otherwise, $P > 0.05$). Sample size shown for each group.

Year, Age, Hatch date, and most of their interactions had a significant effect on gosling size and mass near fledging (Table 1). As expected, goslings from early broods grew faster than goslings from late broods and were larger at fledging. In the second model, which controlled for the effect of the previous variables, *CPQ* had no significant effect on the residual size and mass of goslings from manipulated nests (Table 1; $P > 0.5$), indicating that gosling growth was not affected by the manipulation (Figure 3).

Table 1. Summary of the general linear models. Model 1: the effect of Year, Age and Hatch date on gosling size (PC1 score, $R^2 = 0.66$, $n = 3857$) and mass ($R^2 = 0.57$, $n = 3851$). Model 2: the effect of manipulation (*CPQ*) on the residuals of size ($R^2 = 0.11$, $n = 38$) and mass ($R^2 < 0.01$, $n = 38$) obtained from model 1 for marked goslings from manipulated nests.

		Body size		Body mass	
	d.f.	*F*	*P*	*F*	*P*
Model 1					
Full model	7	1068.1	< 0.001	724.8	< 0.001
Year	1	333.5	< 0.001	371.6	< 0.001
Age	1	1681.6	< 0.001	1127.8	< 0.001
Year*Age	1	308.5	< 0.001	366.5	< 0.001
Hatch Date	1	24.7	< 0.001	39.9	< 0.001
Hatch Date*Year	1	9.0	0.003	1.5	0.2
Age*Hatch Date	1	16.1	< 0.001	24.4	< 0.001
Age*Hatch Date*Year	1	23.7	< 0.001	0.8	0.4
Model 2 (residuals)					
Full model	1	2.1	0.14	0.08	0.8
CPQ	1	2.7	0.11	0.08	0.8
CPQ^2	1	3.6	0.06	–	–

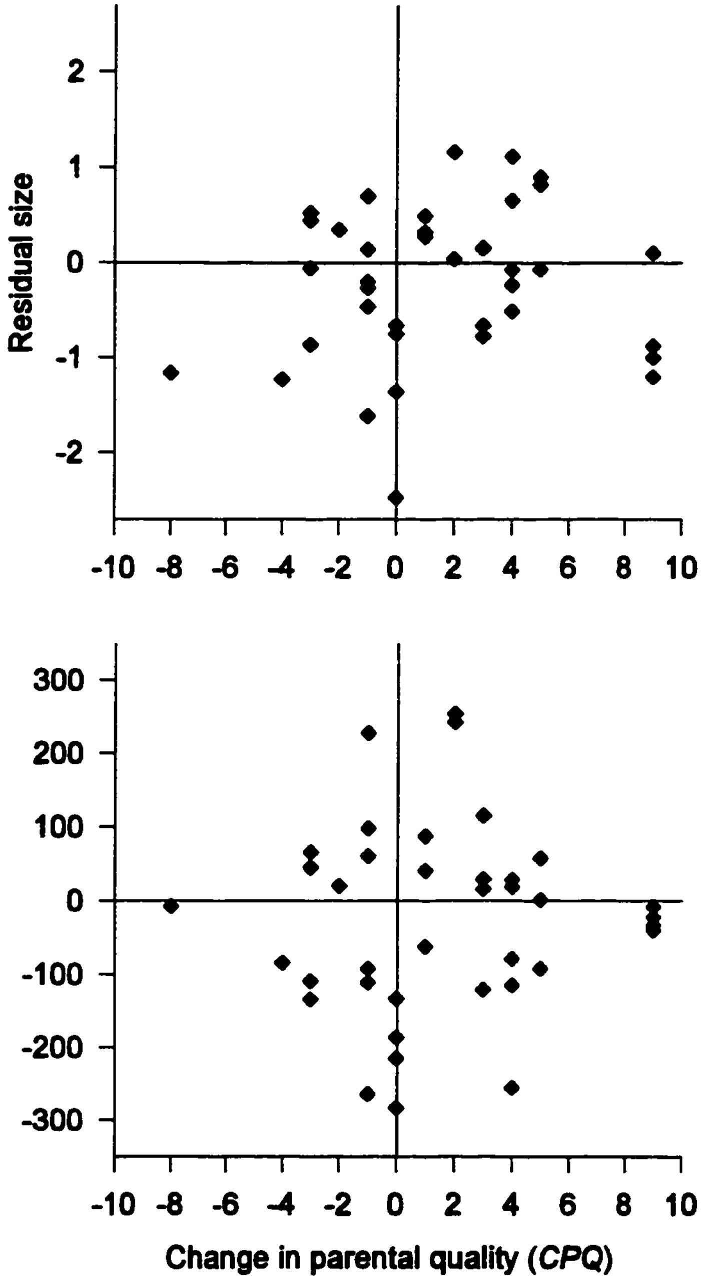

Figure 3. The effect of experimental change in parental quality (*CPQ*) on the residual size and mass of goslings near fledging, after controlling for the effects of year, gosling age, hatch date and their interactions.

DISCUSSION

During our study, we found a seasonal decline in growth, as was observed in other bird populations (Birkhead and Nettleship 1982, Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991, Kersten and Brenninkmeijer 1995). In Arctic-nesting geese, like many other bird species, growth rate is an important determinant of post-fledging survival and recruitment (Perrins 1965, Garnett 1981, Cooke et al. 1984, Owen and Black 1989, Sedinger et. al. 1995) and thus has important consequences on offspring fitness. However, we did not find a seasonal decline of pre-fledging survival during the two study years, although we observed such decline in this population using a larger sample size (chapter 2).

Our manipulations showed that parental quality did not explain the observed seasonal variation in pre-fledging growth rate, strongly suggesting that these variations are essentially caused by seasonal variations in environmental conditions rather than differences in parental ability to raise offspring. Among the environmental factors involved in seasonal variation of growth rate, a seasonal decline in food supply (chapter 3) and colder climatic conditions for late goslings (Fortin 1995) are the two most likely.

An alternative explanation is that growth rate is primarily determined by genes and that eggs laid by early parents produce faster growing goslings. However, Larsson and Forslund (1992) concluded that high heritability of body size in geese was more a consequence of the common environment between parents and offsprings than of genetic factors. A recent experiment by Sedinger et al. (1997) also failed to detect any genetic or maternal effects on seasonal variations in gosling growth in black brant (*Branta bernicla*). Egg quality may also explain a part of the seasonal decline if it varies seasonally and is correlated with offspring success (e.g. Birkhead and Nettleship 1982). However, Williams et al. (1993) and Cooke et al. (1995) found no fitness consequences of egg size variation per se in snow geese.

We cannot exclude the possibility that our manipulations, which prolonged incubation for early parents and shortened it for late parents, reduced the potential effect of parental quality on gosling growth. If, for example, parents with an extended incubation period have to use more body reserves, they may have to devote more time to feeding during incubation or brood rearing at the expense of vigilance, thus reducing potential benefits to their fostered goslings. If present, such bias would affect more the survival probabilities than the growth rate as goslings do not rely on their parents for food provision as in altricial species. However, we showed that nest survival was not affected by the manipulation of the incubation period, thus indicating that this potential bias was probably minimal. This is not surprising since Reed et al. (1995) showed that body mass of female greater snow geese did not decline significantly during the last 10 days of incubation.Moreover, Brinkhof et al. (1993) and Tombre and Erikstad (1996) showed that reproductive success was not affected by experimentally increased incubation effort in European coot *Fulica atra* and barnacle geese *Branta leucopsis*.

The role of parental quality

The role of parental quality in the seasonal variations of reproductive success has recently been investigated in several altricial bird species, using similar manipulation experiments. Some authors found that parental quality contributed to some of the seasonal variation in offspring success (Verhulst and Tinbergen 1991, Wiggins et al. 1994, Brouwer et al. 1995, Verhulst et al. 1995, De Forest and Gaston 1996), while others found that these variations were only attributed to environmental factors directly related to timing *per se* (Parson 1975, Hatchwell 1991, Norris 1993, Brinkhof et al. 1993). Thus, it appears that differences in parental quality can affect the efficiency of parents to provide adequate care for their young, but not in all situations. For instance, Verhulst and Tinbergen (1991) reported that early nesting great tits (*Parus major*) could compensate for the experimental delay of hatch date in one forest, but not in the second one. These authors tentatively explained this result by a higher food availability in the first situation. Other factors, such as the level of intra-specific competition or predation, can possibly also either attenuate or increase the role of parents, but it is probably too early to draw any general conclusion.

In precocial birds, the role of parents after hatch is less prominent and its effect on offspring success could be slight and thus harder to detect than in altricial birds. However, parental quality may still be an important component of the seasonal variation of reproductive success at other stage of the breeding cycle in precocial birds. For instance, only the most efficient parents may be able to accumulate rapidly the nutrients that would allow them to nest early (Drent and Daan 1980, Choinière and Gauthier 1995), thus indirectly providing better growing conditions for their offspring because of the seasonal decline in environmental conditions during the summer.

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CHAPITRE 5

LARGER CLUTCH SIZE INCREASES FLEDGING SUCCESS AND OFFSPRING QUALITY IN A PRECOCIAL SPECIES

RÉSUMÉ

Nous avons testé l'hypothèse que l'habileté des parents à élever leurs jeunes avec succès pouvait limiter la taille de couvée chez la grande oie des neiges (*Chen caerulescens atlantica*), une espèce nidifuge. Durant 2 années, nous avons manipulé la taille de couvée en échangeant des couvées complètes entre des paires de nids, de façon à augmenter ou diminuer la taille de couvée par zéro (nids témoins), un, deux ou trois oeufs dans 314 nids expérimentaux. Nos manipulations ont montré qu'une augmentation de la taille de couvée amenait une augmentation du taux de survie estival chez les oisons, tandis qu'une diminution de la taille de couvée réduisait la survie par rapport aux couvées témoins. En conséquence, les couvées augmentées produisaient plus de jeunes jusqu'à l'envol et les couvées diminuées en produisaient moins. La taille et la masse des jeunes près de l'envol était également plus grande dans les couvées augmentées que dans les couvées témoins, ce qui suggère que la qualité des jeunes a aussi été augmentée par la manipulation. Ce résultat est contraire au compromis habituel entre le nombre de jeunes et leur qualité. Les familles comprenant plus de jeunes étaient dominantes par rapport aux familles moins nombreuses dans les sites d'alimentation et ceci pourrait expliquer l'augmentation de survie et de croissance dans les familles artificiellement augmentées. Nos résultats suggèrent que l'habileté des parents à élever leurs jeunes ne limite par la taille de couvée chez cette espèce et que les parents pourraient augmenter à la fois le nombre de jeunes et leur qualité en pondant plus d'oeufs. Toutefois, le délai requis pour l'addition d'oeufs réduit la viabilité de toute la couvée et pourrait expliquer pourquoi les femelles ne pondent pas plus d'oeufs.

ABSTRACT

We tested the hypothesis that the ability of parents to raise viable offspring limits clutch size in the greater snow goose (*Chen caerulescens atlantica*), a precocial bird. We manipulated clutch size by exchanging complete clutches between pairs of nests to increase or decrease the clutch size by zero (control), one, two or three eggs in 314 nests over two years. Pre-fledging survival of goslings increased in enlarged broods and decreased in reduced broods compared to control. Consequently, enlarged broods fledged more offspring and the reverse was true for reduced broods. Size and mass of goslings near fledging was also higher in enlarged broods than in control, which suggests that offspring quality was also enhanced by the manipulation. This is contrary to the common trade-off between offspring numbers and quality. Large families were dominant over smaller ones in feeding sites, which could explain the increased survival and growth of enlarged broods. Our results suggest that the ability to raise young does not limit clutch size in this species and that parents could be more successful (i.e. increase both the number and quality of their offspring) by laying more eggs. However, the time required to lay additional eggs reduces the viability of all offspring and may explain why females do not lay more eggs.

INTRODUCTION

The hypothesis that clutch size is optimal with respect to the ability of the parents to recruit young is central to the study of life history strategies. In altricial birds, clutch size is generally thought to be limited by the ability of parents to raise young (Lack's optimal clutch size hypothesis) or by the cost incurred by the parents when raising too many young (the cost of reproduction hypothesis) (Partridge and Harvey 1985, Pettifor et al. 1988, VanderWerf 1992, Jacobsen et al. 1995). To test these hypotheses, one must manipulate clutch/brood size, which has seldom been done with precocial birds (Safriel 1975, Rohwer 1985, Lessells 1986, Sandercock 1994). Only Safriel (1975) found a negative effect of enlarged broods on production of young in a precocial species, while others found no effect.

In precocial birds, the hypothesis that the ability of parents to raise young limits clutch size has often been dismissed simply on the ground that these birds do not feed their young (Winklers and Walters 1983). However, precocial birds provide other forms of parental investment shared among offspring (e.g. brooding, Lazarus and Inglis 1986, Schindler and Lamprecht 1987). In geese and shorebirds, there is some evidence that chick mortality increases with brood size (Safriel 1975, Cooke et al. 1995), which suggests that parental ability to raise young may set an upper limit on clutch size (Winkler and Walters 1983). Few studies have examined this hypothesis in precocial birds and they have found mixed results (Safriel 1975, Winkler and Walters 1983, Lessells 1986, Williams et al. 1994).

We experimentally tested the hypothesis that the ability of parents to raise viable offspring may limit clutch size in precocial birds by manipulating clutch size and examining the effects on offspring growth and survival. Using such experiments, one can answer the question: would parents be more successful if they had laid additional eggs? The experiments were conducted in the greater snow goose *Chen caerulescens atlantica*, a large precocial and colonial bird nesting in the High Arctic.

METHODS

Study area

Our study area was located at the Bylot Island colony (73°N 80°W, Northwest Territories, Canada). Much of the island is occupied by mountains and glaciers, except for a plain of ca.

1 600 km^2 in its southern part. Rolling hills, covered by upland tundra and numerous isolated wetland patches used by brood-rearing geese, dominate the landscape of this plain. It is the most important breeding site of greater snow geese (27 000 nesting pairs were censused in 1993, Reed et al. 1992, Gauthier et al. 1996) which occur in several nesting colonies on the island.

Field methods

In 1993 and 1994, nests were found and marked during laying and incubation. Their fate was determined by visiting them regularly until hatching (Lepage et al. 1996). Nesting success was defined as the proportion of nests where at least one young left the nest and was calculated with the Mayfield method (Mayfield 1975, Johnson 1979). Nesting success between different groups was compared using the test suggested by Johnson (1979), which allows two by two comparisons. Hatching success was defined as the proportion of eggs that hatched in successful nests (i.e. those where at least one egg hatched).

Shortly before hatching, in both years, we exchanged complete clutches between pairs of nests to change the clutch size by one, two or three eggs. Paired nests had a similar hatch date, to control for the effect of hatch date on growth rate (Cooch et al. 1991, Lindholm et al. 1994). We also exchanged complete clutches between pairs of control nests with identical clutch sizes. The *change in clutch size* (*CCS*) is the difference between the number of eggs received from the donor nest and the actual number of eggs laid (from -3 to +3), *direction of the manipulation* (*DM*) is the sign of *CCS* (reduced clutches: *CCS* from -3 to -1, control: *CCS* = 0 and increased clutches: *CCS* from 1 to 3), and the *initial clutch size* (*ICS*) is the number of eggs in the nest before the manipulation.

All goslings that hatched from experimental and control nests, as well as goslings from a sample of unmanipulated nests, were individually marked at hatch with numbered web-tags (Alliston 1975). Shortly before fledging, family groups were captured in mass banding drives in nearby brood-rearing areas (Hughes et al. 1994b). All goslings captured were weighed and measured (culmen, head, tarsus and 9th primary length).

During brood-rearing, we observed social interactions between families during a total of 25 hours. Every time a family displaced another family we noted the number of goslings in the winning and losing (displaced) families. Interactions sometimes lasted for more than a minute, but only the final outcome was recorded. Observations could include both manipulated and unmanipulated broods.

Data analysis

Pre-fledging survival of goslings was estimated by the recapture of marked individuals. Probability of recapture is the product of survival rate and capture rate (i.e. probability of capturing a bird if alive). Differences in probability of recapture reflect differences in survival, assuming that capture rate is constant among experimental groups. Goose families were captured over a wide area at our study site and we have no evidence of differential dispersal among our experimental groups. We tested the effect of Year, Hatch date, *ICS*, *DM*, and DM^2 on the proportion of goslings recaptured per brood near fledging with log-linear models (Proc Catmod of SAS Institute inc. 1990). The analysis was restricted to manipulated nests (experimental and control), and only significant variables were retained in the final model. We used *DM* instead of *CCS* in this analysis because small sample size prevented us of using *CCS*, which had too many classes. Even then, we could not test more two independent variables simultaneously. We thus tested all possible two-variable combinations before removing a variable from the model.

Body measurements of goslings caught were used as indices of growth. Body size was defined as the first component of a principal component analysis combining measurements of tarsus, head and culmen. Age of unmarked goslings was estimated by the linear relationship between age of marked goslings (from both manipulated and unmanipulated nests) and length of their ninth primary feather (1993: $n = 102$, $R^2 = 0.63$, $P < 0.001$; 1994: $n = 62$, $R^2 = 0.72$, $P < 0.001$). Age of goslings when measured ranged from 28 to 45 d (mean = 37.1, $n = 3\ 899$ young). An initial generalized linear model was first used to test the effects of Year, Age and Hatch date on goslings size and mass using all goslings captured. To control for the effects of these variables, residuals from this initial model were used to test the effects of Year, *ICS* and manipulation (*CCS* and CCS^2) on marked goslings from manipulated nests only.

RESULTS

The mean clutch size was 4.0 eggs (range: 2 to 6 eggs, *n* = 538 nests). Clutch size was increased or decreased in 151 nests and left unchanged in 163 control nests. Nesting success of reduced nests (69.5% ± 5.7 SE, *n* = 91) was smaller than nesting success of control nests (82.3% ± 3.4 SE, *n* = 163) (*P* = 0.05). This effect could possibly be an artefact of the manipulation (see discussion). However, nesting success of enlarged nests (73.0% ± 6.4 SE, *n* = 60) did not differ from control nests (*P* = 0.19) or from reduced nests (*P* > 0.5). Among successful nests, hatching success after the manipulation did not differ between reduced (89.3% ± 2.4 SE, *n* = 68), enlarged (81.3% ± 3.3 SE, *n* = 40) and control nests (89.8% ± 1.6 SE, *n* =135; χ^2 = 5.6, *P* = 0.062, df = 2) despite a trend for slightly lower hatchability in enlarged clutches. Only successful manipulated nests (i.e. those that hatched) were used in subsequent analyses.

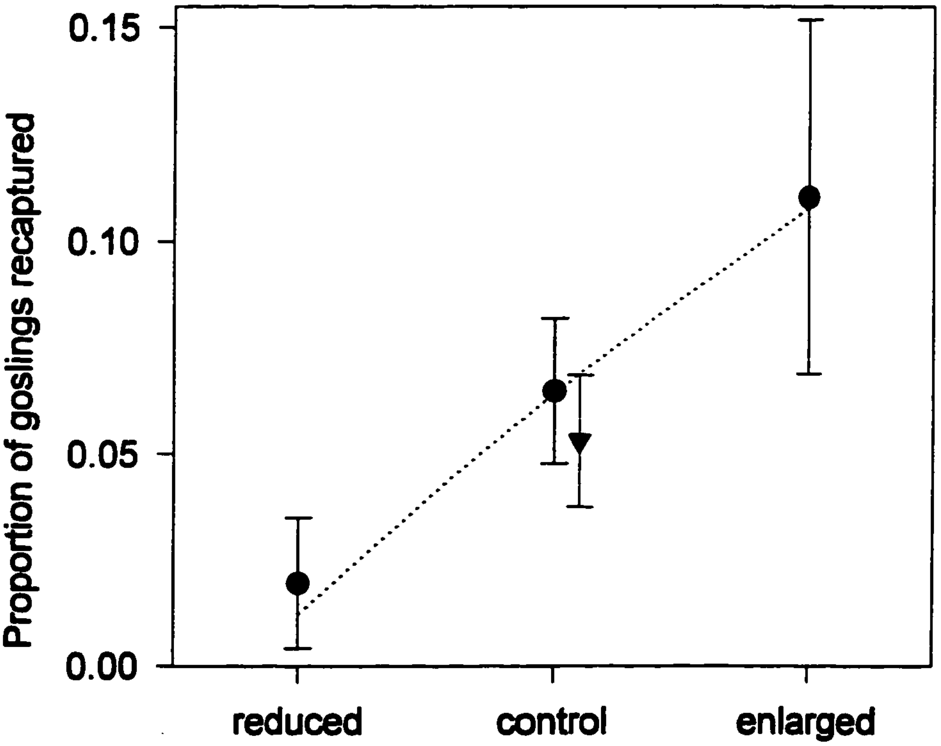

Figure 1. Average proportion of goslings recaptured per brood (± SE) for the three experimental groups (reduced, control and enlarged broods) (●), for unmanipulated broods (▼), and values predicted by the log-linear model (dotted line).

The mean number of goslings leaving the nest 24h after hatching was 3.5 ($n = 391$ nests). On average, manipulations increased the number of goslings leaving the nest in successful nests by 1.4 in enlarged clutches ($n = 40$ nests) and decreased it by 1.6 in reduced clutches ($n = 68$ nests). A total of 871 young were tagged in 243 manipulated nests, and 496 were tagged in 148 unmanipulated nests. Near fledging, 3899 goslings were captured, including 61 marked ones from manipulated broods and 42 from unmanipulated broods.

The proportion of goslings recaptured per brood was positively related to the experimental change in clutch size (*DM*, $\chi^2 = 7.06$, $P = 0.008$, df = 1), indicating that survival of offspring increased in enlarged broods and decreased in reduced broods, compared to controls (Figure 1). None of the other variables tested (Year, Hatch date, *ICS* and *CCS*^{2}) affected the proportion of goslings recaptured ($P > 0.3$). There was no difference in the average proportion of goslings recaptured between manipulated controls (6.6%, $n = 135$ broods) and unmanipulated broods (5.3%, $n = 148$; $\chi^2 = 0.34$, $P > 0.5$, df = 1).

Table 1. Number of goslings recaptured per family in control and experimentally reduced or enlarged broods (clutch size decreased/increased on average by 1.9 eggs; range: 1–3) according to initial clutch size (i.e. before manipulation).

Initial clutch size	Reduced			Control			Enlarged		
	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
1				0.0		10	0.50	0.34	6
2	0.0		2	0.0		7	0.50	0.34	12
3	0.0		8	0.23	0.14	26	0.46	0.33	13
4	0.05	0.22	20	0.20	0.09	56	0.67	0.67	9
5	0.04	0.04	28	0.65	0.23	31			
6	0.0		10	0.0		5			

Since parents with enlarged broods left the nest with more young, and these young survived significantly better, it follows that the number of fledged offspring in enlarged broods was much higher than in control (Table 1). For instance, in parents laying a clutch of three eggs (the group with the largest sample size), enlarging the brood by 1.9 young more than doubled the number of offspring at fledging compared to control. For the same reasons, the number of fledged offspring in reduced broods was much lower than in control broods. It should be reminded, however, that average number of fledged offspring per brood in Table 1 are underestimated for all categories because it is not all broods with live young which are recaptured at fledging.

Year, Age, Hatch date, and most of their interactions had a significant effect on the size and mass of all gosling captured near fledging (Table 2). In the second analysis, which controlled for the effects of the previous variables, Year, *ICS* and CCS^2 had no significant effect on the residual size and mass of goslings from manipulated broods ($P > 0.25$), and these variables were not retained in the final model. However, residual size and mass of goslings from manipulated broods were positively related to *CCS* (Table 2), indicating that goslings were larger and heavier when associated with an enlarged brood (Figure 2).

We observed 20 dyadic encounters involving broods of unequal size. Larger families won 18 of these encounters (sign test: $P < 0.001$) and were therefore dominant over smaller families.

Table 2. Summary of the general linear models. Model 1: effect of Year, Age and Hatch date on body size (PC1 score; $R^2 = 0.66$, $n = 3\,857$) and mass ($R^2 = 0.57$, $n = 3\,851$) of all goslings captured near fledging. Model 2: effect of manipulation (*CCS*) on the residuals of size ($R^2 = 0.08$, $n = 60$) and mass ($R^2 = 0.19$, $n = 61$) obtained from model 1 for marked goslings from manipulated nests.

		Body size		Body mass	
	D.F.	*F*	*P*	*F*	*P*
Model 1					
Full model	7	1068.10	< 0.001	724.81	< 0.001
Year	1	333.50	< 0.001	371.58	< 0.001
Age	1	1681.64	< 0.001	1127.78	< 0.001
Year*Age	1	308.47	< 0.001	366.45	< 0.001
Hatch Date	1	24.70	< 0.001	39.86	< 0.001
Hatch Date*Year	1	9.03	0.003	1.46	0.23
Age*Hatch Date	1	16.08	< 0.001	24.43	< 0.001
Age*Hatch Date*Year	1	23.65	< 0.001	0.76	0.38
Model 2 (residuals)					
Full model	1	5.20	0.026	13.54	<0.001
CCS	1	5.20	0.026	13.54	<0.001

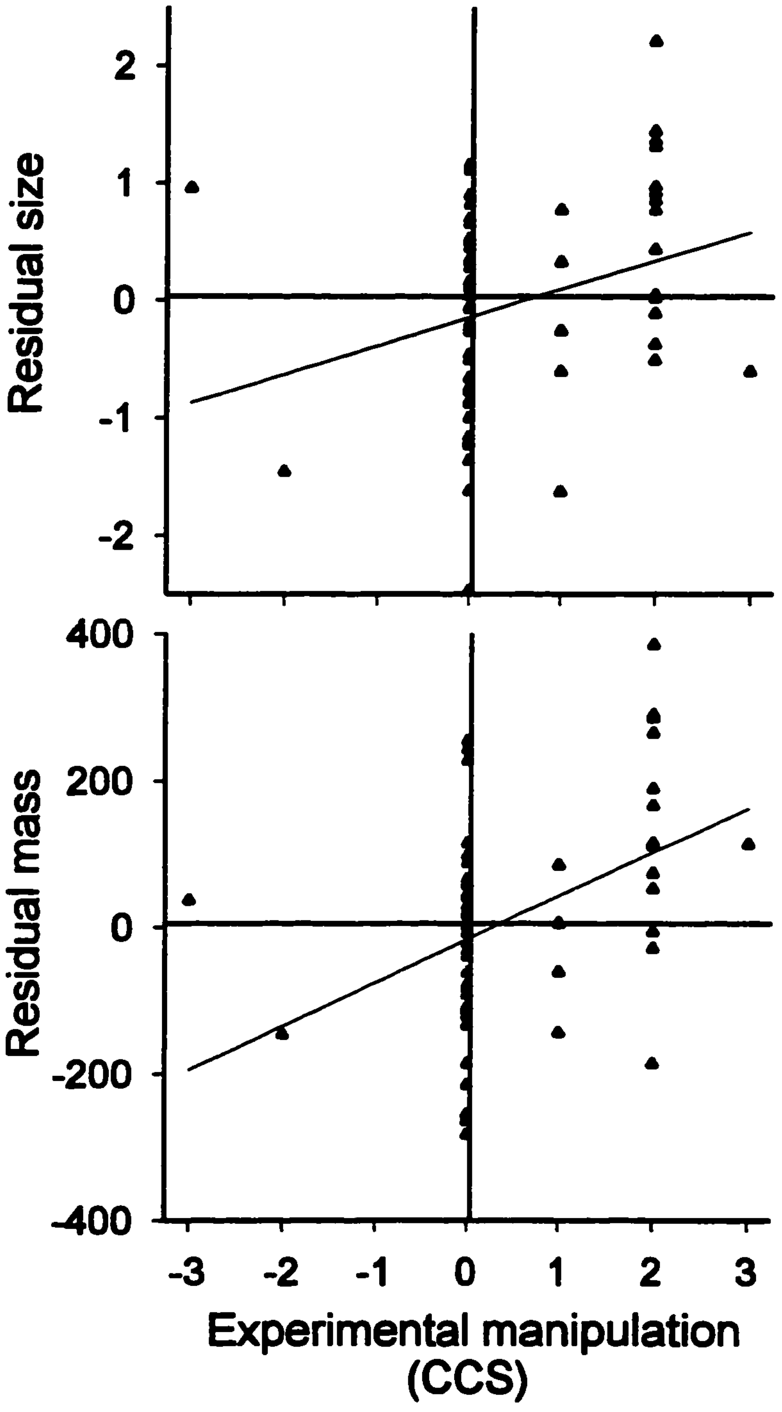

Figure 2. The effect of experimental change in clutch size (*CCS*) on the residual size and mass of goslings near fledging, after controlling for the effects of year, gosling age, hatch date and their interactions.

DISCUSSION

The higher survival and better growth of goslings in enlarged broods compared to control or reduced broods are contrary to the predictions of the hypothesis that parental ability limits clutch size. Although we have no data on post-fledging survival, and hence recruitment, body size of goslings at fledging is positively related with subsequent survival (Francis et al. 1992, Owen and Black 1989, Cooke et al. 1995), recruitment (Sedinger et al. 1995) and perhaps even fecundity (Sedinger et al. 1995). Thus, by laying more eggs, females fledged more offspring, which in turn should have better chances of recruitment because of their larger body size at fledging. This suggests that the number of eggs laid by geese is not optimal with respect to their ability to raise young and that parents would be more successful if they laid more eggs.

Several studies in altricial birds have also found that enlarged broods fledge more young in absolute terms (Pettifor et al. 1988) but this was often obtained at the expense of a lower individual nestling survival or quality (e.g. lower body mass at fledging) (see review in Lessells 1986). To our knowledge, this is the first study that experimentally reported an increase in the quality and survival of individual offspring in larger broods independent of parental quality. This suggests that the common trade-off reported in altricial birds between number of offspring and their quality does not apply in precocial birds (see also Rohwer 1985 and Lessells 1986) and could even be in the opposite direction in geese (i.e. laying more eggs may increase both the survival and quality of individual offspring).

The reduction in the number of eggs in the nest resulted in a lower nesting success. It is possible that a reduction of the number of eggs is perceived by the parents as an act of predation, which may reduce nest attentiveness and create favorable conditions for further predation. However, this would be a transient effect that is unlikely to persist into the brood-rearing period. Moreover, the manipulation of eggs in itself did not appear to have affected nesting success. Another limitation of our study is that it was conducted during only two years. Although environmental conditions during these two years tended to be similar (except for nest predation which was higher in 1994 than 1993) and near average (Lepage et al. 1996, Chapter 1), different results could be obtained in extreme years (e.g. very late snow-melt).

Our protocol did not control specifically for the heritable component of growth rate and body size or for maternal effects. For instance, if larger parents lay larger clutches, they may transmit this trait to their offspring, which would then grow faster and attain larger final body size. Although Sedinger et al. (1995) found a positive relationship between female body size and clutch size in brant geese (*Branta bernicla*), Cooke et al. (1995) found no such relationship in lesser snow geese (*Ch. c. caerulescens*) using a larger data set. Heritability of morphological characters in birds (i.e. size of the various parts of the body) has been estimated at about 60–70% (Boag and van Noordwijk 1987). However, the heritability component is a difficult measure to obtain in the field and most heritability studies may have underestimated the effect of the common environment between parents and offspring. For example, if large parents have a better access to local food supply, this would enhance the growth of their offspring (Boag and van Noordwijk 1987, Larsson and Forslund 1991). This bias is especially important in geese because of their strong female-biased philopatry. A recent experiment by Sedinger et al. (1997) also failed to detect any genetic or maternal effects on seasonal variations in gosling growth in black brant.

A possible explanation for the enhanced growth of goslings in larger broods is that they are socially dominant over smaller ones and lone pairs (Prop et al. 1984, Black and Owen 1989, Grégoire and Ankney 1990, Cooch et al. 1991). Our behavioral observations showed that larger families were indeed dominant over smaller ones during the summer. Dominant families may have better access to sites offering high food quality and the best protection from predators (Prop et al. 1984, Hughes et al. 1994a). The number of goslings may either increase the motivation of the parents to provide parental care or be used by other individuals as a signal of parental quality. The distinction between these two phenomena is important only if there is a cost to parents in raising more offspring (Schindler and Lamprecht 1987).

If the ability to raise young after hatch does not limit clutch size and, on the contrary, laying more eggs increases both the number and quality of offspring, then other factors must constrain clutch size in greater snow geese. We see three hypotheses that could explain why geese do not lay more eggs.

The *egg-production limitation* hypothesis states that the number of eggs laid by a female is limited by the amount of reserves accumulated before laying (Rohwer 1992). In lesser snow geese, females rely almost exclusively on reserves accumulated prior arrival on the breeding grounds for the production of eggs (Ankney and MacInnes 1978, but see Ganter and Cooke

1996). However, in greater snow geese, clutch size is unlikely to be limited by nutrient reserves alone. As in most other precocial birds, this species acquires large amount of nutrients by feeding during pre-laying on the nesting ground (Gauthier and Tardif 1991, Choinière and Gauthier 1995), and hence, by retarding laying and feeding for a longer period, they should theoretically be able to lay more eggs (Drent and Daan 1980).

According to the *cost of reproduction* hypothesis, a survival or fecundity cost could be associated with larger broods (Jacobsen et al. 1995, Daan et al. 1996). Families persist up to one year in geese, and the presence of young could interfere with acquisition of body reserves by parents in spring through competition for feeding sites (Turcotte and Bédard 1989). However, no evidence of such cost was found in lesser snow geese (Williams et al. 1994), nor in experimental manipulation of reproductive costs in other species of geese (Lessells 1986, Tombre and Erikstad 1996). Physiological costs of producing the eggs may also ultimately limit the number of eggs by decreasing future reproductive output. In an experimental manipulation of reproductive costs, Heaney and Monaghan (1995) showed that increased effort in egg production resulted in a lower ability of parents to raise additional chicks in the common tern (*Sterna hirundo*), suggesting that there is a cost to laying the eggs. Similarly, there could be a cost to incubating a clutch too large in terms of reduced hatchability or higher predation risk. This could account for the weak trend toward lower hatchability found in enlarged clutches. However, Rohwer (1985) failed to find such costs in blue-winged teals (*Anas discors*) incubating enlarged clutches.

Actual clutch size could still be optimal at the individual level, according to the laying date and feeding conditions encountered before laying, as stated by the *individual optimization hypothesis* (Pettifor et al. 1988). In arctic-nesting geese, like many other birds, there is a steep seasonal decline of offspring viability (Cooke et al. 1984, Cooke et al. 1995). The number of eggs laid may thus represent a trade-off between the production of more offspring and the delay imposed by the production of more eggs (Drent and Daan 1980, Choinière and Gauthier 1995) because the laying interval between each egg is about 33 h in snow geese (Schubert and Cooke 1993). In great tits (*Parus major*), although clutches enlarged by one egg were more productive, this was compensated by the costly delay in laying the additional egg (Pettifor et al. 1988). This hypothesis could also explain the limitation of clutch size in precocial birds.

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CONCLUSION GÉNÉRALE

Au cours de ma thèse, je me suis attardé à plusieurs aspects de la reproduction des oiseaux, tous centrés autour du thème des variations saisonnières. J'ai tenté de démontrer quels étaient les coûts et les bénéfices associés à la date de nidification et de comprendre quelles étaient les causes des variations.

Facteurs influençant la date de nidification

Les facteurs qui déterminent le moment où les individus vont décider de nicher sont de deux ordres : il y a les causes immédiates (*proximate factors*) et les causes fondamentales (*ultimate factors*). Définir en détail les causes immédiates de la date de nidification n'était pas le but de ma thèse. Toutefois, une meilleure compréhension générale des variations saisonnières et des décisions optimales concernant la reproduction implique de connaître l'importance relative des éléments immédiats impliqués dans la détermination individuelle de la date de nidification. Ces éléments immédiats peuvent être divisés en trois catégories, soit ceux d'ordre environnemental, comportemental et physiologique. Les deux derniers dépendent de ce que j'ai défini en introduction comme étant la qualité parentale, alors que le premier en est indépendant.

Certains auteurs travaillant avec les oies arctiques (Ryder 1970, Ankney et MacInnes 1978) ont proposé que c'était d'abord l'environnement, et en particulier la disponibilité des sites de nidification, qui déterminait la date de nidification. En termes absolus pour une population, il est indéniable que l'environnement influence la date de nidification (chapitres 1 et 3). Ceci est particulièrement vrai de la disponibilité de nourriture, que ce soit au moment précédent la ponte ou durant la croissance des jeunes, bien qu'il n'y ait pas de mécanisme immédiat possible pour ajuster la date de nidification à l'environnement dans ce dernier cas. Toutefois, comme le montre le chapitre 1, la disponibilité des sites de nidification n'est pas toujours une contrainte, puisque les oies sont flexibles dans le choix de leur site.

En termes individuels, puisque tous les individus d'une population vivent dans le même environnement, se sont surtout des différences dans leur physiologie ou leur habileté comportementale qui peuvent expliquer comment des individus réussissent à nicher plus tôt que les autres, du point de vue des causes immédiates. Selon l'hypothèse de contrainte des sites de nidification par exemple, les individus dominants étaient ceux qui réussissaient à obtenir les premiers sites disponibles au printemps (Ankney et MacInnes 1978).

Toutefois, les causes immédiates seules ne peuvent suffire à expliquer ce qui détermine la date de nidification et l'on doit faire intervenir des causes fondamentales, qui se basent sur la théorie de l'évolution. En effet, en plus d'avoir à optimiser le moment de leur nidification, chaque individu doit aussi maximiser le nombre d'oeufs produits, deux besoins qui peuvent être en contradiction, puisque produire plus d'oeufs signifie aussi retarder la nidification. Si les mécanismes physiologiques permettent de comprendre comment se passe le processus individuel de décision, c'est seulement en faisant appel à des notions de succès reproducteur que l'on peut comprendre le pourquoi de ces décisions.

Le modèle de Drent et Daan (1980), présenté en introduction, est très utile en ce sens. Ce modèle requiert notamment des données détaillées sur les coûts et les bénéfices associés à chaque décision reproductrice, particulièrement en fonction de la date de nidification. À cet égard, les chapitres 2 et 3 ont mis en lumière plusieurs effets saisonniers sur les composantes du succès reproducteur entre le moment de la ponte et celui de l'envol des jeunes. Règle générale, le meilleur succès est atteint par les individus qui nichent tôt, bien qu'il y ait aussi certains coûts associés à une nidification très hâtive, notamment un risque accru de prédation du nid. L'une des principales questions soulevées était pourquoi la majorité des individus semblent se comporter de façon sub-optimale en nichant plus tard que le moment qui maximise le succès reproducteur. Le modèle de Drent et Daan semble apporter une solution à ce paradoxe en suggérant qu'il ne serait pas optimal pour tous les individus de nicher tôt. Même si la valeur reproductive de chaque jeune est plus grande tôt en saison, des contraintes font que tous les individus ne peuvent pas pondre beaucoup d'oeufs tôt en saison. La capacité de pondre plus d'oeufs augmente avec le temps durant la ponte puisque la disponibilité de nourriture augmente généralement au cours de cette période. Toutefois, puisque la valeur reproductive des jeunes diminue avec le temps, les parents doivent faire un compromis entre le nombre de jeunes et leur qualité. Selon Drent et Daan, les capacités physiologiques de chaque individu vont déterminer quelle est la meilleure solution possible à ce compromis.

Selon moi, ce chapitre ouvre la voie à de futures études afin de mieux comprendre les phénomènes impliqués dans la prise de décision optimale d'un individu quant à sa reproduction. À quel âge doit-il commencer à se reproduire ? Combien d'oeufs doit-il pondre ? À quel moment doit-il nicher ? Répondre à de telles questions requiert toutefois des études encore plus détaillées sur les coûts et les bénéfices associés à chaque aspect de la reproduction. Le chapitre 2 apporte une partie de ces réponses, mais ne couvre tous les aspects présentés au début de ma thèse (cf. figure 2 de l'introduction), notamment les événements qui surviennent après l'envol des jeunes : la survie annuelle (case 10), le taux de recrutement et le succès de reproduction des jeunes (case 11), et les coûts et bénéfices associés à la date de nidification et à la taille de ponte pour le potentiel reproducteur futur des parents (case 12). De telles études requièrent une quantité impressionnante de données sur des individus marqués et un suivi à long terme de ces individus. Le chapitre 5 montre aussi que la taille de la couvée durant l'élevage devra être prise en compte, puisque le nombre de jeunes influence directement la croissance des jeunes et donc le succès reproducteur des parents. Une fois tous ces éléments connus, il sera alors possible, par exemple, de bâtir des modèles mathématiques qui permettront de connaître précisément la valeur reproductive associée à chaque date de nidification et chaque taille de couvée et de déterminer l'applicabilité du modèle proposé par Drent et Daan (1980) sur la relation entre la taille de ponte, la date de nidification et le fitness.

Les facteurs expliquant les effets saisonniers sur le succès reproducteur

Trois facteurs ont été examinés comme causes potentielles des effets saisonniers sur les composantes du succès reproducteur au cours de cette thèse : la prédation, la disponibilité de nourriture durant la croissance des jeunes, et la qualité parentale.

Nous avons vu que la prédation avait surtout un rôle prépondérant pour expliquer le patron saisonnier du succès de nidification (chapitre 2). Puisque les oies nichent en colonies plus ou moins éparses, les individus très hâtifs et tardifs semblent plus susceptibles aux prédateurs que ceux qui nichent avec l'ensemble des autres individus (i.e. autour de la date médiane de nidification). De plus, puisque les jeunes éclos tardivement sont toujours plus petits que les jeunes hâtifs, il est possible qu'ils soient plus vulnérables à la prédation.

Le deuxième facteur, la disponibilité de nourriture, semble jouer un rôle prépondérant dans les variations saisonnières de la croissance des jeunes (chapitre 3). J'ai montré que le taux de croissance des jeunes, tel que prédit par la littérature, déclinait de façon saisonnière, les jeunes éclos tôt ayant une meilleure croissance que les jeunes tardifs. Toutefois, ce phénomène ne s'est pas produit à tous les ans durant la période couverte par cette étude. À l'aide de données sur la biomasse végétale et le contenu en azote des plantes, j'ai réussi à montrer que les variations dans la disponibilité de nourriture permettaient d'expliquer une grande partie de ce phénomène. Il est aussi intéressant de constater que l'absence de variation dans la disponibilité de nourriture certaines années s'est traduit par une absence de variation dans le taux de croissance. Ceci n'implique toutefois pas que seule la disponibilité de nourriture affecte le succès des jeunes. Des variations dans la qualité parentale, les conditions climatiques ou la dominance sociale (possiblement influencée par la taille de couvée) peuvent aussi jouer un rôle.

Afin de justement évaluer le rôle respectif de la qualité parentale et des conditions environnementales dans les variations du succès reproducteur, telles que décrites aux chapitres 2 et 3, deux expériences ont été réalisées. Au chapitre 4, nous avons examiné le rôle des parents dans le déclin saisonnier de la valeur des jeunes. En échangeant des couvées entre des parents qui nichaient à des dates différentes, nous avons pu séparer les effets possibles de l'environnement et de la qualité parentale. Nos résultats montrent que des différences dans l'habileté des parents à élever les jeunes ne contribuent pas aux variations saisonnières de croissance et de survie des jeunes. Au chapitre 5, nous avons examiné le rôle de la qualité parentale dans la relation qui existe entre la taille de couvée et la croissance et la survie des jeunes. Cette fois, nous avons expérimentalement modifié la taille de couvée des parents. Cette expérience montre d'une part que la qualité des parents n'est pas impliquée dans les variations de croissance et de survie en fonction de la taille de couvée. D'autre part, cette expérience montre que l'habileté des parents à élever les jeunes ne limite pas la taille de couvée. Non seulement une augmentation de la taille de couvée n'a pas eu d'effet négatif sur la croissance des jeunes, comme on s'y attendrait si les soins parentaux étaient limitant, mais en plus, nous avons montré qu'il y avait un bénéfice pour les jeunes à être associé à une grande couvée. Ce bénéfice, qui semble dû à un effet positif de la taille de couvée sur la dominance sociale des familles, devrait être tenu en compte lors d'études subséquentes sur l'optimalité de la taille de couvée.

En conclusion, j'estime que ce travail permet de mieux comprendre les phénomènes de variation saisonnière du succès reproducteur chez les oiseaux. Il met en relief comment le choix de la date de nidification est une des décisions reproductrices les plus importantes pour les individus nichant dans des environnements saisonniers. Il ouvre aussi la voie à des études futures qui pourront estimer plus en détail les composantes additionnelles du succès reproducteur et bâtir des modèles sur l'optimalité des décisions reproductives.

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Drent, R.H., et S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

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ANNEXE 1

On retrouvera dans cette annexe les cartes sur la répartition spatiale annuelle des nids qui n'ont pas été incluses dans le corps de la thèse. Les lignes de contour ont été générées à partir des moyennes harmoniques de la position des nids à chaque année (voir chapitre 1) et illustrent les surfaces occupées par 55, 65, 75, 85 et 95% des nids, à partir du centre vers l'extérieur.

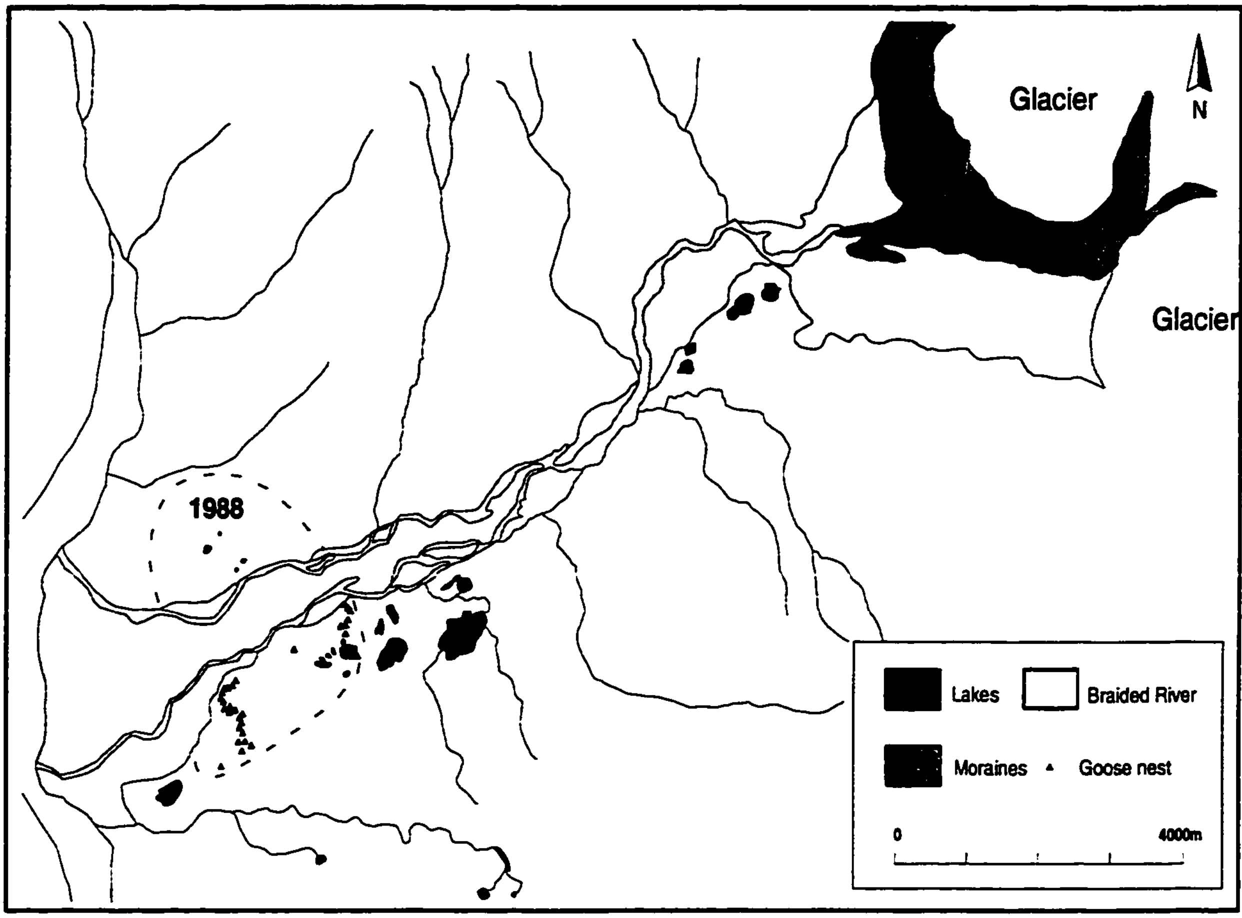

Figure 1. Répartition spatiale des nids dans la vallée principale en 1988.

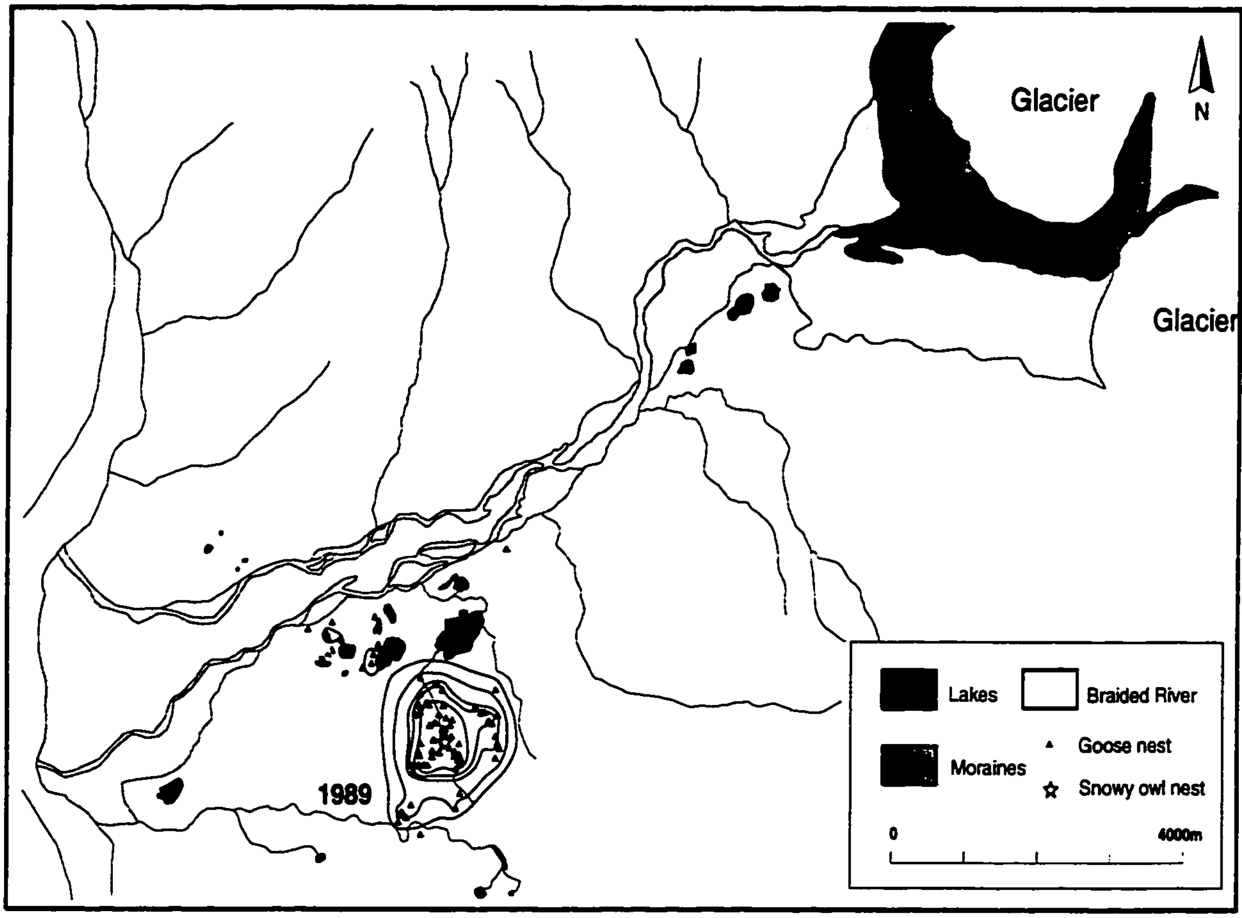

Figure 2. Répartition spatiale des nids dans la vallée principale en 1989.

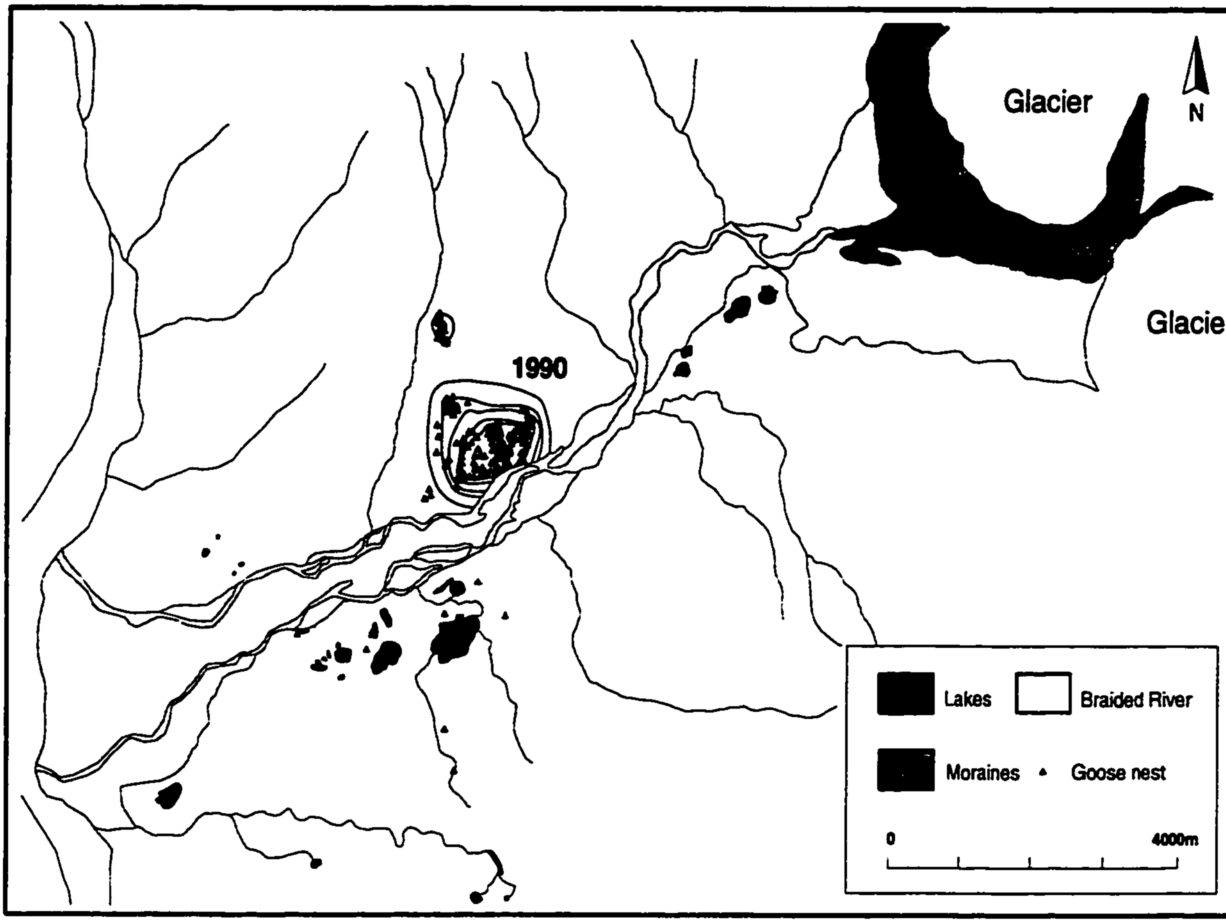

Figure 3. Répartition spatiale des nids dans la vallée principale en 1990.

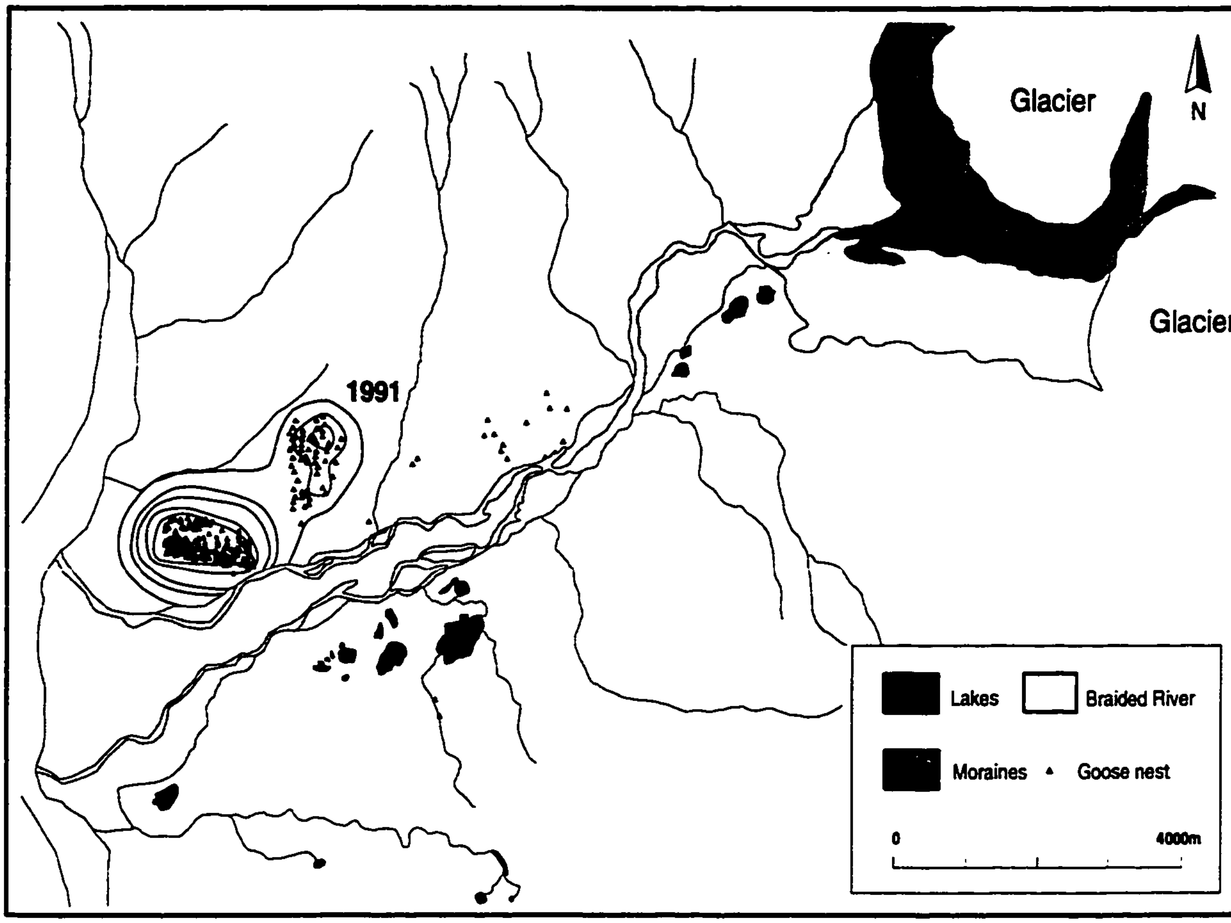

Figure 4. Répartition spatiale des nids dans la vallée principale en 1991.

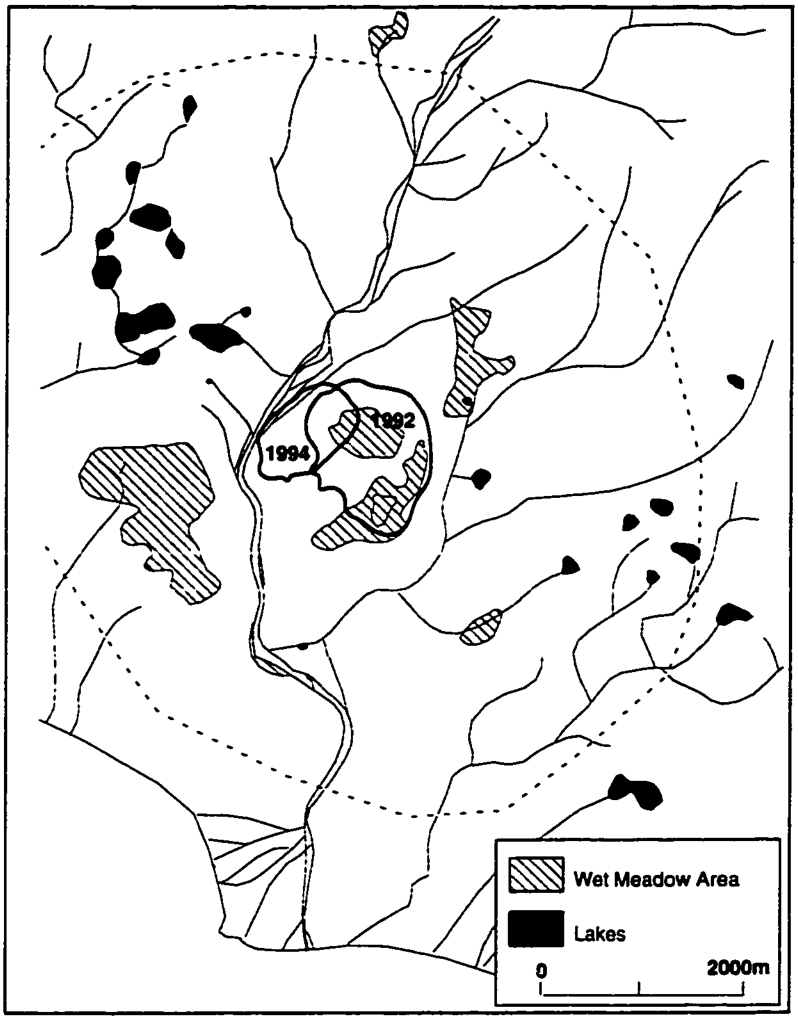

Figure 5. Vue élargie de la colonie secondaire. Les traits en gras délimitent les zones couvertes de façon intensive en 1992 et 1994 durant les visites de nids d'oies. Le pointillé illustre les limites approximatives de l'étendue des nids en 1994.

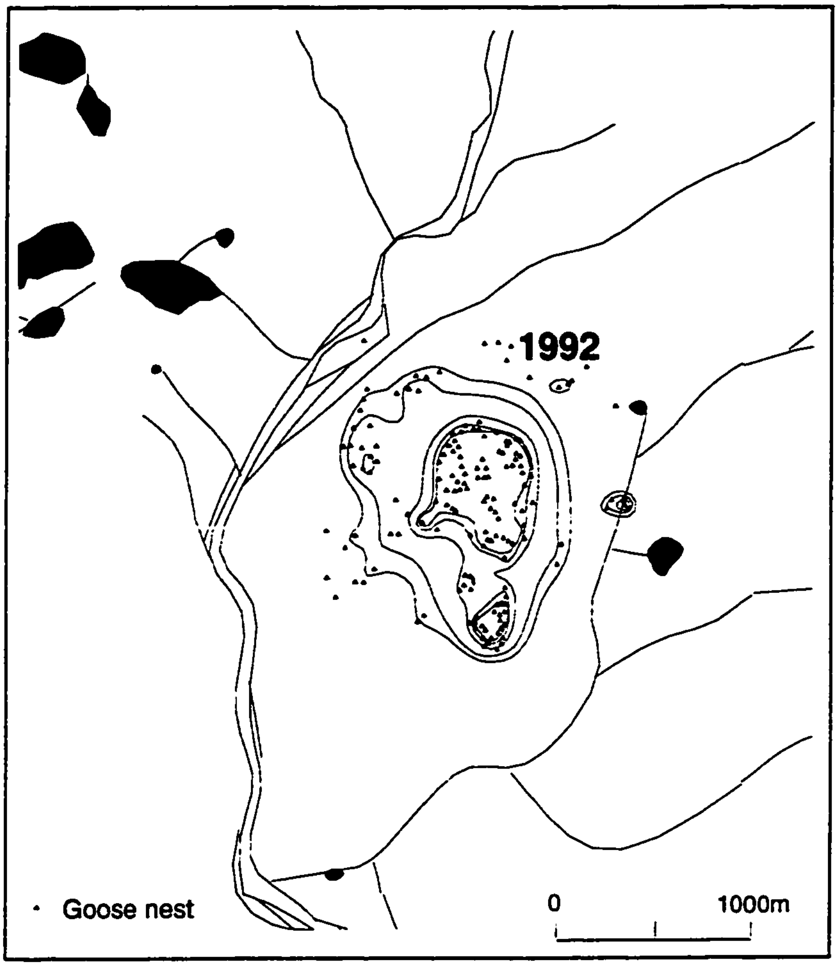

Figure 6. Répartition spatiale des nids à la colonie secondaire en 1992.

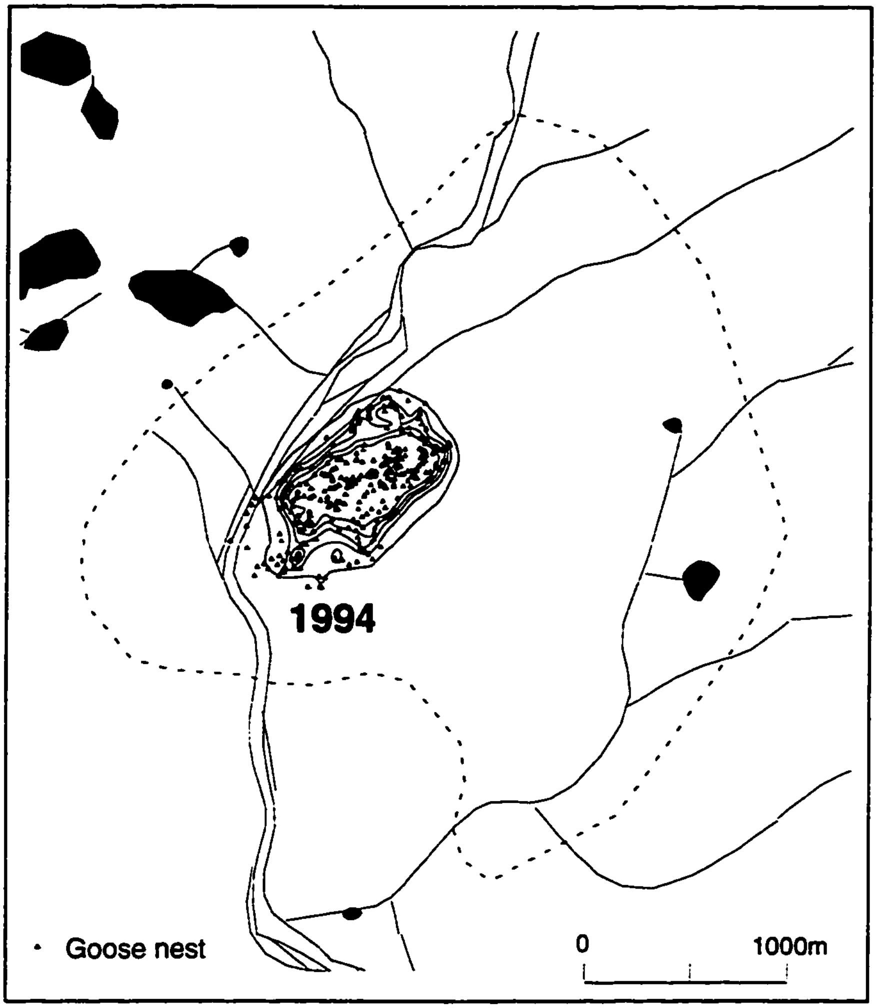

Figure 7. Répartition spatiale des nids à la colonie secondaire en 1994. Le pointillé illustre la limite de la superficie couverte de facon régulière lors de la recherche de nids et le marquage des jeunes au moment de l'éclosion. Les limites approximatives de la colonie sont illustrées à la figure 5.

ANNEXE 2

Estimation des taux de perte de web-tags chez les oisons

Une prémisse importante des modèles de capture-recapture présentés au chapitre 2 est que les marqueurs utilisés pour identifier les individus ne sont pas perdus. En effet, la perte d'une étiquette équivaut à la mort de cet individu pour les calculs des paramètres du modèle puisqu'il n'est plus disponible pour la recapture, causant ainsi une sous-estimation de la survie.

Le taux de perte des web-tags, ou étiquettes de palmure (identiques à celles utilisées pendant mon étude), a été estimé chez la Petite Oie des neiges (*Chen c. caerulescens*) par Séguin et Cooke (1985). Ils ont estimé qu'environ 4% des oisons marqués à l'éclosion perdaient leur étiquette durant les trois premiers mois, mais que cette proportion augmentait à 24% après la première année et 41% après deux ans.

En 1995, nous avons marqué 776 oisons avec 2 web-tags chacun (un sur chaque patte), de façon à pouvoir évaluer leur taux de perte au cours de l'été. Trente-quatre de ces jeunes (4.4%) ont été recapturés à un âge moyen de 35.8 jours et aucun d'entre eux n'avait perdu une des deux étiquettes. La figure 1, qui montre la puissance statistique de notre échantillon (*n* = 34), nous indique que nous pouvons être confiants à 82.5% que le taux réel de perte de web-tags est inférieur à 5%. Les individus qui auraient perdu leurs deux web-tags auraient probablement pu être facilement reconnu grâce aux cicatrices en forme de "V" sur les palmes, caractéristiques d'un web-tag qui est tombé. Nous n'en avons trouvé aucun parmi les 2288 oisons capturés en 1995. De plus, au cours des 5 années de l'étude (1991-1995) une très faible proportion des jeunes capturés montraient des cicatrices potentiellement laissées par la perte de leur web-tag. Bien que nous n'ayons pas évalué le taux de perte jusqu'à l'automne, les résultats de Séguin et Cooke laissent penser que celui-ci est faible.

Nous n'avons donc pas tenu compte de la perte possible de web-tags dans nos calculs des probabilités de survie et de recapture. De plus, pour affecter nos conclusions, les pertes auraient du être non aléatoires et corrélées avec les variables mesurées comme la date de ponte (ce qui est peu probable) puisque nous nous intéressions plus aux différences relatives entre les individus qu'aux valeurs absolues de survie.

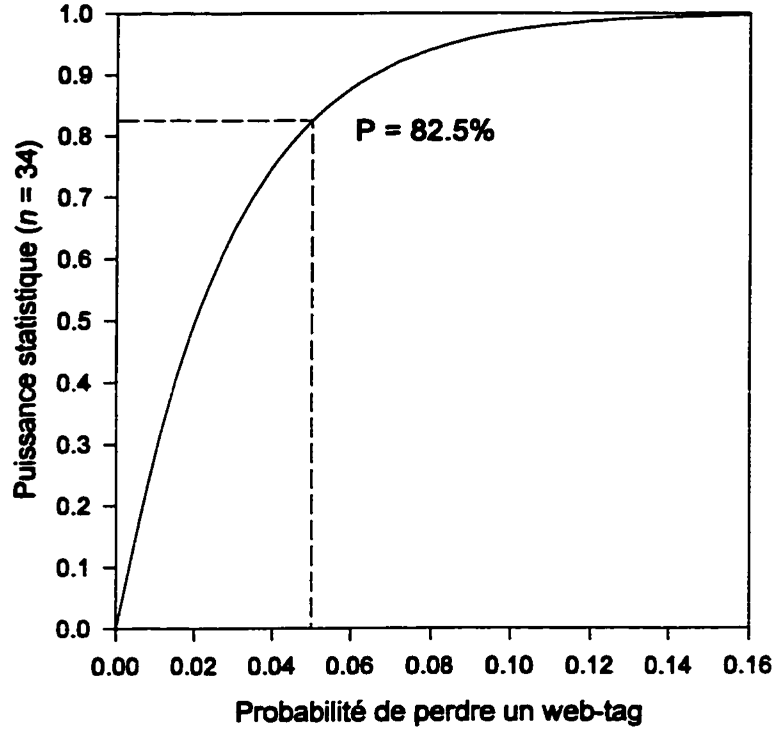

Figure 1. Puissance statistique de l'échantillon de jeunes recapturés avec 2 web-tags (*n* = 34) à détecter différents taux de perte de web-tags.

RÉFÉRENCE

Séguin, R.J., et F. Cooke. 1985. Web tag loss from lesser snow geese. Journal of Wildlife Management 49: 420–422.

ANNEXE 3

Estimation de l'âge par la 9^e primaire

Cette figure illustre la relation, basée sur les individus marqués à l'éclosion et capturés à la fin de l'été, entre l'âge des jeunes et la longueur de leur 9^e primaire. Ces relations ont été utilisées dans les chapitres 3, 4 et 5, pour estimer à chaque année l'âge des jeunes capturés à la fin de l'été et ne portant pas de web-tag. Le détail des modèles est présenté au tableau 2 du chapitre 3.

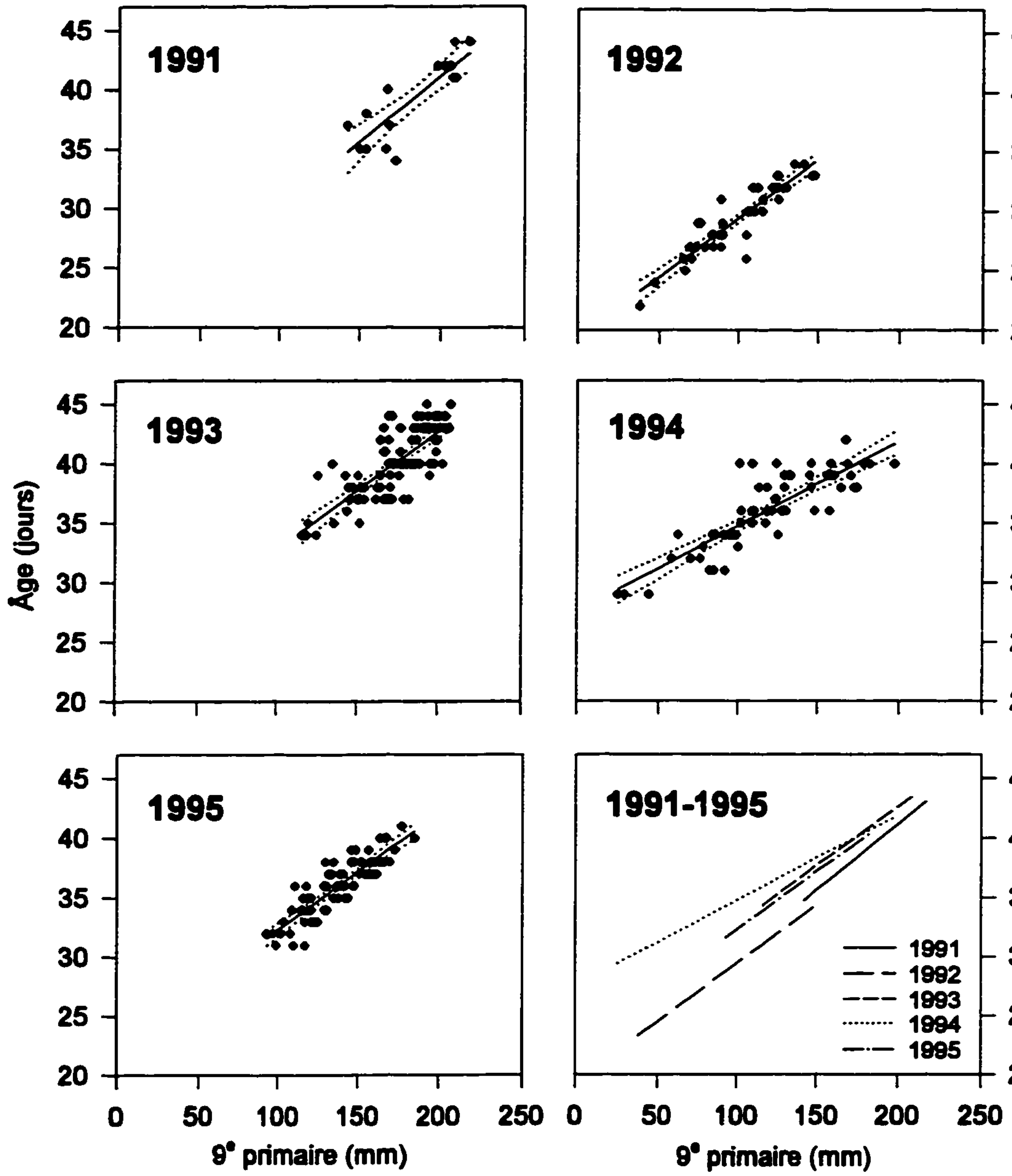

Figure 1. Modèles de prédiction de l'âge des jeunes en fonction de la longueur de leur 9^e primaire. Les points représent les individus d'âge connu qui ont servi à calculer les modèles à chaque année. De 1991 à 1995, les traits pleins représentent le modèle linéaire de régression et les traits pointillés l'intervale de confiance à 95% de la régression. Les modèles des 5 années ont été repris sur la figure en bas à droite de façon à les comparer entre eux.

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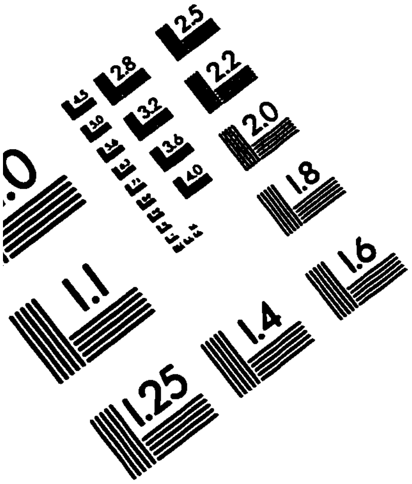

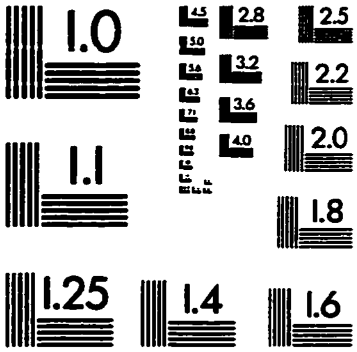

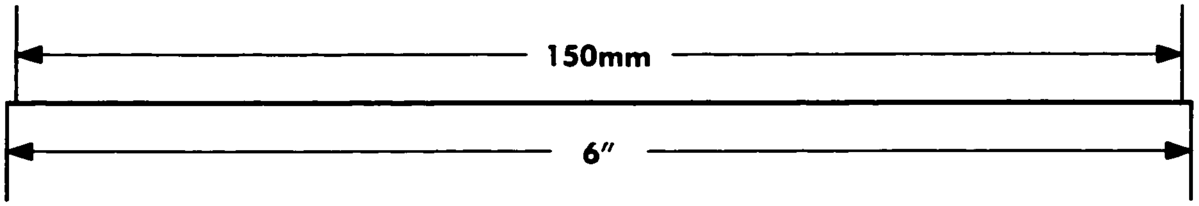

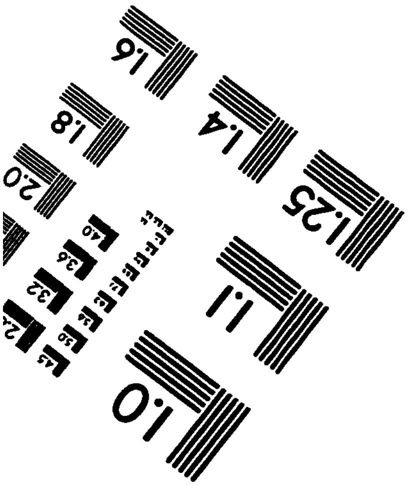

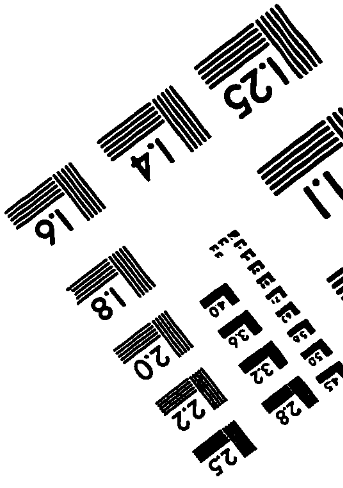

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