

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉLEVAGE ET CROISSANCE DES JEUNES CHEZ LA BERNACHE DU
CANADA RÉSIDENTE (*BRANTA CANADENSIS MAXIMA*) DANS LE SUD DU
QUÉBEC

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AVANT-PROPOS

Ce mémoire de maîtrise est composé de quatre parties. L'introduction générale, en français, commence par donner une brève revue de la littérature sur les populations d'oies et de bernaches en Amérique du Nord, sur le rôle de la croissance des jeunes dans les dynamiques de populations, ainsi que sur l'utilisation d'habitat et le comportement pendant la période d'élevage des jeunes. L'introduction se termine par les objectifs principaux de l'étude. Le corps du mémoire est divisé en deux chapitres écrits sous forme d'articles scientifiques, écrits en anglais dans le but d'être soumis à des revues scientifiques pour publication. Le premier article porte sur la croissance des jeunes Bernaches du Canada pendant l'élevage, en fonction de l'habitat, de l'année et de la date d'éclosion. Le deuxième chapitre porte sur l'adoption et le mélange des jeunes chez la Bernache du Canada. Je serai la première auteure de ces articles, et mon co-auteur sera Jean-François Giroux, mon directeur de recherche. Matthieu Beaumont sera également co-auteur pour le premier chapitre. Finalement, la conclusion générale de ce mémoire revient sur les résultats principaux et les conséquences importantes de cette étude, et ouvre la porte sur des possibilités de recherche futures sur le sujet.

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RÉSUMÉ

Une population nicheuse de bernaches du Canada (*Branta canadensis maxima*) s'est établie sur les îles de Varennes, près de Montréal, depuis 1992. Un suivi de cette population montre que les effectifs augmentent rapidement, ce qui pourrait engendrer des problèmes de surabondance. Chez plusieurs espèces d'oiseaux, il a été démontré que les sites d'élevage deviennent souvent limitants en raison du surbroutage causé par ces herbivores lorsque leurs effectifs augmentent. La majorité de ces études, par contre, ont été réalisées en milieu arctique ou sub-arctique où la productivité primaire est plus faible qu'à des latitudes plus méridionales où les bernaches résidentes se reproduisent.

Les objectifs de cette étude étaient de déterminer si l'habitat d'élevage sélectionné par les bernaches résidentes de Varennes avait un effet sur la croissance des oisons, de vérifier s'il existait des variations saisonnières et inter-annuelles dans leur croissance et de déterminer le potentiel de l'habitat d'élevage comme facteur pouvant limiter la croissance de cette population. Nous avons suivi des femelles nicheuses portant des colliers émetteurs (2004) ou conventionnels (2004 et 2005) afin de connaître l'habitat utilisé lors de l'élevage des jeunes. En 2003, 2004 et 2005, les oisons ont été marqués à l'éclosion à l'aide d'étiquettes de palmure puis recapturés quelques semaines avant l'envol afin d'être mesurés et pesés.

Nous avons observé que les familles de bernaches utilisaient des habitats anthropiques ainsi que des habitats naturels et qu'il y avait peu de mouvements entre les sites d'élevage une fois le site choisi. Les oisons élevés principalement sur des pelouses avaient une masse et une taille structurelle plus élevées que les oisons élevés dans des habitats naturels. Il y avait des différences inter- et intra-annuelles dans la croissance des oisons, mais ces différences n'étaient pas aussi marquées que celles rapportées lors d'autres études portant sur des Ansérinés nichant en régions arctiques. Selon nos résultats, il semble improbable que l'on observe une baisse dans la croissance de la population due à des effets de densité. Nos observations ont aussi montré que les bernaches se regroupaient en groupes familiaux pouvant atteindre près de 200 individus. Un grand nombre de femelles ont abandonné leurs jeunes lors de la période d'élevage et la majorité des jeunes ont été élevés par des adultes autres que leurs parents biologiques. Ces résultats ouvrent les portes à d'autres études sur l'utilisation de l'habitat et le comportement des bernaches du Canada lors de la période d'élevage des jeunes dans le sud du Québec.

Mots clés : adoption, croissance des jeunes, Bernache du Canada, élevage des jeunes, habitats anthropiques, Québec

INTRODUCTION GÉNÉRALE

Augmentation des populations d'oies et de bernaches

Avec l'augmentation constante de la population humaine, les habitats agricoles prennent de plus en plus d'ampleur à l'échelle globale. Bien que l'intensification des pratiques agricoles est souvent associée au déclin de nombreuses espèces animales et végétales (Chamberlain *et al.* 2000; Burel *et al.* 2004), elle a aussi contribué à l'explosion démographique de plusieurs espèces animales qui ont su profiter de l'expansion des habitats agricoles (Wagner *et al.* 1997, Putman et Moore 1998). Les champs agricoles peuvent devenir des habitats alternatifs de haute qualité en valeur nutritive, ce qui sans doute contribue à l'augmentation des populations pour les espèces qui exploitent ces habitats. Les exemples de problèmes causés par une explosion démographique d'espèces animales sont nombreux, tant d'un aspect environnemental que socio-économique. Un cas bien connu est celui du Cerf de Virginie (*Odocoileus virginianus*) qui cause des dommages financiers importants (Wagner *et al.* 1997) et peut avoir des impacts sur l'abondance et la diversité des espèces végétales de son environnement (Anderson *et al.* 2001, Carson *et al.* 2005).

Les populations d'Ansérinés (oies et bernaches) de l'Europe et de l'Amérique du Nord sont en augmentation depuis les 40 dernières années, et plusieurs espèces connaissent une croissance exponentielle depuis le début des années 60s (Madsen 1991; Owen et Black 1991; Ankney 1996). Ces augmentations démographiques seraient dues à plusieurs facteurs, dont une diminution de la chasse et une plus grande disponibilité d'aires d'hivernage reliée à des changements dans les pratiques agricoles qui favorisent la survie des Ansérinés pendant la saison non-reproductrice (Ebbing 1985; Owen et Black 1991).

La bernache du Canada résidente dans le sud du Québec

Les bernaches du Canada résidentes du sud du Québec font partie de la voie migratoire de l'Atlantique, une zone qui comprend les états de la côte est des États-Unis et la région du Canada située au sud du 48° N latitude et à l'est de 80° W de longitude, excluant Terre-Neuve (Atlantic Flyway Council 1999). Les bernaches du Canada résidentes ont d'abord été introduites dans la voie migratoire de l'Atlantique au début du 20^e siècle par des propriétaires privés. Des efforts de réintroduction par des agences de gestion de la faune au centre et dans l'est des États-Unis entre les années 1950s et 1980s ont aussi permis à la sous-espèce *B. c. maxima* de s'établir avec succès dans cette région (Hindman et Ferrigno 1990). Depuis, la population ne cesse de croître et de s'étendre (Ankney 1996, Dennis *et al.* 2000).

La Bernache du Canada est déjà classifiée comme espèce nuisible dans plusieurs régions de l'est des États-Unis et du Canada ainsi que dans plusieurs villes de la côte ouest Américaine (Conover et Chasko 1985; Ettl 1993). Des populations résidentes de bernaches du Canada se sont déjà établies avec succès en Ontario et dans le nord-est des États-Unis (Conover et Chasko 1985; Hindman and Ferrigno 1990; Dennis *et al.* 2000), ainsi qu'en Europe (Madsen et Andersson 1990; Allan 1995). L'augmentation rapide des populations a été la cause de problèmes dans plusieurs régions où les bernaches sont devenues surabondantes. Les bernaches sont herbivores et produisent une grande quantité de fèces (Ettl 1993) qui salissent les terrains de golf, les parcs et les parterres résidentiels (Conover et Chasko 1985; Conover et Kania 1991). Elles sur-broutent le gazon et causent des dommages dans les champs agricoles (Ankney 1996).

La population de bernaches du Canada récemment établie dans le sud du Québec connaît également un taux de croissance élevé. Le taux de croissance de cette population calculé pour la période 1992-2000 était de 1,41 (Giroux *et al.* 2001). En

inclusant les données pour 2001-2003, le taux de croissance atteint 1,42 (J.-F. Giroux, données non publiées). Ce taux de croissance est largement plus élevé que le taux de $1,14 \pm 0.02$ calculé par Ettl (1993) pour d'autres populations de bernaches du Canada recensées dans des régions tempérées (Colombie-Britannique et nord-ouest des États-Unis). Le nombre de nids initiés sur les îles de Varennes augmente rapidement, passant de 3 nids en 1992 à 135 nids en 2004 (Fig. 1). Le nombre de nids diminua à 126 nids en 2005, mais ceci était probablement dû à l'inondation de plusieurs sections des îles suite à une crue printanière importante qui a probablement détruit plusieurs nids avant qu'ils soient trouvés et découragé un certain nombre de nicheurs tardifs.

Bien que les bernaches semblent préférer les îles comme lieu de nidification, elles ne sont pas limitées par la présence de celles-ci pour la reproduction en milieu urbain (Gosser et Conover 1999). Quelques nids ont déjà été localisés sur la terre ferme à proximité de Varennes (J.-F. Giroux et M. Doiron, données non-publiées).

Il devient donc important de développer des outils d'aménagement qui permettraient de contrôler la croissance des populations de bernaches afin de permettre la cohabitation entre cette espèce et l'homme. Pour développer des outils adéquats, il est primordial de connaître la biologie de la Bernache du Canada en relation avec son habitat. Des études ont déjà porté sur la nidification de cette espèce à des latitudes méridionales (Reese *et al.* 1987; Gosser et Connover 1999), mais il existe peu d'informations sur l'habitat utilisé pendant la période d'élevage ou après l'envol.

Croissance des jeunes et dynamiques de population

Puisque la chasse et la disponibilité d'aires d'hivernage ne semblent plus être des facteurs limitants, on peut se demander si des effets de densité de population sur

les aires de d'élevage et de nidification pourraient agir pour réguler la taille des populations d'Ansérinés. En théorie, la population en croissance devrait éventuellement faire face à une diminution des ressources disponibles à la reproduction et à la survie. Dans une population d'oies ou de bernaches, on pourrait penser que l'aire de nidification et/ou d'élevage deviendrait éventuellement saturée et que la disponibilité de la nourriture connaîtrait une diminution saisonnière due au sur-broutage dans la colonie (Owen et Black 1991). Le manque de nourriture pendant la période d'élevage pourrait avoir des effets importants sur la croissance et la survie des individus de la population, particulièrement chez les jeunes en croissance.

Des études récentes portant sur plusieurs espèces d'Ansériformes en milieu arctique ont démontré qu'il existe des variations de taux de croissance des oisons dues à la disponibilité de la nourriture pendant la période d'élevage (Petite Oie des neiges (*C. c. caerulescens*) (Cooch *et al.* 1991; Aubin *et al.* 1993; Williams *et al.* 1993), Grande Oie des neiges (Lepage *et al.* 1998), Bernache cravant (Sedinger *et al.* 1998; Sedinger *et al.* 2001) et Bernache nonnette (*Branta leucopsis*) (Loonen *et al.* 1997)). Des études du même genre ont également porté sur la Bernache du Canada (*B. c. interior*) nichant dans des régions nordiques (Leafloor *et al.* 1998; Cadieux 2002; Hill *et al.* 2003). Ces études suggèrent qu'il existe aussi des effets importants de densité de population sur la croissance et la survie des oisons, reliés à la diminution saisonnière de la quantité de nourriture disponible à cause du sur-broutage dans les aires d'élevage.

Ceci est probablement dû en partie au fait que les oisons sont des herbivores de petite taille qui se nourrissent principalement de feuilles et dépendent donc d'une seule source de nourriture pendant toute leur période de croissance (Owen 1980; Sedinger et Raveling 1984). Les Ansérinés sont nidifuges et les jeunes précoces doivent apprendre à se nourrir par eux-mêmes dans les 24 heures suivant l'éclosion. Contrairement à plusieurs mammifères herbivores, les Ansérinés sont incapables de

digérer la cellulose et la nourriture ingérée passe rapidement à travers le système digestif, ce qui réduit grandement la quantité de nutriments qui peuvent être absorbés (Mattocks 1971). Les plantes dont les oisons se nourrissent contiennent des concentrations faibles en nutriments, particulièrement en protéines, qui limitent la croissance (Sedinger et Raveling 1984; Sedinger 1997). La croissance des jeunes est donc intimement liée à la qualité et la quantité de nourriture disponible sur les aires d'élevage.

Utilisation de l'habitat en période d'élevage

Il existe des relations complexes entre l'habitat d'élevage, l'alimentation, la croissance, la survie et la reproduction chez les populations d'oies et de bernaches. Après l'éclosion, les familles se dirigent vers les habitats d'élevage, où les jeunes effectueront la majeure partie de leur croissance. Chez certaines espèces, comme la Grande Oie des neiges, l'aire d'élevage peut se trouver à plusieurs kilomètres du site de nidification, poussant les familles à effectuer des déplacements importants (Hughes *et al.* 1994b, Mainguy 2003). Ce phénomène est assez répandu chez les Ansérinés nichant en milieu arctique, probablement parce que les besoins changent selon le cycle de vie: un habitat qui possède de bonnes caractéristiques pour la nidification (ex. protection contre les prédateurs) ne possède pas nécessairement de bonnes caractéristiques comme habitat d'élevage (ex. abondance de nourriture de qualité) (Cody 1985; Grand 2002).

En théorie, les familles devraient préférer des habitats qui leur permettent d'avoir accès à de la nourriture de haute qualité et où le dérangement est minimal. Une étude menée par Hughes *et al.* (1994a) sur la Grande Oie des neiges démontre que les oies (avec ou sans jeunes) préfèrent les habitats humides avec lacs ou étangs pendant toute la période estivale, probablement en raison de la qualité supérieure de la nourriture présente dans ces habitats, et parce que les étendues d'eau offrent une

protection contre les prédateurs. Parce que les oissons et les adultes en mue sont incapables de voler pendant une bonne partie de l'été, ils sont vulnérables aux prédateurs terrestres. Ils ont donc tendance à utiliser des habitats qui leur fournissent une certaine protection, comme la proximité d'une étendue d'eau (Giroux *et al.* 1984).

Schmutz (2001) a également suivi des familles d'Oies empereur (*Chen canagica*) pendant la période d'élevage en Alaska et a comparé l'utilisation de six classes d'habitat par rapport à leur disponibilité. Cette étude révèle que les familles d'Oies empereur choisissent préférentiellement les habitats salins pendant la période d'élevage, et que cette espèce utilise des habitats différents que les habitats d'élevage de deux autres espèces de bernaches nichant dans la même région (*B. bernicla* et *B. c. minima*). De plus, Schmutz (2001) et Laing et Raveling (1993) rapportent qu'il n'existe pas de variations saisonnières dans l'utilisation de l'habitat par l'Oie empereur, ce qui concorde avec d'autres études portant sur la Bernache cravant (Lindberg et Sedinger 1998) et la Petite Oie des neiges (Healy *et al.* 1980) selon lesquelles la fidélité à l'habitat d'élevage est élevée et persiste de façon saisonnière malgré des diminutions dans la disponibilité de la nourriture.

La seule étude publiée qui porte sur l'utilisation de l'habitat par des Ansérinés en milieu tempéré est celle menée par Eberhardt *et al.* (1989) sur la Bernache du Canada (*B. c. moffitti*) dans l'état du Washington. Cette étude fut réalisée en suivant 41 femelles équipées de radio-émetteurs et leurs familles pendant toute la période d'élevage des jeunes. La plupart des familles utilisaient des aires bien définies, mais quelques unes se déplaçaient régulièrement d'une région à une autre et ne semblaient pas utiliser une région de façon préférentielle. Les aires d'élevage les plus utilisées comptaient généralement de 8 à 10 familles, et chaque famille utilisait entre 1 et 4 aires d'élevage distinctes entre l'éclosion et l'envol. L'habitat le plus proche de l'aire de nidification était le plus utilisé, mais certaines familles se sont déplacées sur des

distances allant jusqu'à 13 km avant de choisir une aire d'élevage. Le type d'habitat le plus utilisé par les familles était l'habitat riverain et deux tiers des localisations des familles sur la terre ferme se trouvaient à moins de 5 m de la rive. Finalement, les familles avaient tendance à éviter les aires d'élevage à proximité d'habitats humaines, particulièrement pendant les premières semaines suivant l'éclosion.

Les habitats d'élevage pour les bernaches du Canada en milieu péri-urbain dans le sud du Québec peuvent être divisés en deux grandes catégories, soit les milieux naturels (marais, milieux riverains) et les milieux anthropiques (parcs, pelouses entretenues et parfois fertilisées). Les pelouses offrent une source de nourriture plus riche en nutriments que les prairies naturelles, dont la valeur nutritive diminue durant la saison estivale (Sedinger et Raveling 1986; Manseau et Gauthier 1993). Cependant, le dérangement humain pourrait également avoir une influence importante sur la distribution des familles pendant la période de croissance.

Comportement d'élevage des jeunes

Les bernaches du Canada résidentes ont un comportement d'élevage assez bien décrit dans la littérature, et un phénomène couramment documenté est celui de l'adoption et du mélange des couvées pendant cette période (Eadie *et al.* 1988). Les observations effectuées sur les bernaches du Canada nichant dans le sud du Québec ont rapidement révélé que ce phénomène était présent, mais à des taux beaucoup plus élevés que ceux rapportés dans la littérature. L'ampleur inattendue des abandons et adoptions nous a amené à nous interroger sur les mécanismes et l'importance de ce phénomène. En ayant de meilleures connaissances sur cet aspect du comportement d'élevage des jeunes, on pourrait éventuellement soumettre et tester des hypothèses sur son importance évolutive.

Objectifs de l'étude

Les objectifs principaux de cette étude étaient de (1) déterminer l'habitat utilisé par les bernaches pendant la période d'élevage, (2) vérifier si l'habitat utilisé influence la survie et la croissance des oissons (en supposant qu'il y aura une variabilité dans les habitats choisis) (3) évaluer le rôle joué par les milieux anthropiques comme habitat alternatif pour les bernaches du Canada dans le sud du Québec. Ces objectifs seront couverts dans le premier chapitre de ce mémoire. De plus, nous avons comme objectif secondaire de décrire le phénomène d'adoption et de mélange des couvées observés chez cette population de bernaches du Canada résidentes, et cet objectif fera l'objet du deuxième chapitre du mémoire.

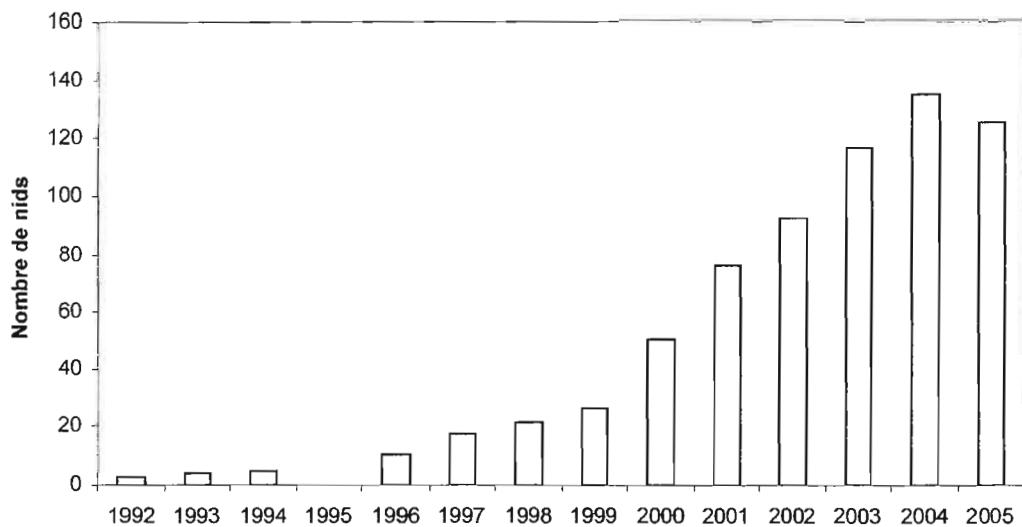


FIGURE 1 : Nombre de nids de Bernache du Canada localisés sur les îles de Varennes, Québec, entre 1992 et 2005.

CHAPITRE 1

**BROOD-REARING BY GIANT CANADA GEESE:
ARE THE SUBURBS A GOOD PLACE TO RAISE A FAMILY?**

Abstract: The brood-rearing habitat is thought to be one of the main limiting factors for population growth in arctic and sub-arctic nesting geese. By studying populations that breed in temperate regions, we can further test the link between brood-rearing habitat and gosling growth. Giant Canada Geese (*Branta canadensis maxima*) have recently began to breed in southern Quebec and the population is increasing rapidly. The main objective of our study was to determine the effect of habitat, hatch date, and year on gosling growth. During the summers of 2004 and 2005, we monitored breeding females equipped with radio-transmitters or conventional alpha-numeric collars to determine habitat used by broods. In 2003, 2004, and 2005, we marked goslings at hatch and recaptured them a few weeks before fledging so they could be measured and weighted. Our observations showed that broods used both anthropogenic habitats (i.e. lawns, agricultural fields) and natural habitats (i.e. islands, marshes). Once a brood-rearing site was chosen, there was little movement among sites or habitat types. Goslings reared mainly on lawns had larger structural size and body mass than goslings reared predominantly in natural habitats. There were annual (2003 and 2004 vs. 2005) variations in body mass and structural size of goslings. No effect of hatch date on body mass was found but structural size significantly decreased with hatch date. Male goslings had larger structural size and mass than female goslings in both years. These results suggest that geese benefit from the presence of anthropogenic habitats such as fertilized lawns which are abundant in suburban areas, though we lack data on food quality and availability to confirm this hypothesis. The factors that affect gosling growth in arctic-nesting geese do not seem to have the same impacts for geese nesting in temperate regions. Shortage of suitable brood-rearing habitat is unlikely and this will probably not limit the growth of this newly-established population in the near future.

Key Words: anthropogenic habitats, *Branta canadensis maxima*, brood rearing, giant Canada goose, gosling growth, habitat use, Quebec, waterfowl.

Introduction

Many goose populations in Europe and North America have been increasing exponentially for the past 40 years (Madsen 1991; Owen & Black 1991; Ankney 1996). These demographic changes have been mainly attributed to a reduced hunting pressure and greater food availability on wintering and staging areas associated with changes in agricultural practices (Ebbinge 1985; Owen et Black 1991; Gauthier *et al.* 2005). The remaining limiting factor for most goose populations, at least for those breeding in arctic and sub-arctic environments, seems to be the availability and quality of brood-rearing areas (Francis *et al.* 1992; Larsson & Forslund 1994).

Although body size in goose species is influenced by genetics (Larsson *et al.* 1998), the growth rate of goslings is highly plastic and directly related to the quality and quantity of the food supply during the growth period (Cooch *et al.* 1991a; Sedinger & Flint 1991; Larsson et Forslund 1991; Lindholm, Gauthier & Desrochers 1994; Sedinger *et al.* 1998). Goslings are thus highly susceptible to variations in nutrient availability during rearing (Sedinger 1997; Lepage *et al.* 1998). The plants on which goslings feed contain only small concentrations of nutrients, particularly proteins. This may limit body growth which can have important effects on fitness (Sedinger & Raveling 1984; Sedinger 1997). Goslings that grow slower are in poorer condition at fledging, which reduces their chances of survival and of being recruited into the population (Cooke *et al.* 1984; Owen & Black 1989; Francis *et al.* 1992; Schmutz 1993; Hill *et al.* 2003). Moreover, the final structural size of an adult goose is highly correlated to its size at fledging, and structural size is in turn associated to reproductive success (Cooch *et al.* 1991b; Larsson & Forslund 1991; Lindholm, Gauthier & Desrochers 1994; Loonen *et al.* 1997). Because size at fledging of goslings has a direct consequence on their survival and reproduction, habitat quality during the rearing period plays a critical role in the processes determining goose population dynamics.

The traditional nesting grounds of most goose populations are located in arctic and sub-arctic regions, where primary production is low and variable within and between seasons (Bliss *et al.* 1973). Nitrogen level in the vegetation reaches a peak soon after snow melts and decreases gradually afterwards (Manseau & Gauthier 1993). Nitrogen is one of the most important limiting factors for the growth of goslings (Manseau & Gauthier 1993; Gadallah & Jefferies 1995). Several studies on different species of geese have shown that goslings hatched later in the season had slower growth and reduced survival than those hatched earlier (Cooch *et al.* 1991a; Sedinger and Flint 1991; Lindholm, Gauthier & Desrochers 1994; Sedinger *et al.* 2001). These differences are thought to be related to the rapid decline in the quality of plants found in arctic regions (Cooch *et al.* 1991b; Aubin *et al.* 1993; Lepage *et al.* 1998). There are also important inter-annual variations in gosling growth in arctic environments attributed to variation in plant production, which is influenced by weather conditions (Lepage *et al.* 1998; Gagnon *et al.* 2004)

We can further test the link between brood-rearing habitat and gosling growth by studying populations that breed in temperate regions. We can then submit the hypothesis that the effects of hatch date and year would not be as important at southern latitudes where primary production is higher and less variable (seasonally and annually) than in the arctic because of the presence of anthropogenic habitats of high quality. However, little is known about gosling growth and the effect of habitat in temperate regions. One exception is the study of a population of Barnacle geese (*Branta leucopsis*) established in Sweden, 1300 km south of their traditional breeding range. Reproductive success and gosling survival rates of these birds are higher than those found for arctic populations of the same species (Larsson & Forslund 1991, 1994; Larsson *et al.* 1998).

The main objective of our study was to determine the effect of habitat, hatch date, and year on gosling growth of a recently-established population of giant Canada

geese (*Branta canadensis maxima*) in southern Quebec (Giroux *et al.* 2001). We predicted that gosling growth would not be affected by hatch date and that annual variation will be limited because of a more constant food supply in temperate regions compared to the arctic, due to the presence of high-quality anthropogenic habitats. We also predicted that geese using enriched anthropogenic habitats will grow better than those using natural habitats. We ultimately want to evaluate the potential of brood-rearing habitat as a limiting factor for the growth of this population.

Study area

This study was conducted near Varennes (45°40' N, 73°27' W), along the St. Lawrence River, approximately 16 km northeast of Montreal (Fig. 1). Canada geese are nesting on four adjacent islands (total area of 111.5 ha) separated by two permanent inland marshes (<5 ha) and several temporary ponds that often dry out during the summer. The islands are characterized by an herbaceous cover, such as red-top (*Agrostis alba*), red fescue-grass (*Festuca rubra*), Kentucky bluegrass (*Poa pratensis*), cow vetch (*Vicia cracca*), reed canary grass (*Phalaris arundinaceae*), and Canada reed-grass (*Calamagrostis canadensis*) with scattered trees and shrubs. Marshes are dominated by cattail (*Typha angustifolia*), big burreed (*Sarganium eurycarpum*) and arrowhead (*Sagittaria* sp.). Until the late 1990s, about 100 cows were pastured on the islands between June and November in a rotational grazing system (Lapointe *et al.* 2000). This has been abandoned since due to a lack of participation from the cattle farmers, whose numbers are rapidly decreasing in the Montreal suburban area to make place for residential development.

The mainland near the Varennes islands consists mainly of residential properties and parks, with large open areas of lawns dominated by Kentucky bluegrass and other species included in lawn mixture. These grassy areas often reach

the shore of the St. Lawrence River. There are numerous agricultural fields, mainly corn and small cereals, further inland and between the municipalities of Varennes and Boucherville (Fig. 1).

The number of goose nests on the Varennes islands has increased from three in 1992 to 135 in 2004 (Giroux *et al.* 2001, J.-F. Giroux & M. Doiron, unpublished data). The number of nests was reduced to 126 in 2005 because of extensive flooding associated with heavy spring run-off. Pairs also nest on nearby islands and we found 69 nests on 12 islands in 2005. Some goslings were marked in these nests. Very few nests (< 5) were found on the mainland. Canada geese generally arrive at Varennes in early April and initiate their nest shortly after. Hatching peak occurs around the 3rd week of May and varies little between years. The geese remain near Varennes during brood rearing and then disperse along the rivers in the Montreal area before leaving in late November (Beaumont 2006).

Methods

Gosling growth

In spring of 2003, 2004, and 2005, weekly searches for Canada goose nests were conducted throughout the Varennes islands. We monitored all nests until hatch and attempted to mark all newly-hatched goslings (sometimes in piped eggs) with an individually numbered web-tag (Alliston 1975). In early July, a few weeks before fledging, which typically occurs at 70 days (Yocom and Harris 1965), the adults moult their primary feathers, and are temporarily unable to fly. Goose families were rounded up and captured during this period in mass banding drives (see Menu *et al.* 2002). Web-tagged goslings were measured (culmen, head, and tarsus bone lengths to the nearest 0.01 mm, and 9th primary length to the nearest 1 mm), weighted to the nearest 50 g, sexed by cloacal examination and banded with a US Fish and Wildlife

Service band. We captured each group of geese present on the study area in distinct drives.

Habitat use

Females were marked with alpha-numeric conventional neck-bands during banding drives in 2003, 2004, and 2005. In 2004, incubating females were captured on their nests using a bow trap or a scoop net and fitted with radio-transmitters affixed to neck collars (Demers *et al.* 2003). The total mass of a transmitter plus collar averaged 56 ± 0.8 g and represented < 1.5% of female body mass. They had an expected longevity of 8 months and the detection range reaches 2 km on land.

In 2004, marked females were searched daily after hatch to determine the habitat used for brood-rearing and the number of adults and goslings accompanying each female. Radio-collared females were tracked by boat or on foot and were located visually every two to three days. We also conducted one or two four-hour observation periods a day (during the diurnal period) from three observation towers erected on the study area (Fig. 1). In 2005, the entire area was searched every 2-3 days to locate groups of geese. During each observation period, we noted the number of birds and age composition (adults and juveniles), the presence of collared females, and the habitat use of all groups of geese we observed.

Habitat was characterized according to landscape features and general vegetation cover and divided into six types: island shores - the shores of the breeding islands; marshes - permanent inland marshes on the islands; natural prairies - unmanaged open fields of heterogeneous herbaceous plants; lawns - managed lawns in parks and residential properties; park shores - the interface between lawns and the St. Lawrence river; agricultural fields - cultivated fields on the south shore. The island shores, the natural prairies, and marshes were grouped into natural habitats

while lawns, park shores, and agricultural fields were considered anthropogenic habitats. Broods observed in movement on open water (i.e. crossing the St-Lawrence River) were excluded from the habitat use analyses.

Isotope measurements

We used stable isotope analyses to examine whether there would be differences in gosling diets during the brood-rearing period in 2004. Stable isotope values of newly grown feathers should be a reliable indicator of food intake during the period when these feathers are grown (Mizutani, Fukuda & Kabaya 1991; Hobson 1999). We collected samples from the 8th primary feather of goslings captured during banding drives, to examine whether gosling feathers had different isotopic signatures of carbon and nitrogen depending on the habitat type in which they were reared.

Feather samples were cleaned in a 2:1 mixture of methanol/chloroform for 48 hours, rinsed twice with methanol, and dried for 24 hours under a hood. Between 0.6 and 0.75 mg of feather material was combusted using a Carlo-Erba NA1500 elemental analyser. The resulting CO₂ and N₂ gas from the samples was separated chromatographically and introduced into a VG Optima triple collector isotope-ratio mass-spectrometer via an open split. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were expressed in delta (δ) notation, as parts per thousand (‰) deviation from the PDB (Pee Dee Belemnite) and the AIR (atmospheric nitrogen) standard, respectively. Measurement precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was estimated to be $\pm 0.2\text{‰}$.

Statistical analyses

Because most goose families formed several large groups (up to 190 individuals) with a high proportion of brood-mixing, we were unable to use individual families as a sampling unit. Instead, we regrouped all geese in family groups using locations and observations of radio-marked and neck-collared females. These large groups formed distinct entities, and the total number of goslings in each group remained relatively stable. We used the observations of each marked female to associate each capture group to different habitat types and to determine in which habitat goslings had been reared. Habitat use was determined for each group using a correspondence analysis of females found in capture groups and habitat types in which they were observed. This allowed us to display graphically the associations between the levels of the two-way contingency table (Sall, Lehman & Creighton 2001).

Growth of known-age goslings (marked at hatch) was measured before fledging using two variables: body mass and structural size. The latter was obtained by extracting the first axis (PC1) from a principal components analysis on the correlation matrix of the lengths of head, culmen, and tarsus-bone of each gosling. The PC1 of these variables is commonly used as an index of structural size (Alisauskas & Ankney 1990; Lindholm, Gauthier & Desrochers 1994; Lesage & Gauthier 1997).

We examined the effects of sex, year (2003, 2004, and 2005), and habitat (natural vs. anthropogenic in 2004 and 2005) on body mass and structural size (PC1) with hatch date as a linear covariate (Cooch, Lank & Cooke 1996). We proceeded in two steps because data on habitat use was missing in 2003. We first ran an analysis using data for the 3 years without the habitat variable and then by including habitat with the 2004 and 2005 data. We used relative hatch date ($\pm n$ days from annual mean

hatch date) to include inter-annual variations. To control for differences in gosling age at capture, we analyzed residuals of regressions of body mass and structural size on age in all analyses (see Cooch et al. 1991a; Cooch, Lank & Cooke 1996). References to body mass and structural size from hereon refer to these adjusted values. We conducted the analyses by including a weight based on the inverse of the number of recaptured goslings that hatched in the same nest. that were recaptured.

While body mass and structural size are obviously correlated (structurally larger goslings have higher body masses), it has been shown that body mass is more sensitive to changes in environmental conditions than structural size (Cooch et al. 1991a; Cooch, Lank & Cooke 1996). We used the residuals of a regression of body mass on structural size (PC1) as a measure of gosling body condition; a higher mass/PC1 ratio would translate into a higher proportion of fat or muscle tissue. We used an analysis of covariance to test the effects of year, sex, relative hatch date, and brood-rearing habitat on this body condition index.

Finally, we used a two-tailed ANOVA to verify whether the isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of primary feathers were affected by sex and rearing habitat. All statistical analyses were performed with JMP IN version 4.0.4 (SAS Institute Inc. 2001) and R version 2.0.1 (R Development Core Team 2004). Significance for all statistical tests was set at $P = 0.05$.

Results

A total of 17 and 36 collared females nested with success and were regularly sighted after hatch in 2004 and 2005, respectively. In addition to this number, 19 females were equipped with radio-transmitter collars in 2004. The broods were recaptured in 10 distinct drives (4 in 2004 and 6 in 2005). Group size ranged from 17 to 240 individuals, with an average of 115 ± 52 , of which goslings represented 2 to

61%, with an average of $40 \pm 26\%$. Groups were relatively stable, as recaptured marked females were observed an average of 92 % of the time ($n = 302$ observations) within the same group. Only 12 and 2 marked females out of the 50 that we recaptured had been observed with two and three different groups of geese, respectively.

We recaptured 141 goslings out of a total of 300 marked at hatch (47.0%) in 2003, 258 recaptured out of 462 (55.8%) in 2004 and 202 out of 323 (62.5%) in 2005. Goslings were web-tagged in 63, 106 and 71 nests in 2003, 2004, and 2005, respectively. Goslings recaptured in 2004 were older than those recaptured in 2003 and 2005 (2003: 46.7 ± 6.5 days; 2004: 53.4 ± 5.9 days; 2005: 46.4 ± 3.8 days; $F = 135.9$, $df = 527$, $P < 0.0001$). This was explained by the later hatching peak in 2003 (2003: 25 May; 2004: 19 May; 2005: 19 May), and by the fact that the banding drives were conducted a few days earlier in 2005 (2 - 13 July) compared to 2003 (8 - 14 July) and 2004 (6-14 July). The hatching period was relatively long, with a difference of 27, 36, and 25 days between the first and last nest hatched during the 3 years, respectively.

Habitat use

Broods used both anthropogenic habitats (i.e. lawns, agricultural fields) and natural habitats (i.e. islands, marshes). Once a brood-rearing site was chosen, there was little movement among sites or habitat types. When the percentage of observations in the two most heavily used habitats by each group is added and averaged, we found that geese spent 88.4% of their time in these two habitats. In 2004, the correspondence analysis of capture groups and habitat types revealed that goslings from group 1 were predominantly reared on anthropogenic habitats, whereas goslings from groups 2, 3, and 4 were mainly reared in natural habitats (Fig. 2a). The proportion of observations among the habitat types differed between group 1 and the

other three groups ($\chi^2 = 141.3$, df = 126, P < 0.0001). The same pattern was observed in 2005; goslings from group 6 were mainly reared in anthropogenic habitats and the proportion of observations in this habitat was significantly greater for this group than for groups 5, 7, 8, 9, and 10 (Fig. 2b; $\chi^2 = 98.0$, df = 168, P < 0.0001). However, the group that predominantly used anthropogenic habitats was much smaller in 2005 than in the previous year (Table 1).

Gosling growth

The first principal component (PC1) explained 84.4, 78.6, and 73.5% of the variance in the initial measures of culmen, head, and tarsus-bone in 2003, 2004, and 2005, respectively. In our first analysis with the 3-year data set, we found significant differences between males and females, both in body mass and structural size (Table 2). There was no intra-annual variation in age-adjusted gosling mass, i.e. no effect of hatch date on body mass, but there was an effect of hatch date on structural size. Structural size significantly decreased with hatch date, so that goslings hatched later in the summer were smaller than those hatched earlier ($F_{1, 527} = 15.75$, P < 0.0001). Year was a significant variable in both body mass and structural size (Table 2). A post hoc Tukey-Kramer HSD test revealed that goslings reared in 2005 had larger age-adjusted body masses ($F = 13.2$, df = 527, P < 0.0001) and structural sizes ($F = 27.8$, df = 527, P < 0.0001) than those reared in 2003 and 2004. Goslings in 2005 were 3 and 7% heavier compared to 2003 and 2004, respectively.

The interaction between sex and year was significant (Table 2). A post hoc Tukey-Kramer HSD test revealed that males were larger than females in all three years, but males recaptured in 2003 had lower body masses than males recaptured in 2004 and 2005. The pattern was different for females; they had larger body masses in 2005, but there were no differences between 2003 and 2004.

In the second analysis, we found a significant effect of habitat on gosling body mass and structural size (Table 3). Goslings reared predominantly in anthropogenic habitats were heavier and larger than those reared mainly in natural habitats during both years (Fig. 3 and 4). There was a significant interaction between habitat and year on body mass and structural size (Table 3), and a post hoc t-test showed that goslings were heavier in 2005 than in 2004 in anthropogenic habitats (445 g heavier in 2005; $t = 4.76$, $P < 0.0001$), but that the difference between years was much smaller in natural habitats (77 g heavier in 2005; $t = 2.34$, $P = 0.0197$). Hatch date had no significant effect on body mass when habitat was included in the model, but had a significant effect on structural size (Table 3). There was significant interaction between habitat and sex on structural size (Table 3). We found that males had significantly higher PC1 values in anthropogenic habitats in both years. However, there was no such effect for females (Fig. 4).

There was a significant effect of year, habitat, and hatch date on the body condition index (residual values for the regression of body mass on structural size) of goslings (Table 4). Goslings reared in 2005 were in better condition than those reared in 2004 and those reared predominantly in anthropogenic habitats were in better body condition than those reared mainly in natural habitats (Fig. 5). Goslings hatched earlier in the season were in better body condition than those hatched late. There was no significant effect of sex on the body condition index of goslings.

Isotope measurements

There was no difference between male and female goslings in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values ($P > 0.05$). $\delta^{13}\text{C}$ values did not differ between habitat types ($P > 0.05$) but feathers of goslings reared in natural habitats had higher $\delta^{15}\text{N}$ values than those of goslings reared in anthropogenic habitats (natural: 9.29 ± 0.64 ; anthropogenic: 8.51 ± 0.36 ; $t = 2.94$; $df = 14$; $P = 0.0108$).

Discussion

This study examines the effects of year, hatch date, sex, and brood-rearing habitat on the growth of goslings reared in a temperate region. There was no effect of hatch date on body mass, but there was an effect on structural size and body condition. Males were significantly larger than females and goslings reared in anthropogenic habitats were larger than goslings reared mainly in natural habitats. However, contrary to our prediction, goslings were larger and heavier in 2005 than during the other 2 years but the magnitude of the difference was not very important compared to the effect of sex or habitat.

Effects of hatch date and year on gosling growth

Several studies have shown a seasonal decline in body mass and structural size of goslings according to hatch date (Sedinger & Flint 1991; Cooch *et al.* 1991a; Lindholm, Gauthier & Desrochers 1994; Lepage *et al.* 1998), but these studies were all conducted in arctic or sub-arctic regions. Nest densities in those goose colonies were generally high, implying an important grazing pressure on the vegetation of brood-rearing sites. The difference in size at fledging of goslings according to hatch date is linked to the rapid decline in the quantity and quality of herbaceous food plants. According to these studies, differences as small as 5 to 7 days in hatch dates could have major consequences on the fitness of individuals. From an evolutionary point of view, this has probably promoted the highly synchronized hatching observed in arctic regions. For example, most goslings hatch within a 7-day period in Greater Snow Goose (Lesage & Gauthier 1998) and within a 12-day period in artic-nesting migrant Canada Goose (Cadieux 2002). The peak of hatch generally corresponds to a maximum in the availability and quality of food supply (Sedinger & Raveling 1986).

While the Canada goose population of southern Quebec is increasing, their total numbers are still relatively low (approximately 1000 individuals) and it is unlikely that grazing causes a significant decline in the availability of food plants on brood-rearing sites. The absence of difference in body mass related to hatch date leads us to believe that the food supply at southern latitudes remains adequate, both in quality (nitrogen content) and quantity to fulfill a gosling's energetic needs throughout the brood-rearing period. The population we studied remains in the Montreal area long after the young acquire flight capacity, and observations conducted in 2004 showed that migration takes place between October 9 and December 19, the median date being December 3 (Beaumont 2006). The long hatching period in southern Quebec may partially be explained by some couples re-nesting after an unsuccessful attempt.

Contrary to our predictions, there was a significant effect of year on size at fledging. Summer temperatures in 2005 reached record highs in the St-Lawrence and Great Lakes region, with an average of 2.2°C higher than normal; it was recorded as the warmest summer of the previous 57 years, which may have impacted gosling growth. Comparatively, the summer of 2004 was on average 0.7°C lower than the norm, and was the coldest summer in the previous 12 years (Meteorological service of Canada 2005). The results we obtained may also be due to the fact that the goslings were measured earlier in 2005, which may have caused us to overestimate their size at fledging if growth is non-linear.

Lepage *et al.* (1998) compared the growth of Greater Snow Goose goslings over five consecutive years, and found that the smallest gosling produced in the “best” year was larger than the largest gosling produced in the “worst” year. Although the goslings measured in southern Quebec were larger in 2005, the differences observed were nowhere near as important as those reported by Lepage *et al.* (1998).

Effects of habitat on gosling growth

Goslings reared in anthropogenic habitats had higher mass, structural size, and a higher proportion of fat and muscle tissues (body condition index) than goslings reared predominantly in natural habitats. Although we have not measured food intake, food quality or food availability for goslings, it is likely that these differences are closely linked to the food supply in these different habitats. It has been shown in several studies concerning gosling growth that body size variations are closely linked to food supply and that goslings are highly plastic in their growth rates (Larsson & Forslund 1991; Lindholm, Gauthier & Desrochers 1994; Leafloor *et al.* 1998).

The anthropogenic habitats in our study area consist mainly of mowed lawns in parks or residential properties, where grass is regularly mowed throughout the summer. New leaves have higher nitrogen concentrations than older leaves (Ydenberg & Prins 1981), and the higher nitrogen content of plants grazed by herbivores is often maintained by grazing (Cargill & Jefferies 1984). Furthermore, it has been shown that gosling growth in the Black Brant (*Branta bernicla nigricans*) was positively related to the areal extent of grazing lawns, which are maintained by grazing (Person *et al.* 2003). In an experiment that consisted in physically removing part of the growing biomass of plants to simulate goose grazing, Fox *et al.* (1988) showed that the biomass of preferred tissue available to geese was doubled. Thus, we would expect mowed lawns to be richer in nitrogen concentration than plants found in natural fields, even if the lawns are not fertilized regularly.

While the isotopic analyses do not provide direct information about the quality of the food resource during the period when feathers are grown, our results show that the $\delta^{15}\text{N}$ values of feathers differed between anthropogenic and natural habitats. This confirms the difference in the diet of goslings from these two habitat types. Mean $\delta^{15}\text{N}$ values in bird feathers are strongly correlated with the proportion of

agricultural land through the entry of excess fertilizer into local water bodies (Hebert & Wassenarr 2001). The habitats that we classified as ‘natural’ consisted mainly of island shores and natural prairies in proximity to numerous agricultural habitats. This could explain the higher $\delta^{15}\text{N}$ values found in feathers of goslings reared in natural habitats.

Another potential advantage of using lawns rather than natural fields or marshes would be a reduced interval of time between each bite. As lawns are typically very homogeneous, goslings probably spend less time looking for appropriate food plants and thus have a higher food intake than goslings reared mainly in natural habitats. Additionally, a study on Dark-bellied Brent geese (*Branta bernicla*) has shown that grazing efficiency decreases for high-standing crops, which means that it is profitable for geese to graze on continuously grazed or mowed vegetation (Bos, van de Koppel & Weissing 2004).

Sexual size dimorphism

We found a consistent difference between males and females in our population, both in body mass and structural size of goslings. Previous studies on various goose species showed that there is a small degree of sexual size dimorphism for both growth rates and size at fledging (Cooch *et al.* 1991a, 1996; Larsson & Forslund 1991; Sedinger & Flint 1991; Leafloor, Ankney & Rusch 1998; Sedinger *et al.* 1998). Other studies have found no differences between males and females in gosling growth (Lesage *et al.* 1998; Cadieux 2002), but this may simply be due to the fact that in these studies, goslings were captured when they were much younger (30–35 days vs 45–55 d in our study) possibly before a sexual size dimorphism appears. There was no difference between males and females in the body condition index suggesting no difference in the physiological condition between sexes, despite differences in size.

Conclusion

The goal of this study was to test the predictions that hatch date and year would not have a significant effect on gosling growth of Canada geese in southern Quebec, and that goslings reared in enriched anthropogenic habitats would have a better growth than those reared in natural habitats. Our results showed that factors that limit the growth of arctic-nesting goslings, such as an important seasonal decline in food quality and availability, are probably negligible for southern populations, or at least mitigated by the presence of anthropogenic habitats. Thus, managers must be cautious when using data from artic-nesting populations to make decisions concerning southern populations. On the other hand, annual variation can occur at southern latitudes, but the impact of these variations does not appear as strong as what has been observed in the arctic. We showed that anthropogenic habitats are not only adequate brood-rearing environments for giant Canada geese, they seem to be superior to natural habitats. Considering that the population studied nests in an urban/suburban area where lawns and agricultural fields are abundant, this suggests that shortages of adequate brood-rearing habitat will probably not limit the growth of this population in the near future nor of other populations breeding at temperate latitudes.

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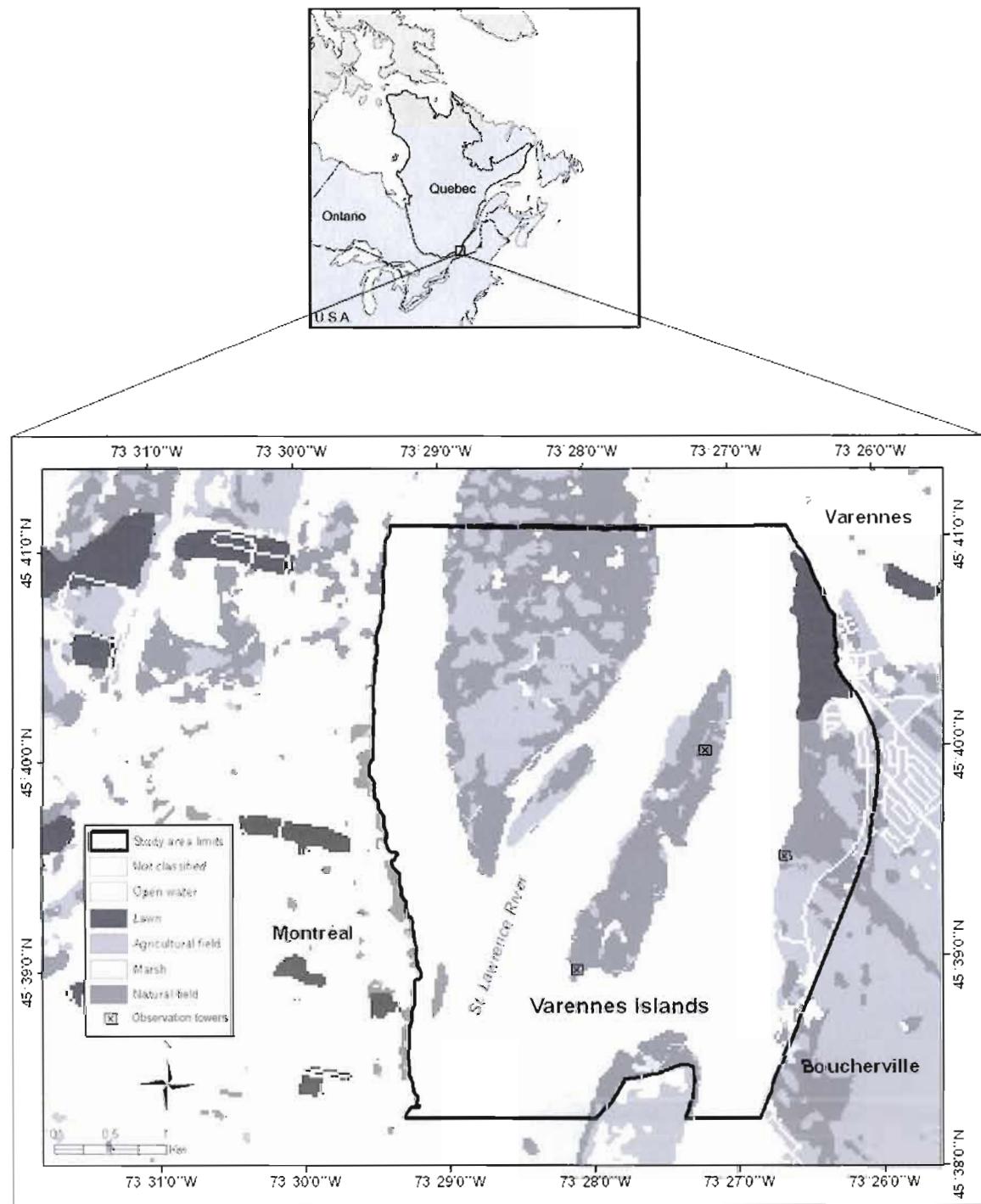


FIG. 1. Location of the Varennes islands on the Saint-Lawrence river, Quebec.

TABLE 1. Habitat use by marked female Giant Canada geese associated to different capture groups near Varennes, Qc, 2004-2005.

Group	Year			Habitat type (% observations)									
		Nb of marked females	Total nb of locations	Natural			Agricultural			Park		Total natural	Total anthropogenic
				Marsh	field	Island shore	field	Lawn	shore				
1	2004	6	81	0	3.7	0	7.4	44.4	44.4	3.7	96.2		
2	2004	3	17	17.6	0	70.6	11.8	0	0	88.2	11.8		
3	2004	2	15	13.3	26.7	53.3	6.7	0	0	93.3	6.7		
4	2004	1	14	28.5	35.7	35.7	0	0	0	100	0		
5	2005	5	20	60.0	0	35.0	5.0	0	0	95.0	5.0		
6	2005	3	26	0.0	7.6	23.1	0.0	15.4	53.8	30.7	69.2		
7	2005	8	46	26.1	2.2	71.7	0	0	0	100	0		
8	2005	5	17	64.7	0	29.4	5.9	0	0	94.1	5.9		
9	2005	12	46	71.7	8.7	19.6	0	0	0	100	0		
10	2005	5	13	23.1	0	76.9	0	0	0	100	0		

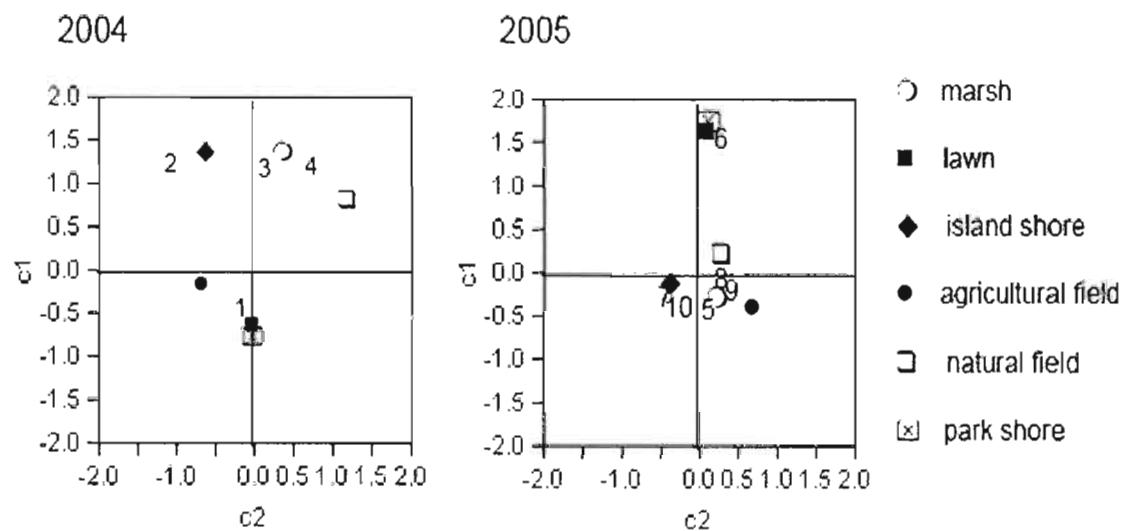


FIG. 2. Correspondence analysis of habitat use by collared adult Canada goose females with goslings during the brood-rearing period according to their capture group in 2004 and 2005. Numbers represent capture groups (see Table 1). C1 and C2 represent the first two axes of correspondence analysis.

TABLE 2. Effects of year and sex on body mass (g) and structural size (PC1 scores: first axis of a principal components analysis on head, culmen, and tarsus lengths) of Canada goose goslings near fledging in 2003, 2004, and 2005, using relative hatch date ($\pm n$ days from annual mean hatch date) as a covariate. F and P values are shown for the complete model and for each independent variable in the model ($n = 528$). Only significant interactions are included in the model.

Parameters	Mass ($R^2 = 0.17$)			Size ($R^2 = 0.28$)	
	d.f.	F	P	F	P
Model	7	15.59	< 0.0001	34.44	< 0.0001
Year	2	12.50	< 0.0001	30.11	< 0.0001
Sex	1	43.90	< 0.0001	85.89	< 0.0001
Hatch Date ^a	1	1.95	0.1634	19.76	< 0.0001
Sex x Year	2	4.73	0.0091	4.11	0.0168
Sex x Hatch Date	1	6.66	0.0101		

^aRelative hatch date

TABLE 3. Effects of year, sex, and habitat on body mass (g) and structural size (PC1 scores: first axis of a principal components analysis on head, culmen and tarsus lengths) of Canada goose goslings near fledging in 2004 and 2005, using relative hatch date ($\pm n$ days from annual mean hatch date) as a covariate. F and P values are shown for the complete model and for each independent variable in the model ($n = 433$). Only significant interactions are included in the model.

Parameters	Mass ($R^2 = 0.33$)			Size ($R^2 = 0.35$)	
	d.f.	F	P	F	P
Model	6	35.44	< 0.0001	38.30	< 0.0001
Year	1	62.45	< 0.0001	63.17	< 0.0001
Sex	1	96.94	< 0.0001	118.78	< 0.0001
Hatch Date ^a	1	0.0143	0.9049	7.20	0.0076
Habitat	1	95.19	< 0.0001	18.28	< 0.0001
Sex x Hatch Date	1	4.55	0.0335		
Habitat x Year	1	31.69	< 0.0001	7.72	0.0057
Habitat x Sex				6.64	0.0103

^aRelative hatch date

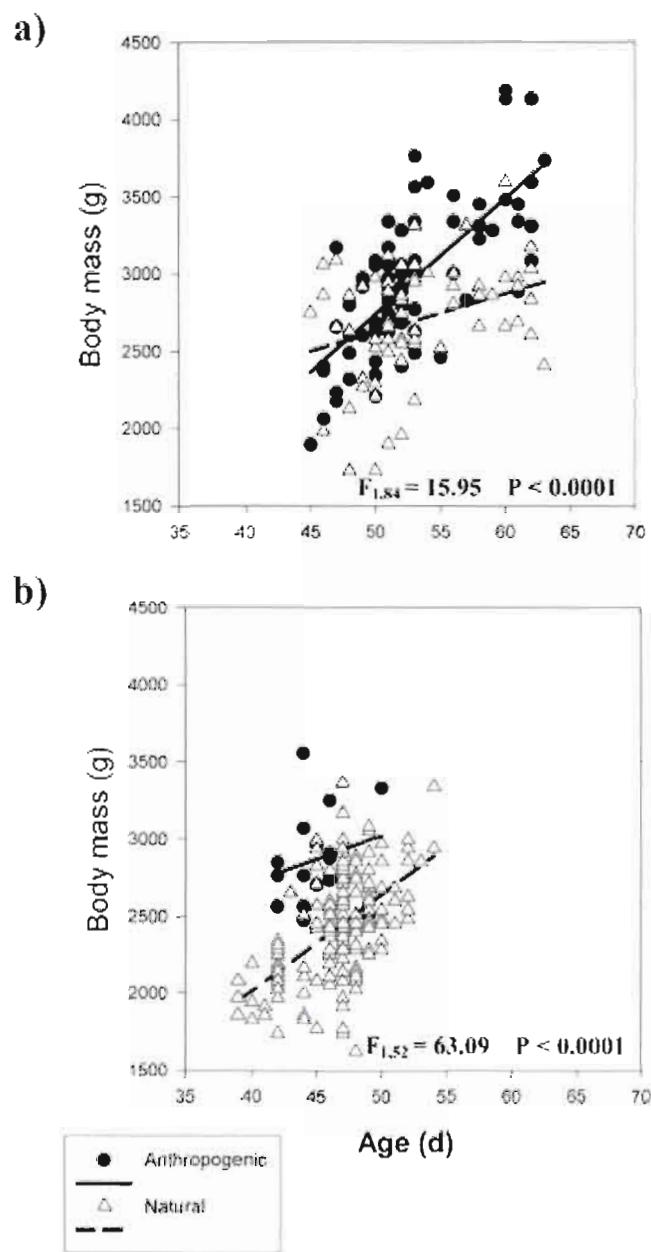


FIG. 3. Relationships between age of Canada goose goslings and their body mass according to the brood-rearing habitat (anthropogenic vs. natural) on Varennes islands in a) 2004 and b) 2005. The F and P-values represent the habitat effect.

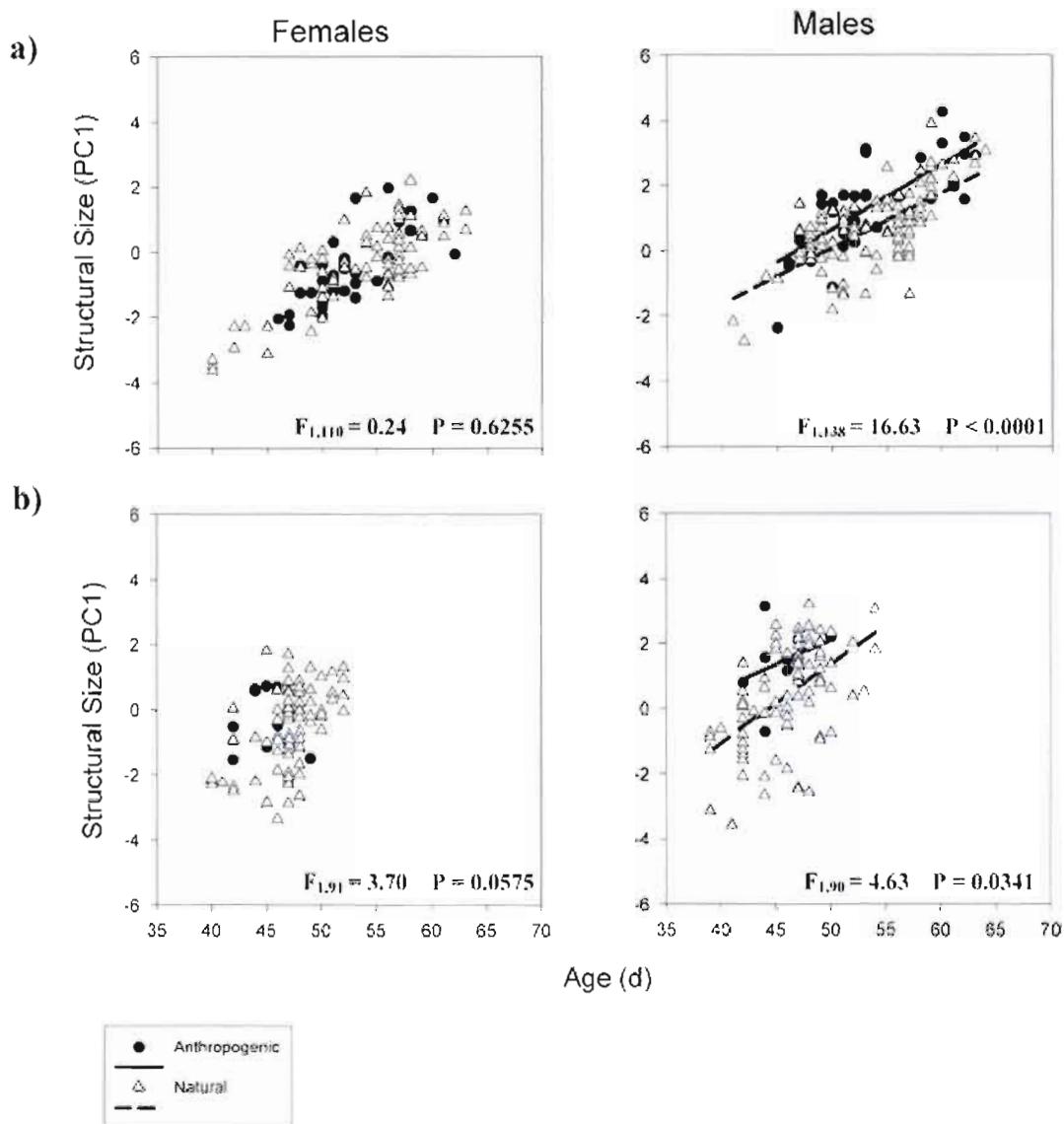


FIG. 4. Relationships between age of Canada goose goslings and their structural size according to the brood-rearing habitat (anthropogenic vs. natural) on Varennes islands in a) 2004 and b) 2005. The F and P-values represent the habitat effect.

TABLE 4. Effects of year, sex and habitat on the body condition index (residual values for the regression of body mass on structural size) of Canada goose goslings near fledging in 2004 and 2005, using relative hatch date ($\pm n$ days from annual mean hatch date) as a covariate. F and P values are shown for the complete model and for each independent variable in the model ($n = 433$). Only significant interactions are included in the model.

Parameters	Body condition index ($R^2 = 0.39$)		
	d.f.	F	P
Model	5	53.52	< 0.0001
Year	1	40.05	< 0.0001
Sex	1	8.27	0.0043
Hatch Date ^a	1	3.86	< 0.0001
Habitat	1	27.12	< 0.0001
Habitat x Year	1	14.61	0.0002

^aRelative hatch date

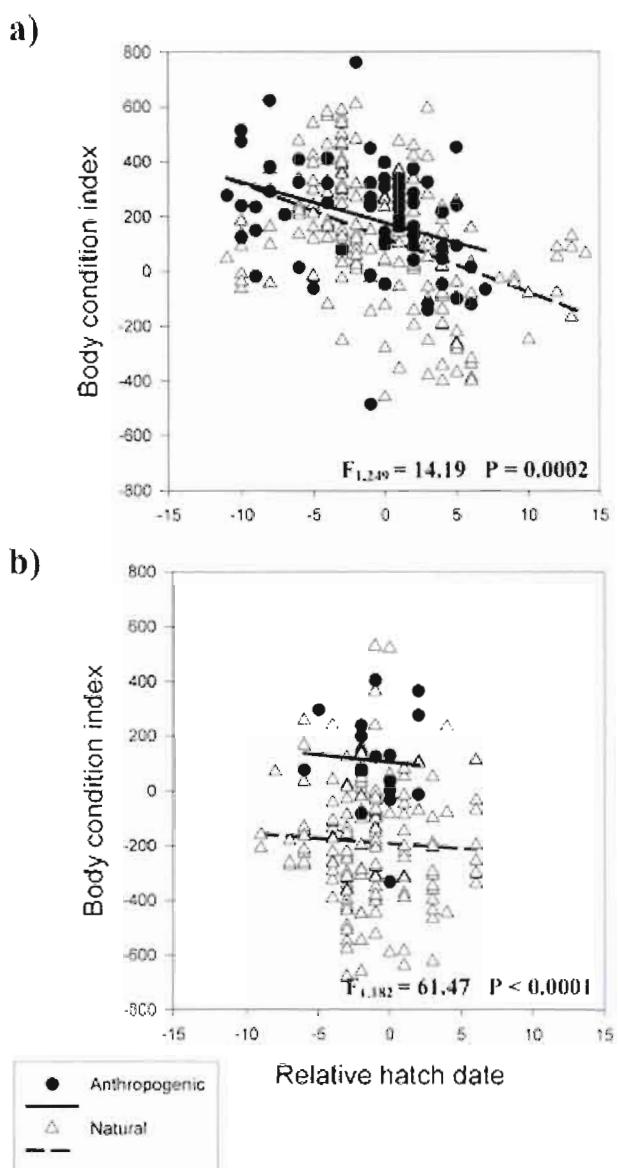


FIG. 5. Body condition index (residuals of the regression of body mass and structural size) of Canada goose goslings against their relative hatch date, according to the brood-reading habitat (anthropogenic vs. natural) in 2004 and 2005. The F and P values represent the habitat effect.

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CHAPITRE 2

**BROOD-MIXING, ADOPTION, AND ABANDONMENT IN
GIANT CANADA GEESE**

Abstract: Since 1992, we are monitoring a nesting population of giant Canada geese (*Branta canadensis maxima*) on the Varennes islands, near Montreal. In 2004 and 2005, we observed that brood amalgamation and adoption of goslings was common. In this paper, we describe the extent and timing of the phenomenon, the parents' characteristics and the mobility of the broods. We marked goslings at hatch and recaptured them a few weeks before fledging. We also marked adult females with radio-transmitters and conventional alpha-numeric collars and monitored them throughout the summer to determine how many goslings accompanied them. Broods formed several large groups that varied in size between 6 and 197 individuals. The majority of females abandoned their young early in the summer. Females that kept their goslings had slightly higher brood sizes at hatch than those that abandoned, but they did not show any differences in hatch date and initial clutch size. Globally, 71 and 51% of recaptured goslings were reared by adults other than their biological parents in 2004 and 2005, respectively. Hatch date, sex, and difference from peak hatch did not affect a gosling's probability of being abandoned. However, their chance of being abandoned and adopted was negatively correlated to brood size at hatch and was higher in 2004 than in 2005. The information gained from this study should help to address specific questions about the significance of this behaviour.

Key Words: adoption, alloparental care, *Branta canadensis maxima*, brood rearing, giant Canada goose, Quebec, waterfowl

Introduction

Adoption, or alloparental care, is defined as the care of young by individuals other than the genetic parents. Alloparental care by conspecifics has been reported in over 150 species of birds and 120 species of mammals (Riedman 1982). Alloparental care in birds can occur in two ways: (1) pre-hatch, when a female lays her eggs in the nest of another female, and (2) post-hatch, when a female loses her young because they become mixed with the young of another female (Eadie *et al.* 1988). Post-hatch alloparental care, often defined as brood-mixing, occurs in at least 28 waterfowl species in North America, and is considered common in 14 species (Eadie *et al.* 1988).

The cost associated with rearing an increased number of offspring is much less clear for precocial than altricial species because precocial parents do no feed their offspring. The main cost incurred by these parents after hatching is vigilance (Schindler & Lamprecht 1987). Studies on common eiders (*Somateria mollissima*) have shown that females that abandon their young are in poorer body condition at time of hatch, which suggests that females abandon their young as a salvage strategy to ensure their own survival and lifetime reproduction (Bustnes and Erikstad 1991, Bustnes *et al.* 2002). The advantages for the adopted young or for the young of the adoptive parents have received more attention. According to Nastase and Sherry (1997), mixed broods improved the survival of natural goslings by exploitation of adoptive goslings, as adopted goslings were more often on the periphery of the group and thus more vulnerable to predators. It has also been suggested that larger groups provide increased dominance ranks against other broods when there is competition for feeding sites (Mulder *et al.* 1995; Loonen *et al.* 1999). Different hypotheses have been put forward to explain the occurrence of brood-mixing in waterfowl species (see review by Eadie *et al.* 1988), but it remains unclear whether this phenomenon is

adaptive or accidental, and what are the payoffs of such a strategy for the individuals involved. A better understanding of the mechanisms by which alloparental care takes place is therefore required to evaluate the adaptive significance of this behaviour.

The recent establishment of a nesting population of giant Canada geese (*Branta canadensis maxima*) in southern Quebec was reported by Giroux *et al.* (2001). This population is growing rapidly, at similar or higher rates than other Canada goose populations in temperate regions (Ettl 1993; Ankney 1996; Giroux *et al.* 2001). During a study on brood ecology, we observed that brood amalgamation and adoption of goslings was common. The objectives of this paper are to describe the extent and timing of the phenomenon, the parents' characteristics and the mobility of the broods. This information should help to address specific questions about the significance of this behaviour.

Methods

Our observations were conducted on and around the Varennes islands ($45^{\circ}40'$ N, $73^{\circ}27'$ W), on the St. Lawrence River, approximately 16 km northeast of Montreal. The Varennes islands are characterized by open vegetation mainly composed of herbaceous plants and a few small trees and shrubs. The area surrounding the islands consists of residential properties and recreational parks, agricultural fields and a few large industrial developments. The Varennes islands represent the main nesting area of giant Canada geese in southern Quebec, with 135 and 126 nests found in 2004 and 2005, respectively (1.2 and 1.1 nests/ha) (J.-F. Giroux & M. Doiron, unpublished data). Breeding geese generally arrive on the study area in early April, and hatching peak occurs around the 3rd week of May.

In 2004 and 2005, we conducted nests searches on the Varennes islands and the surrounding area and marked all goslings at hatch with individually numbered web-tags and recaptured them in banding drives a few weeks before fledging (mean age of 53 days). A sub-sample of adult females were equipped with radio-transmitters (2004 only, n=19) or conventional alpha-numeric collars (2004 and 2005, n=60) and were monitored to determine their habitat use and the number of adults and goslings accompanying each female. Radio-collared females were tracked by boat or on foot and were located visually every two to three days. We also conducted one or two four-hour observation periods a day (during the diurnal period) from three observation towers erected on the study area. In addition, we opportunistically noted all collared females or broods while traveling around the study area. Goslings observed were considered part of solitary families when all the goslings appeared to be of the same age and they were accompanied by only two adults. Goslings were considered part of mixed groups when the goslings appeared to be of varying ages and were accompanied by 3 adults or more.

We considered a female as having abandoned her young when she was observed twice successively without goslings, in a group of adults only or alone with her mate, and when at least one of her goslings was recaptured in July during the banding drives to eliminate the possibility of total brood loss. Pairs that kept and/or adopted goslings are referred to as “attending pairs”, while pairs that successfully nested but eventually abandoned/lost their goslings are referred to as “non-attending pairs”. Attending pairs may include couples that have abandoned their own goslings and adopted others afterward, as we were unable to verify this. A gosling was considered as abandoned when it was recaptured in a group where its mother was not present but known to be alive (recaptured in another group or observed on the study area). In our study area, most geese formed stable distinct groups that remained several hundred meters that could be captured by driving them independently (M. Doiron, unpublished data).

We compared the breeding parameters of attending and non-attending pairs. Additionally, logistic regressions were used to examine the effects of year, brood size at hatching, and hatch date on the probability of a female to abandon/lose her goslings. We also used logistic regressions to determine the effects of females' collar type (radio vs. conventional), year, hatch date, difference from gosling sex, annual mean hatch date, brood size at hatch, and gosling condition at marking on the probability of a gosling to be abandoned.

Results

Only solitary families were observed during the 17 days that followed the beginning of hatching (Fig. 1). However, the number of goslings in these families ranged from 1 to 25 (mean = 6.4 ± 4.3), indicating that brood mixing had already occurred. The number of goslings leaving a successful nest averaged 4.5 ± 1.6 ($n = 352$, range = 1 - 8) and did not differ between years. Adults and goslings started to congregate and form groups towards the end of May when most of the nests (85%) had hatched. Group size ranged between 6 and 197 individuals with a mean of 68 ± 47 individuals. Groups were composed of an average of $59 \pm 22\%$ goslings, but these proportions greatly varied among groups (6 - 91%). An average of 32 ± 40 adults accompanied the goslings, but this number ranged between 3 and 185. The number of young in each group remained relatively stable until the banding operations in early July. It was not uncommon to observe young within the same group that had an age difference of up to 25 days. This pattern was consistent in both 2004 and 2005.

A total of 42 and 41 marked females left the islands with goslings in 2004 and 2005 and we observed 38 and 36 of them during the brood rearing period,

respectively. In 2004, two of the missing females were subsequently observed during the fall (M. Beaumont, pers. comm.) indicating that they temporarily left the study area to moult at an unknown location. The other 2 females may have dispersed or died during the summer. A high proportion of collared females that successfully left their nest with at least one gosling were subsequently observed with no goslings during the brood-rearing period: 26 out of 38 (68%) in 2004 and 13 out of 36 (36%) in 2005. We recaptured at least one gosling that belonged to 24 of the 26 females that were observed without young in 2004 and from all 13 of those females in 2005, which shows that most non-attending females had not suffered total brood loss through mortality of all the goslings, but through abandonment as well. These non-attending females were observed for the first time without goslings between 5 and 15 days after hatch. The attending females were observed with young throughout the summer and captured with their goslings during the banding drives.

Mean clutch size (number of eggs laid) and hatch date did not significantly differ between attending and non-attending pairs in 2004 or 2005 (Table 1). Brood size at hatching was greater for attending than non-attending females but the difference was at the limit of significance in 2005. When both years were pooled, the difference was significant ($t = 2.35$, $P = 0.021$). Pairs had a higher chance of abandoning their goslings in 2004 than 2005 ($\chi^2 = 4.685$, $df = 1$, $P = 0.030$) and this was negatively correlated to brood size at hatching ($\chi^2 = 4.777$, $df = 1$, $P = 0.029$). The effect of hatch date was not significant.

A total of 13 collared successful females (≥ 1 young hatched) were observed regularly after hatch in both years. Out of the 5 attending females in 2004, 3 also attended a brood in 2005. In contrast, 4 out of the 8 non-attending females in 2004 attended a brood in 2005. Pairs that attended goslings in 2004 were not more likely to

attend goslings in 2005 than pairs that did not (Fisher's exact test, $P = 0.821$). Only 7 out of the 13 females adopted the same behaviour in both years.

In 2004 and 2005, 186 and 206 web-tagged goslings left the islands, respectively. During these 2 years, we recaptured 102 (55%) and 104 (51%) of these goslings. Among them, 72 (71%) and 53 (51%) goslings were recaptured in groups that did not include the female associated to the nest in which they hatched during the two respective years. Their putative mothers were either recaptured in other catches, sometimes in groups comprised of adults only, or not recaptured at all. The 15 females not recaptured in 2004 were all observed later in the summer or the following year, indicating that the young had not been orphaned through mortality of their mother, but were really abandoned.

There was no significant effect of hatch date, sex, and difference from peak hatch on the probability of a gosling to be abandoned or adopted ($P < 0.05$). However, goslings had higher chances of being abandoned/adopted in 2004 than in 2005 ($\chi^2 = 7.429$, $df = 1$, $P = 0.006$), and their chances of being abandoned/adopted was negatively correlated to brood size at hatch ($\chi^2 = 8.578$, $df = 1$, $P = 0.003$).

Discussion

Brood-mixing is common in Canada geese (Hanson and Eberhardt 1971; Zicus 1981; Eadie *et al.* 1988; Seddon and Nudds 1994; Nastase and Sherry 1997), and easily identified by differences in ages of goslings within a brood or by abnormally large brood-size. Hanson and Eberhardt (1971) reported that adoption was common in a western Canada goose population, and large broods of up to 28 goslings were observed. In all cases, these broods were escorted by only one pair of adults. Zicus (1981) observed that 46% of Canada goose pairs in Wisconsin adopted

at least one gosling, and that broods attended by more than one pair were very rare. In contrast, most of the goslings around the Varennes islands were reared in large groups with goslings of varying ages accompanied by several adult pairs. These groups of birds that fed, moved and loafed together started forming as early as 17 days after the first nests hatched.

Brood abandonment rates reported in these studies were much lower than what we observed in southern Quebec. Zicus (1981) found that 24% of the successful nesting pairs did not raise broods to flight, probably through abandonment. These pairs had lower egg fertility, egg success and average brood size at hatching, tended to be younger and probably less experienced than adults that reared goslings to fledging. In southern Quebec, 68% and 36% of successful nesting pairs abandoned/lost their young in 2004 and 2005, respectively. This annual variation may be a result of the low production of goslings in 2005. Due to abnormally high precipitation in the spring of 2005 and a record-high run-off in the river, 20% of Canada goose nests on the Varennes islands were submerged and subsequently abandoned. A further 10% were destroyed, probably by a family of red foxes (*Vulpes vulpes*) that was observed several times over the summer. We estimated that 501 goslings left the nest in 2004, compared to 318 in 2005, a difference of 36% (M. Doiron, unpubl. data). It is possible that the lower rate of adoption that year simply resulted from the lower number of goslings and the lower frequency of encounters between broods. It may also be because the less-experienced, younger females had already lost their nests leaving a higher proportion of more maternal females among the pairs that managed to produce young in 2005.

The non-attending pairs had lower brood sizes at hatching than the attending adults in 2005, but their initial clutch sizes did not differ in either year. This means that non-attending pairs in 2005 had a lower hatching success than attending pairs, and that they had a higher proportion of eggs that were either preyed upon from the

nest, that were infertile, or that had stillborn goslings. Because of the presence of terrestrial predators in 2005 (red foxes), we can assume that the predation risk was greater that year than in 2004. It is possible that the non-attending females were also less attentive or maternal even at the incubation stage, and that they were more vulnerable to partial predation, which would explain the difference in brood size at hatching between attending and non-attending females in 2005. This could also be related to the age/experience of the females with younger less experienced females being more prone to abandon their young.

The cause of the high rates of abandonment and adoption in this population is unclear. It has often been suggested that adoption in various waterfowl species occurs due to accidental brood mixing after disturbances and to incomplete imprinting resulting in an inability of goslings to recognize their own parents, even after parent-offspring recognition should be well developed (Warhurst & Bookhout 1983; Choudhury *et al.* 1993, Williams 1994). However, after hundreds of hours of observation, we did not observe any direct evidence that brood-mixing occurred after a disturbance in southern Quebec, even though disturbances related to human activities were relatively frequent. Furthermore, this is only a proximate explanation of how broods mix.

The fact that adults easily adopt goslings that are not their own suggests that the costs of adoption are low for parents, or that it may even be beneficial for them. Williams (1994) suggests that adoption is a mutually beneficial strategy that is beneficial for both adopted young and adopting parents.

Goslings may be exposed to a lower predation risk when in large groups, due to a simple dilution effect. Although adoptive parents may incur costs in terms of increased vigilance due to larger broods (Williams 1994), they may compensate if their own goslings grow and survive better in large groups (Lepage *et al.* 1998).

However, it seems unlikely that predation is higher in southern Quebec than for other studies that have reported lower rates of brood-mixing. Canada geese are susceptible to nest depredation by red foxes, gulls (*Larus spp.*) or ravens (*Corvus corax*) during the incubation period, and goslings may be vulnerable in the first week of life, but once they reach about 10 days of age, they likely become too big for these predators. The only predation event we witnessed was on a small gosling of less than a week by a Great Black-backed Gull (*Larus marinus*) in 2003. If predation risk was the main driver in brood-mixing, we should expect low rates of adoption in this population compared to other populations.

Eadie *et al.* (1988) suggested that females may abandon young as a salvage strategy if they find themselves unable to provide adequate parental care for their goslings, either because they lack breeding experience, they are in poor body condition, or brood-rearing habitat is limited. Compared to arctic-nesting geese, for which lower rates of adoption have been reported, it seems unlikely that females in southern Quebec would have a poorer body condition, forcing a large number of them to abandon their goslings to ensure their own survival.

The occurrence of such high rates of brood-mixing in this population may simply be a case of competition for brood-rearing sites if more than one pair attempt to use the same sites and that one pair is evicted by the other. However, we never observed such interactions between broods during several hundreds hours of observation. Eadie *et al.* (1988) have noted that brood-mixing occurs more frequently in species for which resources are limited. A long-term study examining age, relatedness and fitness of individuals is needed to yield solid conclusion on the factors that cause brood-mixing in this Canada goose population.

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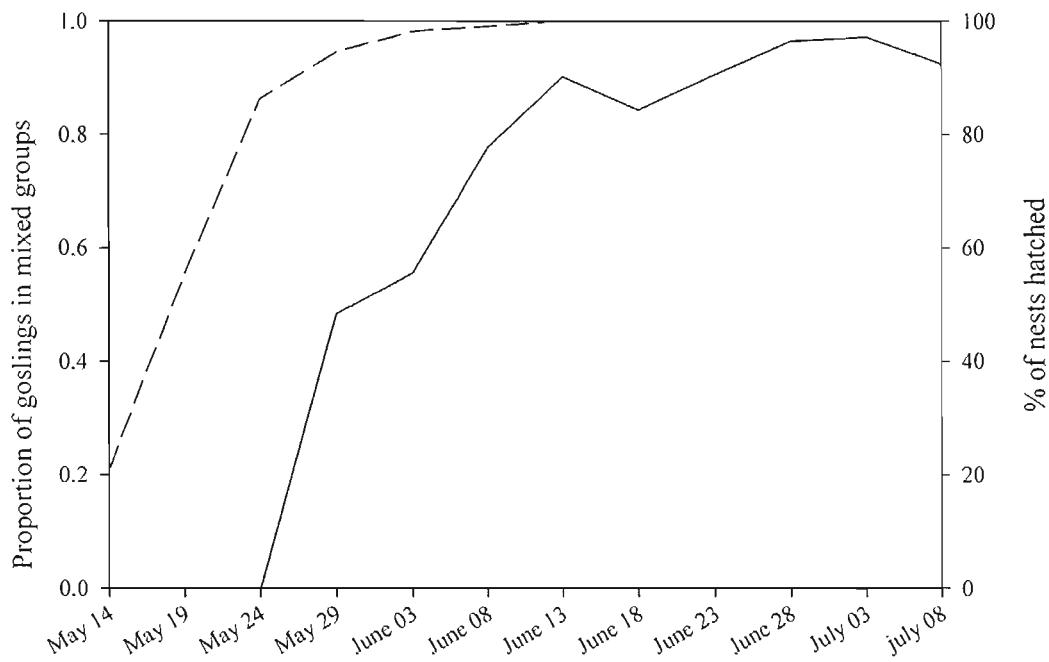


Figure 1. Proportion of Canada goose goslings observed in mixed groups near Varennes, Quebec, in 2004. Before May 24th, all observed goslings were in solitary families. The dashed line represents the cumulative percentage of nests hatched.

Table 1. Breeding parameters of attending and non-attending pairs of Canada geese in Varennes, Quebec, 2004- 2005.

a) 2004

<i>Characteristic</i>	<i>Non-Attending</i>				<i>t</i>	<i>P</i>
	<i>Attending (N=12)</i>		<i>(N=24)</i>			
	mean	SE	mean	SE		
Clutch size	5.7	0.6	5.3	1.2	0.916	0.366
Brood size at hatch	4.9	1.0	4.3	1.7	1.102	0.278
Hatch date	May 20	8	May 22	7	-0.643	0.524

b) 2005

<i>Characteristic</i>	<i>Non-Attending</i>				<i>t</i>	<i>P</i>
	<i>Attending (N=23)</i>		<i>(N=13)</i>			
	mean	SE	mean	SE		
Clutch size	6.0	1.0	5.9	1.0	0.097	0.924
Brood size at hatch	5.3	1.1	4.3	1.8	1.984	0.049
Hatch date	May 19	4	May 20	4	-1.239	0.224

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CONCLUSION GÉNÉRALE

La population de bernaches du Canada résidentes du sud du Québec niche principalement en milieu péri-urbain et utilise en grande partie les habitats anthropiques de la région tels que les parcs, les terrains de golf et les terrains privés couverts de pelouse ainsi que les champs agricoles. Les oisons élevés principalement sur ces types d'habitats avaient des tailles structurelles et des masses corporelles supérieures à celles des oisons élevés sur des habitats considérés plus naturels tels que les marais et les prairies naturelles. Comme ces habitats anthropiques sont abondants dans la vallée du Saint-Laurent, et que les îles propices à la nidification sont nombreuses le long du fleuve, il semble improbable que l'on observe une baisse dans la croissance de la population due à des effets de densité. Bien que nous n'avons pas mesuré cet aspect directement, la survie des jeunes semble élevée, du moins jusqu'à l'envol, et ce malgré des différences annuelles dans la croissance des jeunes.

Les facteurs influençant la croissance des jeunes dans les populations arctiques ne semblent pas applicables aux populations d'oies des régions tempérées, quoique le climat semble aussi avoir dans une moindre mesure un effet dans les régions du sud. En effet, une « mauvaise » année semble avoir des conséquences beaucoup moins drastiques dans le sud du Québec que dans les régions arctiques, probablement en raison des variations moins extrêmes du climat. La période de nidification est longue, ce qui suggère que la date d'éclosion joue un rôle moins important dans le sud du Québec que dans le nord, où les éclosions sont très synchronisées au début de la saison (Lesage et Gauthier 1998; Cadieux 2002). Tous ces facteurs portent à croire que cette population va continuer à croître rapidement au cours des prochaines années.

Il semble inévitable que des mesures de gestion active seront nécessaires pour garder la population de bernaches résidentes à un niveau acceptable pour la

cohabitation avec la population humaine de la vallée du Saint-Laurent. Il serait recommandé d'évaluer le niveau de support du milieu, tant du point de vue de la population humaine que du point de vue écologique, afin de pouvoir établir un seuil qui permettrait aux gestionnaires de la faune d'évaluer la nécessité de contrôler la population et d'éviter les problèmes déjà rencontrés ailleurs dans le nord-est de l'Amérique du Nord (Conover et Chasko 1985; Conover et Kania 1991; Ettl 1993; Ankney 1996). Historiquement, les mesures de gestion concernant la Bernache du Canada résidente ont toujours eu lieu après que les effectifs aient atteint des niveaux dits de « nuisance ». Il serait beaucoup plus avantageux et efficace d'entreprendre ces mesures bien avant que le seuil de tolérance soit atteint (Ettl 1993). Des études supplémentaires sur l'effet de certaines méthodes de contrôle, telles l'arrosage des œufs, l'abattage d'un certain nombre d'adultes ciblés, la stérilisation des adultes, etc., seraient souhaitables pour pouvoir produire un plan de gestion à long terme pour cette sous-espèce bien adapté à la situation du sud du Québec.

Les taux élevés de mélange des couvées et d'adoption observés sur notre aire d'étude peuvent aussi jouer un rôle non-négligeable sur le taux de croissance de la population, s'ils ont un effet sur la croissance ou la survie des oissons. Il a été suggéré que le mélange des couvées procure un avantage pour la survie des jeunes en offrant une plus grande protection contre les prédateurs) ou un accès à des sites de meilleure qualité (Hanson 1953; Black et Owen 1989; Seddon et Nudds 1994; Williams 1994; Loonen *et al.* 1999). Ce comportement serait une stratégie qui bénéficierait aux adultes qui adoptent ainsi qu'aux jeunes qui sont adoptés (Eadie *et al.* 1988; Williams 1994). Le mélange des jeunes pourrait ainsi accélérer le processus de croissance démographique de manière considérable, et il devient important de considérer cet aspect du comportement d'élevage dans les plans de gestion de cette espèce.

Il serait intéressant de pouvoir combiner l'aspect du comportement d'élevage des jeunes à des aspects de dynamique de la population. Il est facile d'imaginer

comment le mélange des jeunes, la taille d'un groupe, la vigilance des adultes et la prédatation peuvent tous être reliés et avoir des effets importants sur un aspect fondamental de la démographie, soit la survie des jeunes. Les taux d'adoption élevés rapportés lors de mon étude soulèvent des questions intéressantes, surtout dans le contexte particulier du sud du Québec. Mon mémoire n'est que le début d'une série d'études possibles examinant de plus près l'importance de ce phénomène, et illustre bien le besoin d'effectuer un suivi à long terme qui tiendrait compte non seulement d'aspects de dynamique de populations mais également de comportement animal.

Outre la nécessité d'étudier cette population à cause des problèmes de gestion qu'elle pourrait engendrer, les bernaches résidentes de la vallée du Saint-Laurent pourraient devenir un modèle intéressant car elles sont faciles à observer, capturer et marquer, leurs nids sont presque toujours faciles d'accès et elles ont une longue espérance de vie, ce qui facilite les études à long terme basées sur des individus marqués. Finalement, mon étude représente un point de départ pour un suivi à long terme de cette population de bernaches du Canada afin d'acquérir les connaissances requises pour permettre une bonne gestion et une meilleure connaissance de l'écologie de cette sous-espèce.

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