

**The Foraging Behavior of Lesser Snow
Geese and Ross's Geese on La Pérouse Bay**

By Barbara Pezzanite

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Date

Chair of Examining Committee

Date

Executive Officer

Robert F. Rockwell, Ph.D.
City College, CUNY

Sheila Chase, Ph.D.
Hunter College, CUNY

Louis Levine, Ph.D.
City College

Peter Moller, Ph.D.
Hunter College

Carol Simon, Ph.D.
City College

Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK

Signed approval page archived with the Graduate Center of CUNY

Abstract

The Foraging Behavior of Brood Rearing Lesser Snow Geese

and Ross's Geese on La Pérouse Bay

by

Barbara Pezzanite

Advisor: Professor Robert F. Rockwell

Two behavioral studies were conducted on La Pérouse Bay's intertidal feeding flats to determine: 1) long-term changes in foraging behavior of breeding lesser snow geese coincident with over 20 years of degrading habitat conditions, and 2) differences in foraging behavior of breeding lesser snow geese and Ross's geese on this degraded habitat. Data were collected from June to August, using focal animal protocols. The first study utilized foraging data collected in 1980, 1984, 1985, 1988 to 1990, and 1998 to 2000. The second study examined foraging by lesser snow geese and Ross's geese during the 1999 brood rearing period.

Coincident with habitat degradation from 1980 to 2000, the pecking rates of adult female snow geese increased from 168 to 204 pecks per minute. Time spent searching for food increased 7% in males and 12% in females. In contrast, snow goose goslings spent 12% less time feeding than in earlier years. From 1984 to 1998, the mass of gosling snow geese declined approximately 2% in males and 5% in females, and structural measurements (culmen and tarsus) declined 7% and 3% in females, and 5% and 4% in males. In 1999, snow goose brood size declined by 74% from early June to early August.

These changes appear to reflect a decrease in food availability without compensatory changes in the goslings' foraging tactics.

Adult and gosling Ross's goose pecking rates were approximately 30% and 35% higher than those of snow geese. Walking rates of adult male and female Ross's geese were 44% and 39% faster than those of adult snow geese. Higher pecking rates and use of larger feeding areas appears to have contributed to the high survival rate of gosling Ross's geese.

Results from this research highlight the need for behavioral studies in wildlife management and conservation by demonstrating how a degraded habitat can differentially affect two species. Data can now be used by conservationists to monitor the population dynamics of these species, and their potential impact on other ecosystems.

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CHAPTER 1

INTRODUCTION

This dissertation includes two studies on the foraging behavior of the lesser snow goose (*Chen caerulescens caerulescens*) and the Ross's goose (*Chen rossii*) in the intertidal salt marsh at La Pérouse Bay (58°43.29' N 93°25.71' W), along the western shores of Hudson Bay in Manitoba, Canada. Specifically the studies addressed foraging strategies during the breeding season.

The first paper examines the past two decades of lesser snow goose foraging data on the La Pérouse Bay marsh. The study addresses the issue of changes in snow goose foraging by, comparing the early years to the later years, in relation to La Pérouse Bay's degrading coastal habitat. Data were analyzed and evaluated with respect to environmental change.

The second paper is a comparative study of the foraging behavior of lesser snow and Ross's geese on the La Pérouse Bay intertidal salt marsh during the 1999 breeding season. Because Ross's geese have only started breeding on La Pérouse Bay within the past several years, little is known about their foraging behavior, and interaction with snow geese, on this habitat. Specifically, the relationship between foraging behavior and gosling condition was a key issue addressed. Direct observational methods were employed and data from banding drives analyzed.

The "General Discussion & Conclusions" section of the dissertation is followed by an annotated bibliography. It was included for the purpose of identifying variation in body size, potential differences in feeding habits and behavior between lesser snow geese

and Ross's geese, as well as calling attention to contradictory studies on which I will opine.

Feeding behavior of Arctic breeding geese. Theories of optimal foraging assume that animals have been shaped to behave in ways that will maximize their inclusive fitness, typically measured in terms of lifetime reproductive success. In terms of foraging this goal may be achieved by maximizing the net rate of energy intake while feeding (MacArthur and Pianka 1966, Schoener 1971). However for Arctic breeding geese such maximization does not come without constraints which must be considered when conducting research designed to evaluate foraging behavior.

Salt marsh vegetation on Arctic habitats tends to be low in protein content and high in fibre. Geese have simple digestive tracts, with rapid passage rates of food through the gut (Harwood 1974), and are not efficient at processing high fibre foods. Therefore, the rate at which they can process plant matter is limited. As a result they cannot compensate for low nutrient foods by increasing the quantity eaten (Sedinger et al. 1995). Instead, geese optimize energy intake with behavioral adaptations, searching for quality food. Strong selection pressures favor behaviorally flexible feeding strategies (Harwood 1974).

Geese are strictly herbivorous, feeding primarily on graminoid vegetation during the breeding season (Owen 1980). Arctic grasslands, however, are typically low in annual productivity due to the short growing season and unstable weather patterns. When geese arrive in spring the ground is still snow-covered and food is limited. In order to feed, geese must use different feeding strategies directly after arrival than during summer

(Abraham and Jefferies 1997). Additionally, during spring females initiate egg laying and incubation and can lose up to one-third of their body weight (Ankney and MacInnes 1978), subsequently necessitating maximization of nutrient uptake. For a species without a complex digestive system, such maximization must be achieved via flexible behavioral tactics.

The Lesser Snow Goose and La Pérouse Bay. For at least the past 50 years La Pérouse Bay has been a traditional breeding ground for lesser snow geese. Snow geese exhibit a tendency towards philopatric behavior (*sensu* Greenwood 1980), making long-term use of La Pérouse Bay. They choose mates on their wintering grounds, and because only the female is natively philopatric, the male returns to the feeding and nesting areas where his mate was reared as a gosling (Cooke et al. 1995, Cooke and Abraham 1980).

Behaviorally, philopatry can be a highly advantageous strategy. Familiarity with local resources and local habitat may increase efficiency at finding food and facilitate escape from predation. Levels of aggression may also be reduced as a consequence of familiarity with family and neighbors (Shields 1982). However, natal philopatry may become maladaptive when environmental conditions change. Rockwell et al. (1993) have shown declines in reproductive success of aging breeding females returning to their environmentally deteriorated natal colony and traditional feeding areas.

Over the past 20 years such a change has occurred to the intertidal salt marsh in La Pérouse Bay. Between 1979 and 1991 vegetation estimates of standing crop decreased from about 50 g m^{-2} to about 25 g m^{-2} (Williams et al. 1993). Currently, total plant cover is estimated at less than 2%, with the remaining intertidal area composed of

bare sediment (Jefferies and Rockwell 2002). The cause of this loss of vegetation is twofold: 1) an increase in the population of lesser snow geese in the region of La Pérouse Bay, from approximately 1,300 breeding pairs over two-square kilometers in 1968 (Cooke et al. 1995) to approximately 44,500 breeding pairs over 300-square kilometers in 1997 (Jefferies and Rockwell 2002), as well as an increase in the number of staging geese on route to more northerly nesting colonies, and 2) destructive foraging habits (Srivastava and Jefferies 1996, Kerbes et al. 1990).

The increase in numbers of geese on La Pérouse Bay is part of a general increase in the North American mid-continent population of lesser snow geese: approximately 7% annually as of the year 2000 (Jefferies and Rockwell 2002). Traditionally, snow geese wintered along coastal salt marshes on the Gulf Coasts. The amount of available forage limited their over-winter survival, maintaining their population at stable levels. Beginning in the 1940's these marshes were lost or degraded through increased commercial development. Snow geese responded by expanding their foraging areas to include rice prairies developed adjacent to coastal marshes. They then began wintering further north, feeding on corn, wheat and other cereal grains (Abraham et al. 1996). Finally the development of wildlife refuges, providing augmented food supplies and sanctuary from hunters, further expanded their winter ranges and improved migration staging areas. The combination of increased nutrient resources and protection from hunters increased their survival rate and reproductive success.

Destructive foraging -extensive grubbing, shoot pulling, and intense grazing – by increasing numbers of both La Pérouse Bay breeding geese and geese awaiting snowmelt of their nesting colony further north, has resulted in significant habitat destruction of La

Pérouse Bay's coastal habitat. When geese arrive in the spring they uproot, or "grub," for roots and rhizomes of graminoid plants. In fresh-water areas, they pull shoots of sedges, eating the basal portion and discarding the remainder. During the summer months geese graze the tips of plant stems (Abraham and Jefferies 1997). Such intensive foraging results in the loss of vegetation cover, exposure of surface sediments and increased soil salinity (Jefferies and Rockwell 2002). The increase in salinity levels then inhibits the growth and survival of plants (Srivastava and Jefferies 1996).

Given the degraded state of La Pérouse Bay's intertidal salt marsh, used primarily for feeding, a density-dependent decline in the snow goose population should have resulted. On the contrary, many snow geese began dispersing from this traditional intertidal feeding area to less degraded fresh water areas further inland, and northerly along the eastern coast (Cooke et al. 1995), possibly increasing adult survival (Francis et al. 1992). Goslings from dispersed broods were found to be structurally larger, heavier, and had higher first-year survival rates than goslings from broods that did not disperse (Cooch et al. 1993). Goslings remaining underwent an average 15% reduction in body mass, 2% reduction in tarsus length, and 4% reduction in culmen length (Cooch et al. 1991). Adult female lesser snow goose have undergone declines in body size, tarsus, and culmen of 13%, 6%, and 4% respectively (Cooch et al. 1991), and a decline in reproductive success (Cooch et al. 1989, Cooch et al. 2001, Francis et al. 1992, Williams et al. 1993).

Arrival of the Ross's Goose to La Pérouse Bay. Over the past several years there has been an increase in the number of breeding and nonbreeding Ross's geese on the

intertidal marsh. They had previously been observed on La Pérouse Bay, but only in small numbers and typically as broodless pairs or mated to snow geese (Didiuk et al. 2001).

Structurally, Ross's geese are smaller than snow geese: their average body mass is 67% that of snow geese, culmen an average 30% shorter, tarsus an average 17% shorter, and total body length an average 16% shorter. They too are primarily herbivorous, feeding on the same vegetation types as snow geese (Ryder and Alisauskas 1995). Pair formation in Ross's geese is thought to occur during winter. Their incubation behaviors similar to those of snow geese: males guard the nest while females incubate the clutch (Ryder and Alisauskas 1995). Their behavior in salt marshes during brood rearing, however, is unknown.

Why they have begun brood rearing on an already degraded habitat is unknown. Perhaps exploitation competition - wherein snow geese depressed the Ross's goose population through the use of shared resources - historically excluded Ross's from the marsh. Interference competition, the use of aggressive behaviors to limit other populations' access to a resource, may also have taken place (*sensu* Krapu et al. 1997). The presence of high numbers of the larger, potentially more threatening snow geese may have inhibited Ross's geese from using the marsh.

Grazing facilitation may be a factor as well. Ross's geese may benefit from grass already grazed by snow geese. It has been shown that nutritional quality of vegetation is enhanced by grazing, such that shorter swards of grass have higher nitrogen content (Cargill and Jefferies 1984, Riddington et al. 1997). Brent geese, for example, prefer to forage on vegetation previously grazed by barnacle geese (Stahl 2001). And, because

Ross's geese have a smaller bill morphology it is conceivable that they are better able graze on shorter blades of grass - grass already grazed by snow geese (Abraham and Jefferies 1997).

General Methodology. In order to conduct the first study I made use of un-analyzed behavioral data on brood rearing geese from 1980, 1984, 1985, and 1988 – 1990 (the “early” years). Although this data is property of the Hudson Bay Project, they were laboriously collected by former La Pérouse Bay researchers Chris Davies, Randy Seguin, and Maarten Loonen, whose permission was respectfully sought for their use and for whom co-authorship in the publication of the study will be granted. Data from 1998 – 2001, the “later” years, were collected by myself. Due to a scarcity of geese on the marsh in 2001, this year was not included in the analyses.

For the second study, I collected data on lesser snow geese and Ross's geese from 1998-2001, however only data from 1999 was used. In 1998, there was too few Ross's geese on the marsh, therefore behavioral data was insufficient to use in analyzes. In 2000, spring arrived late resulting in the lack of available nest sites. Consequently, most geese on La Pérouse Bay did not breed. Behavioral data on geese with broods, particularly Ross's geese, was not obtainable. And, in 2001, vegetation on the marsh was so scant that many geese moved inland and did not forage on the traditional feeding flats. Again, due to an insufficient amount of behavioral data collected, comparisons of the two species could not be made.

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CHAPTER 2

**THE FORAGING BEHAVIOR OF LESSER SNOW GEESE AT
LA PÉROUSE BAY: 1980 - 2000**

INTRODUCTION

The La Pérouse Bay intertidal salt marsh has been used almost exclusively as a brood rearing habitat by the mid-continent US population of lesser snow goose (*Chen caerulescens caerulescens*) for at least the past 50 years (Cooke et al. 1995). Females are natively philopatric, returning to the nesting area where they were reared as goslings, and are faithful to traditional feeding areas (Cooke et al. 1975, Cooke and Abraham 1980). From 1968 to 1997 the density of snow geese using La Pérouse Bay has increased from 1300 breeding pairs over two-square kilometers to an estimated 44,500 breeding pairs over 300-square kilometers, an annual geometric increase of approximately 7% (Cooke et al. 1995, Jefferies and Rockwell 2002). This colony is part of the Mid-continent Population which has increased at approximately 5% annually (Jefferies and Rockwell 2002). La Pérouse Bay is used as a staging area for geese from the Mid-continent Population nesting further north.

Over the past two decades the condition of the intertidal marsh in La Pérouse Bay has become degraded. As of 1999, total maximum standing crop was half of what it was from 1979 to 1986 (Jefferies and Rockwell 2002). The increase in the density of geese utilizing the marsh is not in and of itself the problem. The problem lies in the manner in which geese forage: digging up roots and rhizomes of graminoid plants in spring, and overgrazing the remainder in summer. The combined effect of increased numbers of

geese and their destructive foraging behaviors has virtually denuded this ecosystem of all vegetation.

Within the past several years many snow geese have dispersed from the traditional intertidal feeding area to freshwater areas inland and north along the eastern coast of La Pérouse Bay (Cooch 1993, Cooch et al. 2001). However, because salt-marsh vegetation is a preferred food source of geese especially during the early brood rearing period (Gadallah and Jefferies 1995), and snow goose females tend to be loyal to traditional nesting and feeding areas, some geese still nest and rear broods on La Pérouse Bay. The quality as well as quantity of vegetation is especially important during the breeding season. Females deplete their nutrient reserves during egg formation and incubation, and goslings must increase their body weight from about 80 grams to between 1500-1800 grams in approximately 7 weeks (Kerbes et al. 1990). As such, declines in vegetation quantity or quality may affect the physical condition of the geese (Cooch et al. 2001). Additionally, declines in food resources may lead to changes in the foraging strategies and/or foraging tactics of geese. For example, geese may spend more time searching for food and feeding (Sedinger and Raveling 1988, Sedinger et. al Raveling 1995) — a strategic change — or they may vary their uptake rates as fluctuations in vegetation arise — a tactical change (Madsen 1985, Owen 1992).

Given the continued increase in the snow goose population and the concomitant decrease in vegetation, the key issue to be addressed in this study is how the geese may have adjusted their foraging behaviors in response to a degrading salt marsh. Data on the behavior of lesser snow geese at La Pérouse Bay is available from 1980 – 2000, over which time vegetation on the intertidal salt marsh has become steadily degraded.

Differences in behavior between adult lesser snow goose males, females, and between goslings were examined to determine the extent to which behaviors may have changed coincident with changing environmental conditions.

METHODS

Behavioral data were collected during brood rearing in 1980, 1984, 1985, 1988 - 1990, and 1998 - 2000 from a 5-meter high observation tower on the coastal La Pérouse Bay intertidal feeding flats (58°43.29' N 93°25.71' W), located in Wapusk National Park (Figure 2.1). In all years observations were begun in either mid June or July and ended the second or third week of August. Observers entered the tower the evening before the start of observations to allow geese to begin undisturbed normal morning activities.

Observations were conducted during daylight hours beginning approximately between 0500 and 0700 hours, and ending between 2200 and 2400 hours. Observational hours were not consistent throughout the observation period due to unavoidable circumstances including inclement weather, polar bears, bald eagles, and human disturbance, all of which scared the birds out of viewing range.

Behavioral observations were made using standard focal animal protocols and focal animal sampling on randomly selected individual pairs of geese with and without broods, as well as lone geese (Altmann 1974, Gregoire and Ankney 1990, Williams et al. 1994, Mulder et al. 1995). For data collected in 1980, geese wearing tarsal bands were chosen whenever possible enabling identification of gender and age through banding records. Otherwise, identification of gender in adult geese was based on the presence or absence of a brood patch on females (for up to approximately 4 weeks post hatch), body size (males are typically larger than females), or brooding (goslings typically only sit

with, or under the wing of, the female). Because this study focused on adults with broods, families of one to five goslings only were included. Families of 6 goslings or more were omitted from the analyses since large family sizes usually indicate intraspecific nest parasitism and/or adoption which is not atypical of colonially breeding waterfowl (Lank et al. 1989a, Lank et al. 1989b, Williams 1994).

Geese were videotaped with a SONY Hi-8 Handycam (Optical Zoom 18x, Digital Zoom 72X) during the 1998-2000 field seasons from which forage and time-budget observations were analyzed. Observations in 1980 were conducted in real time. Given the difference in methodology between collecting data using a video camera and collecting data in real time, there was concern that results from the statistical analyses may not be valid. However, it was concluded that the only possible discrepancy would have been in data collected on pecking rates since these rates were recorded via slow-motion video. To determine if this was the case, a sample of videotaped pecking rates were recorded without slowing down the tape. Pecking rates taken using both methods were comparable, therefore it was concluded that the difference in methodology would not affect the conclusions. Demographic data (species, goose color, sex, brood size, band information), date, and time of day were recorded from the tower. Families may have been sampled more than once in scans and behavioral observations. Data may therefore not be strictly independent.

Gosling Morphometrics & Mass

Weights and measurements of banded gosling snow geese measured on La Pérouse Bay during all study years were utilized to evaluate annual changes in structural size and body mass of goslings using the intertidal marsh as a foraging habitat (see

Dzubin and Cooch 1992 for methods). Goslings may or may not have been part of the observations performed in this study, however these analyses were conducted simply to estimate changes that may have occurred over the 20-year period. Differences in structural measurements (tarsus bone, culmen 1) (Appendix A) and mass were evaluated with analyses of variance and pairwise contrasts with Bonferroni adjustments to avoid inflation of overall alpha error rate (Rice 1989). Analyses were performed with GLM procedure from SAS[®] 8.02 (SAS Institute 1999-2001).

Principal component analyses on head length (Appendix A), culmen 1 and tarsus bone are typically used to derive a single variable, the first principal component (PC1), to serve as an index of structural size (Cooch et al. 1991a, Cooch et al. 1999). The PC1 is used to evaluate changes in body condition over time. However, because of missing headlength measurements, the derivation could not be performed as PCA must be based on three or more variables (P. Flint, personal communication). Analyses on annual body condition were then attempted, scaling mass for structural size using tarsus bone and culmen length. However, preliminary covariance analyses indicated that the relation of mass to tarsus and mass to culmen varied over year. Neither tarsus nor culmen length, then, could be used as a covariate to adjust for annual differences in structural size in evaluating whether condition has changed over time.

Mean hatch dates for each year were estimated to determine if variation in hatch date could be accountable for differences in structural size or mass.

Any evaluation of annual changes in gosling size must address the fact that there are annual differences in the age of the goslings when measured. This annual age difference reflects the reality that while annual differences in hatch dates are a function of

annual differences in seasonal phenology, the dates birds are caught and measured are generally fixed by year-constant logistic schedules of aircraft and personnel. In the earlier days of the La Pérouse Bay project, precise ages of the goslings were known owing to a web-tagging program (Cooke et al. 1995). Using these known ages, annual variation in age could be simply controlled in statistical analyses. As the population grew, this approach became unmanageable and a surrogate method was sought. Cooch et al. (1999) showed that the length of the 9th primary (Appendix A) could be used as a surrogate for age. The logic underlying this approach was that demands for flight south led to growth of the primary flight feathers being a constant with respect to age, a constant invariant over years. They cautioned that this assumption could be constrained under environmental stress. As such, the reasonably robust but empirically derived relation between 9th primary and age could change and the use of 9th primary as a surrogate for age should be used cautiously.

Activity Budgets

Data on activity budgets were available for 1980 and 1998-2000. Observations were recorded to examine foraging behavior in relation to brood rearing season and sex. Behaviors of adults and goslings were recorded for up to 10 minutes at 5- or 10-second intervals during all study years, up to approximately 100 meters of the observation tower. In 1980, behavioral observations were conducted in real time, and from 1998-2000 behavioral observations were videotaped. Behavioral activities included: feeding, head-up and extreme head-up (Lazarus and Inglis 1978), swimming, walking, preening, stretching, bathing, drinking, sleeping, attack or threats to other geese, and social interactions (usually intrabrood) (Williams et al. 1994).

Activities were categorized as feeding (while walking and sitting), comfort (bathing, preening, stretching, resting, social), motor (swimming, running, walking while not feeding), agonistic (threats, attacks) and vigilant (head-up and extreme head-up) (Williams et al. 1994, see Appendix B for behavioral diagrams).

Evaluations of annual changes in behavior must address the fact that there are annual differences in the age of adults and goslings at the time observations were conducted, both of which may affect behavioral responses. The term “age” in the case of adults is simply being used to represent weeks from mean hatch, and the term “age” in the case of goslings is an approximate age (in weeks) based on mean hatch date. Because annual hatch dates varied across the study period, it was necessary to scale the ages of geese to adjust for differences in annual hatch dates. Based on an approximate two week hatch period (Cooke et al. 1995), and known date of first nest hatched, mean hatch dates were estimated and weekly age classes were assigned to geese based on observation date. Data for adults were summarized into a frequency distribution of behavioral activities (the response variable) cross-classified by year, sex, and age class (the classification variables). Data for goslings were summarized into a frequency distribution cross-classified by year and age class only since gender was not known. Behavioral activities were evaluated using log-linear models, a procedure sometimes referred to as Multidimensional Contingency analysis (Bishop et al. 1975). Loglinear models are important for the analysis of frequency data and are appropriate when there is no clear distinction between the response and explanatory variables, i.e. when all variables are observed simultaneously. The loglinear model point of view treats all variables as response variables, with the focus being on statistical independence and dependence. It is

analogous to correlation analysis for normally distributed response variables and is useful in assessing patterns of statistical dependence among subsets of variables (Stokes et al. 2000). Since the objective was to determine the dependency of the response variable on year, sex, and age class for adults, and year and age class for goslings, only second and higher order terms were included in the Results. The log-linear models used to determine dependency of the behavioral response variables on year, sex, and age class were generated using the CATMOD procedure from SAS[®] 8.02. Effects were evaluated statistically using the Wald statistic, and the log ratio of the unsaturated model chi-square was used to confirm the significance of the second and higher order terms (Stokes et al. 2000). To avoid inflation of overall alpha error rate, Bonferroni adjustments were made.

Foraging Behavior

Observations were conducted to examine finer details of foraging behavior. Foraging data on adults were available for 1985 and 1998-2000, and on goslings for 1984, 1985, 1988 - 1990, and 1998-2000. Data on foraging behavior for 1998-2000 were videotaped, whereas data for all other years were collected in real-time. Observations were conducted for up to 10 minutes, up to approximately 100 meters of the observation tower. An observation began when the individual assumed a head-down posture and took its first peck and ended either at the end of the observation period, if the bird went out of visual range, or if a disturbance occurred. Total observation time, number of steps taken while feeding (“feeding bout steps” = number of steps/total time feeding), and the number of pecks taken in 10 seconds were recorded.

As in activity budget analyses, age classes were assigned to geese to adjust for differences in annual mean hatch dates (see “Activity Budgets,” Methods section).

Pecking rates and feeding bout steps were then analyzed with the GLM procedure, using age class as a covariate to adjust for annual differences in age. Again Bonferroni adjustments were used to avoid inflation of overall alpha error rates.

RESULTS

Gosling Morphometrics & Mass

Preliminary analyses of gosling morphometric and mass data using 9th primary as a covariate to adjust for annual variation in gosling age revealed that for the 20-year time span examined here, the second order year \times 9th primary term was highly significant. This indicates that the relation of “morphometric and mass variables” to 9th primary length itself varies over year, thus precluding the use of 9th primary as a surrogate to adjust for age differences. The most likely biological explanation for the result is that the growth rate of 9th primary as a function of age has itself changed over the span of the study and that this most likely reflects on the habitat degradation demonstrated at La Pérouse Bay.

As a consequence, annual differences were evaluated without adjustment for annual variation. For both males and females, mass showed roughly steady declines from 1980 to 2000 (Figures 2.2 and 2.3). Culmen 1 (Tables 2.1 and 2.2), and tarsus bone (Tables 2.3 and 2.4) declined the greatest from year 1980 to year 2000, with measurements fluctuating between years 1984 and 1999. Methods to ascertain whether the declines in structural measurements and mass over time were related to a systematic decline in gosling age related to a systematic annual delay in nesting, annual mean hatch dates were evaluated using linear regressions (Figure 2.4). The non-significant regression is not consistent with such shift in nesting. It is more likely that the declines in size and

mass are related to the long-term decline in habitat condition (Jefferies and Rockwell 2002).

Activity Budgets

Adults

Due to missing age classes in years 1998 and 2000, only years 1980 and 1999 were used in the analyses. For these two years, behavioral data on age classes two to five were available. The fourth-order term of adults (year \times sex \times behavior \times age class) was significant indicating that behavioral patterns were dependent on a unique combination of year, sex, and age class. This is examined further in the full set of third-order models (sex \times behavior \times age class, year \times behavior \times age class, and sex \times year \times behavior). Third-order terms sex \times behavior \times age class, and year \times behavior \times age class were significant indicating that behavioral patterns were dependent on unique combinations of sex and age class, and year and age class. The third order-term sex \times year \times behavior was only significant for week two post hatching, indicating that behavioral patterns two weeks after the hatching of goslings was dependent on a unique combination of sex and year (Table 2.5).

Third-order analyses were examined further in the second-order models (behavior \times age class, behavior \times sex, and year \times behavior) and summarized in Table 2.6. Second-order term behavior \times age class was significant, indicating that time spent in behaviors varied with age class, however the only clear pattern was an increase in the percentage of time 1980s males fed from age class two to five (Table 2.8). Second-order term behavior \times sex was significant for ages two to four weeks in 1980, and for ages two and three weeks in 1999 indicating a significant difference in behavior pattern between males

and females during these weeks for each year. Across both years the percentage of time spent feeding by females was greater than that of males, while males spent twice as much time in vigilance behaviors than females (Tables 2.7 and 2.8). Such behavioral patterning is consistent with that of Arctic breeding geese and is not assumed to change through time (Lazarus and Inglis 1978, Lessells 1987, Sedinger and Raveling 1990). Comfort and motor activities varied with changes in the percentage of time feeding, but were generally low throughout all years. And, second-order term year \times behavior was significant for both females and males for age classes two to four only, indicating that the percentage of time spent in behaviors during these weeks differed across years (Tables 2.7 and 2.8).

Goslings

Because of missing age classes in years 1998 and 2000, only years 1980 and 1999 were used in analyses. For these two years behavioral data on age classes two to four were available. Data for goslings were cross-classified by year and age class. Despite the non-significant third-order Wald statistic, the difference in second-order analyses for 1980 and 1999 indicate that some aspect of the behavior or its dependence on age classes did change (Table 2.9). Second-order models behavior \times age class was significant for 1999 only, indicating that behavior during this year varied with age. Goslings fed more, engaged in comfort activities less and motor activities more at four weeks post hatch versus two weeks post hatch (Table 2.10), whereas percentage of time spent in behaviors in 1980 was fairly consistent from two to four weeks post hatch. Second-order model behavior \times year was significant for all age classes, indicating that the percentage of time spent in behaviors during these weeks differed across years. Overall goslings fed less in 1999 (85%) than in 1980 (97%) and spent more time in comfort (10%) and motor (5%)

activities in 1999 than in 1980 (2% and 0.07%). Vigilance behaviors in goslings across both years were negligible.

Foraging Behavior

Pecking Rate

Adults

Pecking rate was not dependent on unique combinations of year and age class for females ($P = 0.0937$) or males ($P = 0.5835$). Analyses were then conducted to evaluate between year differences and showed that pecking rates of females were faster in 1998, 1999 and 2000 than 1985 (Tables 2.11 and 2.12). Males' pecking rates did not differ between years (Tables 2.13 and 2.14).

Goslings

Pecking rate was dependent on unique combinations of year and age class (Tables 2.15 and 2.16). Overall, rates tended to increase in goslings of older age classes, which may reflect goslings approaching a rate close to their physical limit (Harwood 1974). Rates of 4-week old goslings were higher in 1999 and 2000 than in 1985 or 1988 (Figure 2.5), however due to missing age classes it cannot be concluded that significant increases in annual pecking rates have occurred.

Feeding Bout Steps

Adults

Feeding bout steps were found to depend on unique combinations of year and age class for females (Table 2.17). Results from preliminary analyses of variance evaluating feeding bout steps from 1998-2000 were not significantly different and were therefore pooled. Analyses of bout steps were then conducted classified by year, "old" 1985 and

“new” 1998-2000. Because of missing cells, bout steps were examined only for weeks two to six post hatch for all years. For all weeks post hatch, females walked more while feeding in years 1998, 1999, and 2000 than in 1985 (Table 2.18).

For males, feeding bout steps were not dependent on unique combinations of year and age class ($P = 0.4377$). Again, because results from the preliminary analyses showed no differences in steps for years 1998 - 2000, these years results were pooled. The pooled data indicate that males walked more during feeding in 1998, 1999, and 2000 than in 1985 (Table 2.19).

Goslings

Since preliminary analyses indicated that feeding bout steps did not depend on unique combinations of year with age class ($P = 0.06$), the analysis was then rerun without the second-order term. After Bonferroni adjustments were made, no significant differences were found in feeding bout steps across years.

DISCUSSION

The density of breeding pairs of lesser snow geese in La Pérouse Bay has increased 34-fold from 1968 - 1997 (Jefferies and Rockwell 2002, Cooke et al. 1995). Within the past two decades destructive foraging by increasing numbers of snow geese has resulted in considerable loss of graminoid vegetation on La Pérouse Bay (Jefferies and Rockwell 2002). Grubbing for roots and rhizomes in spring by staging geese, as well as the local population of breeding geese, has resulted in the destruction of salt-marsh swards (Srivastava and Jefferies 1996). In the absence of grubbing, intense grazing by geese is essential for the maintenance of primary production and species composition of plants (Kerbes et al. 1990). Grazing increases the quantity and quality of vegetation

allowing for further goose grazing, creating a positive feedback (Srivastava and Jefferies 1996). However, at high goose densities initial intense spring grubbing, followed by overgrazing in summer, causes a second, destructive, positive feedback, initiating a terrestrial trophic cascade destroying salt-marsh graminoids (Jefferies et al. 2002). As a result of such destructive foraging, food availability on La Pérouse Bay is now severely limited.

Food limitation has been attributed to reductions in both snow goose gosling structural measurements and body mass between 1980 and 2000. However, because mean hatch date in 2000, for example, was approximately 12 days later than mean hatch date in 1980, the change in measurements and mass could be attributed to the differences in age. This appears not to be the case. In 1984 goslings were approximately 33-36 days old when measurements were conducted, and in 1998 goslings were approximately 43 days old when measured. Yet, both male and female goslings in 1998 had smaller structural measurements and mass even though they were approximately 7-10 days older than 1984 goslings at the time measurements were taken. Culmen lengths of females declined by 7%, tarsus length declined by 3% and mass declined by 27%. These reductions in culmen, tarsus, and mass, correspond to annual geometric declines over this 14-year period (1984-1998) of approximately 1% ($\lambda = 0.987$), 0.5% ($\lambda = 0.994$), and 2% ($\lambda = 0.978$) respectively. Measurements of males, culmen, tarsus, and mass, declined by 5%, 4%, and 27% corresponding to annual geometric declines over 14 years of approximately 0.8% ($\lambda = 0.991$), 0.7% ($\lambda = 0.992$), and 5% ($\lambda = 0.947$) respectively.

The present study is not the first to record reductions in body size attributed to food limitation (Cooch et al. 1991a, Cooch et al. 1991b, Cooch et al. 1993, Cooch et al. 2001).

A long-term study by Cooch et al. (1991a) recorded declines in gosling mass (16%), culmen length (2%) and tarsus length (4%) between years 1976 and 1988. Additionally, in a comparative study on prefledged goslings feeding on non-traditional, well-vegetated sites, Cooch et al. (1993) showed that birds on the non-traditional areas had significantly higher survival rates than La Pérouse Bay birds. In a study evaluating changes in brood size of snow geese during the 1999 brood rearing period, survival of prefledged goslings on La Pérouse Bay was found to decline (see chapter 3, page 68). The two studies attribute the decline in gosling survival to the deteriorated conditions of the traditional La Pérouse Bay feeding area.

Coincident with and likely in response to reductions in available forage, the foraging behavior of snow geese has changed at La Pérouse Bay. The distribution of time spent in behavioral activities such as feeding and vigilance between adult males and females has remained constant throughout the years. However, changes have occurred in the allocation of time spent searching for food, and the rate at which geese feed. Both females and males spent more time searching for food in later years than earlier ones, as evidenced by the increased number of steps taken while feeding. Increases in search time have been associated with declining resources (Sedinger and Raveling 1988).

Additionally, females' rate of pecking increased by approximately 15% from 1984 and average 1998-2000. No change occurred in males' pecking rate. The sex-related difference in pecking rate is likely related to the breeding ecology of female and male geese. Females deplete nutrient reserves during egg formation and incubation, and can lose between 11% and 32% of their body mass (Ankney and MacInnes 1978, Lazarus and Inglis 1978, Aldrich and Raveling 1983, Ankney 1984, Thompson and Raveling

1987, Afton and Paulus 1992). Males do not share in incubation and do not incur such dramatic losses in weight (Ankney 1977). Because the brood rearing period of Arctic breeding geese is short, approximately 7 weeks, females have a greater amount of body mass to regain than males before the commencement of fall migration.

Increased pecking rates, leading to increased uptake rates, may be the means by which females are adapting their foraging behavior to degraded habitat conditions. Faster pecking rates may result in an increase in food taken per unit time (Owen 1992, Boysen et al. 2001). Owen et al. (1992) found that Barnacle geese (*Branta leucopsis*) tended to increase their pecking rate towards late in the day effectively lengthening their feeding day, and increased their peck rate as biomass decreased. Lazarus and Inglis (1978) have demonstrated that male Pink-footed geese may compensate for reductions in feeding by increasing their pecking rate. Lessells (1987) found that male snow geese increase their pecking rates to compensate for reductions in feeding resulting from more time spent in vigilance behaviors. Madsen (1985) found that when grazing on patchily distributed pasture vegetation, Pink-footed geese (*Anser brachyrhynchus*) also increased their pecking rate.

Although the overall mean percentage of time spent feeding by goslings decreased from 1980 (96%) to 1999 (87%), goslings at La Pérouse Bay appear to have responded to declines in food by increasing the percentage of time spent feeding as the brood rearing period progresses. At two weeks post hatch, goslings fed for 83% of the time, with this percentage steadily increasing to 88% by four weeks post hatch. In 1980, the percentage of time spent feeding by goslings was fairly consistent throughout the season, only increasing by approximately 7% from two to four weeks post hatch. In

light of reductions in available food, a common behavioral response has been to increase foraging time since rates of food intake are assumed to be lower (Sedinger and Raveling 1988, Sedinger et al. 1995). Coincident with declining food availability, the percentage spent feeding by Black Brant (*Branta bernicla nigricans*) on the Yukon-Kuskokwim Delta increased with date following hatch. Overall declines in the percentage of time feeding, however, may be the way in which La Pérouse Bay goslings are attempting to conserve energy in a habitat that offers inadequate amounts of available food. Feeding requires more energy than resting, so any increase in the amount of time spent feeding will increase daily energy requirements (Wooley and Owen 1978). The observed declines in structural size, mass, and survival have already demonstrated that if this is indeed a foraging strategy meant to cope to the deteriorating condition of the marsh, it is not working.

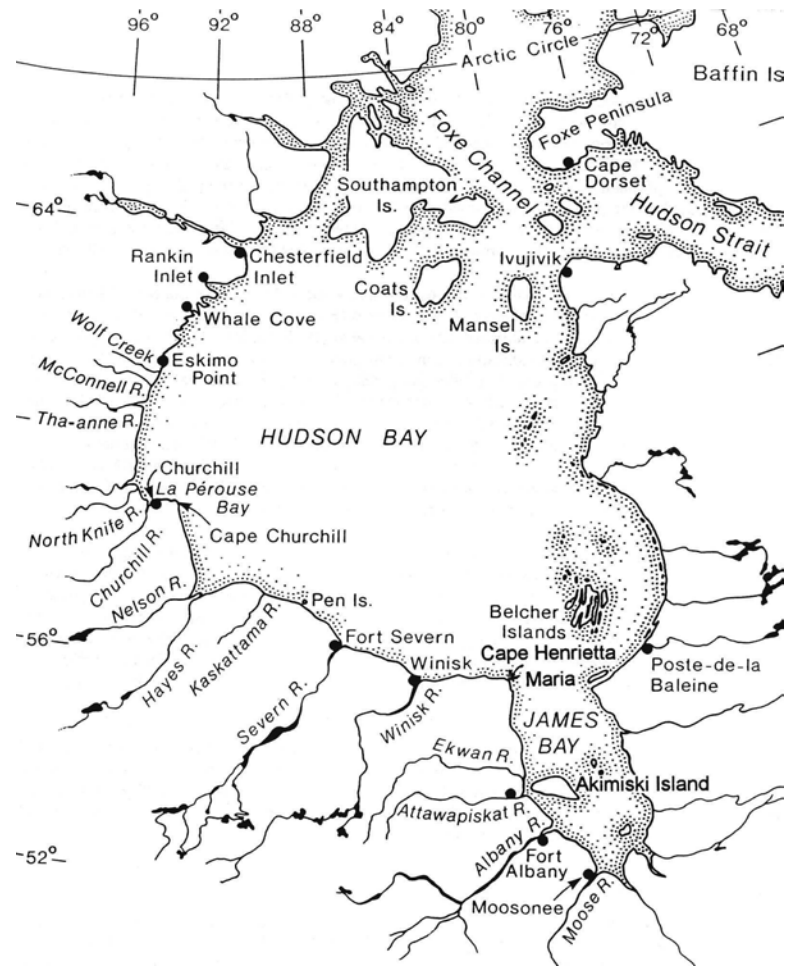
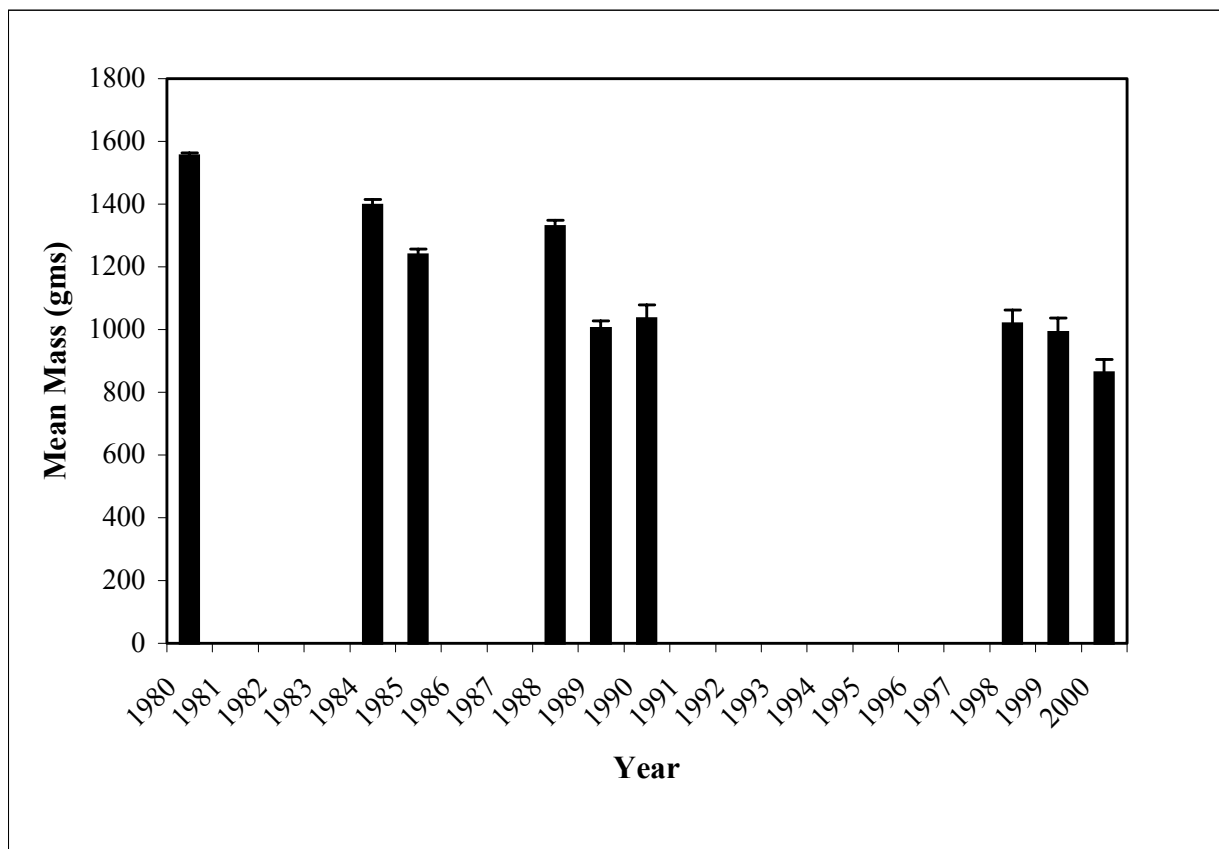


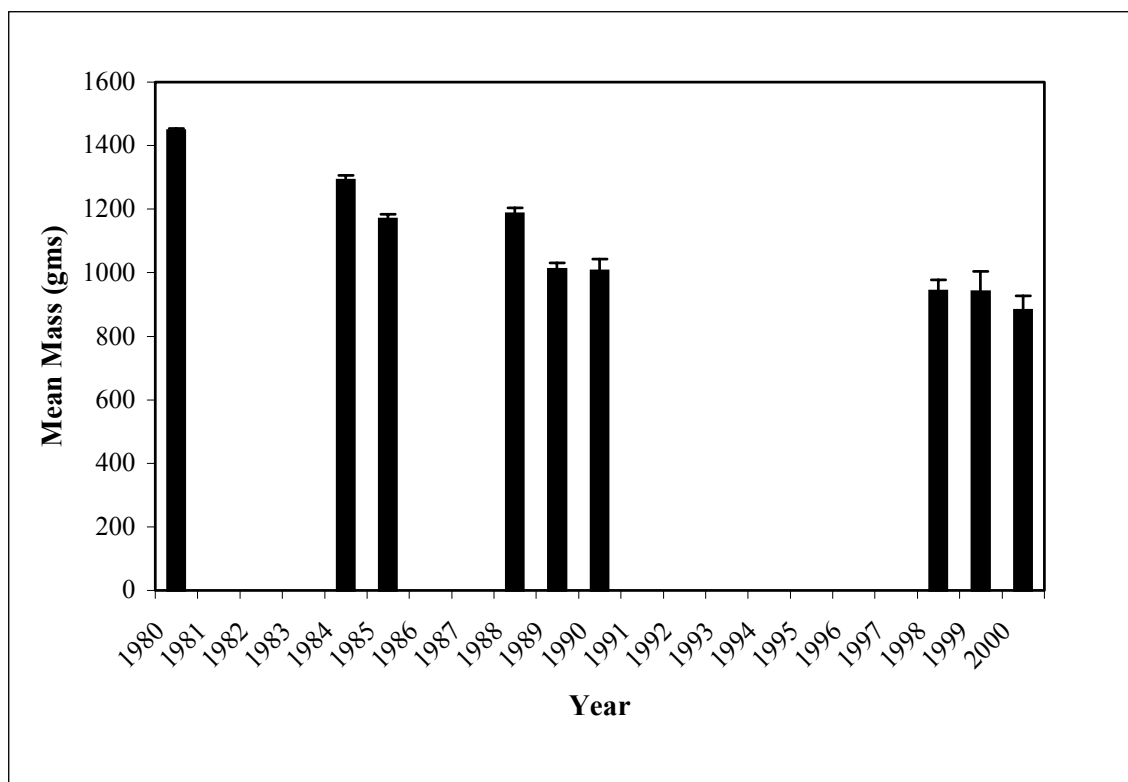
Figure 2.1. Map of the Hudson Bay Region, including La Pérouse Bay ($58^{\circ}43.29' N$ $93^{\circ}25.71' W$), located in Manitoba, Canada. From: Abraham, K.F., and R.L. Jefferies. 1997. High goose populations: Causes, impacts and implications. (pp. 7-72). In: B. Batt (ed.) *Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group*. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa and US Fish and Wildlife Service, Washington, D.C. (ISBN 0-9617279-3-4).

Figure 2.2. Declines in mass of lesser snow goose gosling males from 1980 – 2000 on La Pérouse Bay indicating a significant linear change over time.



Least square means of mass and + standard errors. ANOVA - $df = 8, 639$, $F = 132.39$, $P < 0.0001$.

Figure 2.3. Declines in mass of lesser snow goose gosling females from 1980 – 2000 on La Pérouse Bay indicating a significant linear change over time.



Least square means of mass and + standard errors. ANOVA - $df = 8, 761$, $F = 131.84$, $P < 0.0001$

Table 2.1. Analyses of variance of La Pérouse Bay lesser snow goose gosling culmen 1 across years 1980, 1984, 1985, 1988, 1989, 1990, 1998, 1999 and 2000. Culmen 1 declined the greatest from year 1980 to year 2000, with measurements fluctuating between years 1984 and 1999.

Source	df	MS	F	P
Females				
Year	8	275.16	50.41	<0.0001
Error	762	5.46		
Males				
Year	8	365.10	48.82	<0.0001
Error	640	7.48		

Table 2.2. Least square mean culmen 1 lengths and standard errors of La Pérouse Bay lesser snow goose goslings.

	1980	1984	1985	1988	1989	1990	1998	1999	2000
Females									
Mean (mm)	43	42	39	41	40	39	39	38	34
Stderr	0.11	0.24	0.25	0.29	0.33	0.58	0.58	1.04	0.73
Males									
Mean (mm)	44	43	39	42	40	40	41	40	32
Stderr	0.14	0.32	0.32	0.34	0.41	0.78	0.75	0.82	.75

Table 2.3. Analyses of variance of La Pérouse Bay lesser snow goose gosling tarsus bone lengths across years 1980, 1984, 1985, 1988, 1989, 1990, 1998, 1999 and 2000. Tarsus bone declined the greatest from year 1980 to year 2000, with measurements fluctuating between years 1984 and 1999.

Source	df	MS	F	P
Females				
Year	8	792.59	86.26	<0.0001
Error	762	9.19		
Males				
Year	8	994.82	75.14	<0.0001
Error	638	13.23		

Table 2.4. Least square mean tarsus bone lengths and standard errors of La Pérouse Bay lesser snow goose goslings.

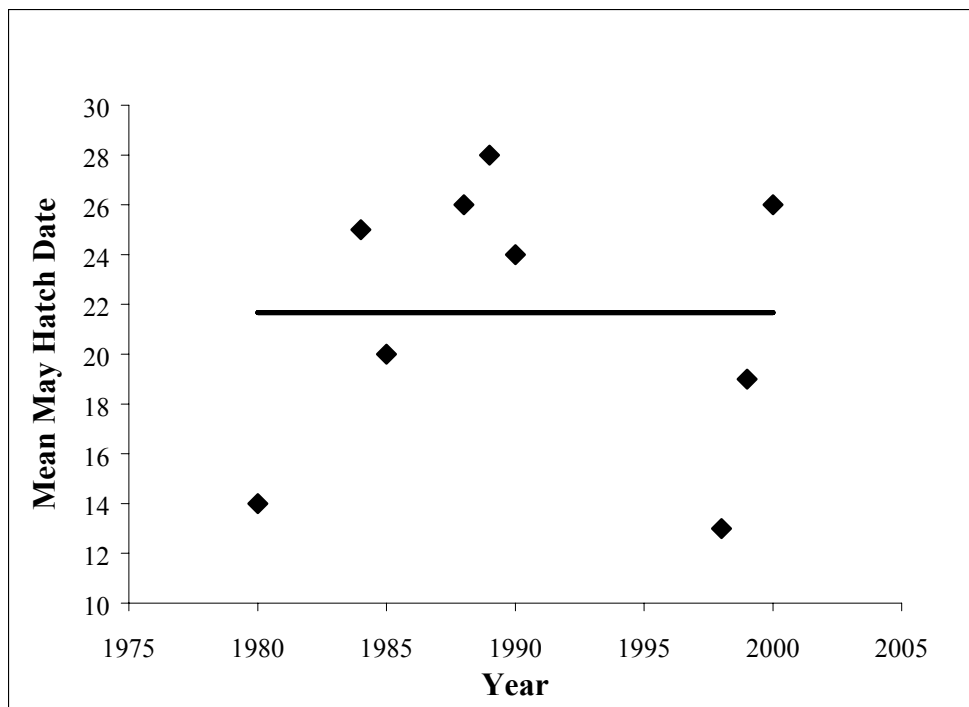
	1980	1984	1985	1988	1989	1990	1998	1999	2000
Females									
Mean (mm)	79	75	72	77	75	73	73	72	69
Stderr	0.14	0.32	0.33	0.38	0.42	0.75	0.75	1.35	.95
Males									
Mean (mm)	83	79	75	81	76	77	76	77	69
Stderr	0.19	0.42	0.43	0.46	0.55	1.05	1.05	1.09	1.00

Table 2.5. Results of log-linear modeling of activity budget data for La Pérouse Bay lesser snow goose adults. The fourth-order term was significant indicating that behavioral patterns were dependent on a unique combination of year, sex, and age class, and third-order terms sex \times behavior \times age class, and year \times behavior \times age class were significant indicating that behavioral patterns were dependent on unique combinations of sex and age class, and year and age class. The third order-term sex \times year \times behavior was only significant for week two post hatching, indicating that behavioral patterns two weeks after the hatching of goslings was dependent on a unique combination of sex and year.

Model	Source	df	Wald Statistic	P
<u>Fourth-order</u>	year \times sex \times beh \times age class	7	33.06	<0.0001
<u>Third-order</u>				
1980	sex \times beh \times age class	7	39.01	<0.0001
1999	sex \times beh \times age class	9	34.04	<0.0001
Females	year \times beh \times age class	7	33.51	<0.0001
Males	year \times beh \times age class	7	27.79	0.0002
Age: 2 weeks	sex \times year \times beh	2	22.03	<0.0001
3 weeks	sex \times year \times beh	3	6.33	0.0968
4 weeks	sex \times year \times beh	3	10.49	0.0148*
5 weeks	sex \times year \times beh	2	2.41	0.3000

*Not significant after Bonferroni adjustment $.05/4 = 0.0125$

Figure 2.4. Graph of hatch dates showing that declines in structural measurements and mass of snow goose goslings were not due to variation in mean hatch dates across years.



Linear regression analysis of annual mean hatch date of lesser snow goose goslings on year at La Pérouse Bay.

Table 2.6. Results of log-linear modeling of activity budget data for La Pérouse Bay lesser snow goose adults. Second-order term behavior \times age class was significant, indicating that time spent in behaviors varied with age class. 1980s males fed more 2-5 weeks post hatch. Second-order term behavior \times sex was significant for ages 2-5 weeks in 1980, and for ages 2 and 3 weeks in 1999 indicating a significant difference in behavior pattern between males and females. Females fed longer than males, and males spent were twice as vigilant as females. Second-order term year \times behavior as significant for both females and males for age classes 2-4 only, indicating that the percentage of time spent in behaviors during these weeks differed across years.

Model	Source	df	Wald Statistic	P
<u>Second-order</u>				
1980 Females	beh \times age class	7	18.89	0.0085
1980 Males	beh \times age class	7	96.63	<0.0001
1999 Females	beh \times age class	9	39.46	<0.0001
1999 Males	beh \times age class	9	23.06	0.0061
1980 2 Weeks	beh \times sex	2	134.42	<0.0001
1980 3 Weeks	beh \times sex	3	112.95	<0.0001
1980 4 Weeks	beh \times sex	3	80.71	<0.0001
1980 5 Weeks	beh \times sex	2	2.24	0.3266
1999 2 Weeks	beh \times sex	3	29.15	<0.0001
1999 3 Weeks	beh \times sex	3	22.10	<0.0001
1999 4 Weeks	beh \times sex	3	4.51	0.2112
1999 5 Weeks	beh \times sex	3	4.38	0.2229
Females Week 2	year \times beh	2	19.54	<0.0001
Females Week 3	year \times beh	3	28.18	<0.0001
Females Week 4	year \times beh	3	32.60	<0.0001
Females Week 5	year \times beh	2	1.33	0.5139
Males Week 2	year \times beh	2	31.36	<0.0001
Males Week 3	year \times beh	3	21.57	<0.0001
Males Week 4	year \times beh	3	56.81	<0.0001
Males Week 5	year \times beh	2	5.27	0.0717

Table 2.7. Percentage of time spent in behavioral activities by La Pérouse Bay female lesser snow geese by age class.

	Age Class							
	2		3		4		5	
	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>
Comfort	7.0	.40	5.8	2.2	4.6	6.5	7.0	3.6
Feeding	82.6	87.3	84.6	90.7	86.1	72.8	81.2	77.3
Motor	0.0	4.4	0.1	3.3	0.1	10.3	0.0	8.2
Vigilant	10.4	8.0	9.5	3.8	9.3	10.3	11.8	10.9

Table 2.8. Percentage of time spent in behavioral activities by La Pérouse Bay male lesser snow geese by age class.

	Age Class							
	2		3		4		5	
	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>
Comfort	5.0	7.1	4.7	3.5	2.4	2.4	6.1	4.4
Feeding	68.7	74.0	73.4	70.3	78.8	76.9	79.9	65.5
Motor	0.0	5.1	0.1	4.1	0.5	8.7	0.0	9.7
Vigilant	26.3	13.8	21.9	22.1	18.2	12.0	14.0	20.3

Table 2.9. Results of log-linear modeling of the cross-classified activity budget data for La Pérouse Bay lesser snow goose goslings. Second-order models behavior \times age class was significant for 1999 only, indicating that behavior during this year varied with age. Goslings fed more, engaged in comfort activities less and motor activities more at four weeks post hatch versus two weeks post hatch, whereas percentage of time spent in behaviors in 1980 was fairly consistent from two to four weeks post hatch. Second-order model behavior \times year was significant for all age classes, indicating that the percentage of time spent in behaviors during these weeks differed across years. Goslings fed less in 1999 (85%) than in 1980 (97%) and spent more time in comfort (10%) and motor (5%) activities in 1999 than in 1980 (2% and 0.07%). Vigilance behaviors in goslings across both years were negligible.

Model	Source	df	Wald Statistic	P
<u>Third-order</u>	year \times beh \times age class	3	2.22	0.5280
<u>Second-order</u>				
1980	beh \times age class	4	5.92	0.2053
1999	beh \times age class	5	15.13	0.0098
2 Weeks Old	beh \times year	2	130.95	<0.0001
3 Weeks Old	beh \times year	2	150.77	<0.0001
4 Weeks Old	beh \times year	2	44.87	<0.0001

Table 2.10. Percentage of time spent in behavioral activities by La Pérouse Bay lesser snow goose goslings by age class.

	Age Class					
	2		3		4	
	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>	<u>1980</u>	<u>1999</u>
Comfort	2.1	12.3	1.7	11.0	1.3	6.2
Feeding	96.3	82.7	96.7	85.5	97.4	88.2
Motor	0.0	4.9	0.2	3.5	0.0	5.4
Vigilant	1.7	0.1	1.3	0.0	1.3	0.2

Table 2.11. Analysis of variance of pecking rates between La Pérouse Bay adult female lesser snow geese across years 1985, 1998, 1999 and 2000. Females pecked faster in 1998, 1999 and 2000 than 1985.

Source	df	MS	F	P
Year	11	243.52	15.12	<0.0001
Error	360	16.10		

Table 2.12. Least square mean La Pérouse Bay adult female lesser snow goose pecking rates and standard errors in 1985, and 1998 - 2000.

	Mean	Stderr
1985	28	0.45
1998	33	0.81
1999	32	0.73
2000	34	0.80

Table 2.13. Analysis of variance of pecking rates between La Pérouse Bay adult male lesser snow geese across 1985, 1998, 1999 and 2000. No difference occurred in male pecking rates across years.

Source	df	MS	F	P
Year	10	37.72	1.71	0.0823
Error	148	22.00		

Table 2.14. Least square mean La Pérouse Bay adult male lesser snow goose pecking rates and standard errors in 1985, 1998 - 2000.

	Mean	Stderr
1985	28	1.21
1998	33	1.15
1999	32	0.89
2000	32	1.08

Table 2.15. Analysis of variance of pecking rates between La Pérouse Bay lesser snow goose goslings in 1985, 1988, 1999 and 2000. Pecking rate was dependent on unique combinations of year and age class. Overall, rates tended to increase in goslings of older age classes.

Source	df	MS	F	P
Year	20	325.59	21.06	<0.0001
Error	390	15.45		

Table 2.16. Least square mean pecking rates and standard errors for four week old La Pérouse Bay lesser snow goose goslings in 1985, 1988, 1999 and 2000.

	Mean	Stderr
1985	26	2.14
1988	21	1.23
1999	34	1.23
2000	33	1.43

Figure 2.5. Graph of pecking rates (least square means and standard errors) of La Pérouse Bay snow goose goslings during week four post hatch showing that pecking rates were higher in 1999 and 2000 versus 1985 and 1988.

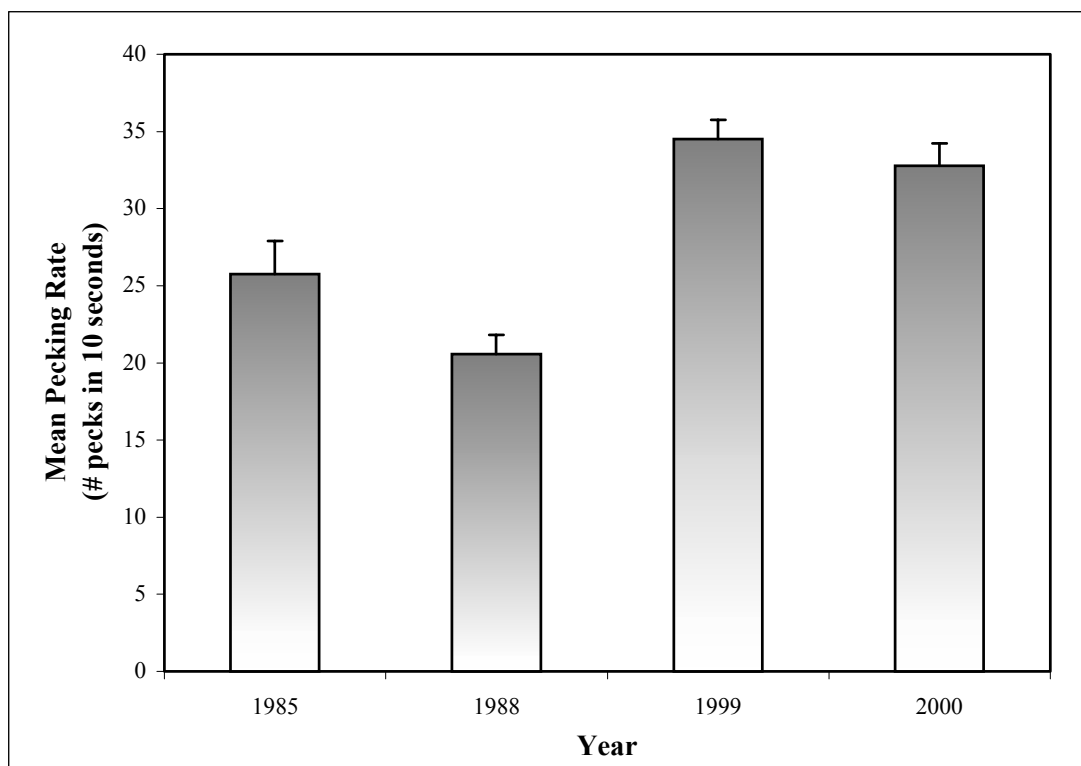


Table 2.17. Analysis of variance of feeding bout steps between La Pérouse Bay adult female lesser snow geese across 1985, and 1998 - 2000. Females walked more while feeding in years 1998, 1999, and 2000 than in 1985.

Source	df	MS	F	P
Year	20	510.25	12.76	<0.0001
Error	364			

Table 2.18. Comparison of feeding bout steps of La Pérouse Bay lesser snow goose females in 1985 to 1998-2000 (pooled) at 2, 3, 4, 5 and 6 weeks post hatch. For all weeks post hatch, females walked more while feeding in years 1998, 1999, and 2000 than in 1985.

Source	df	MS	F	P
Week 2				
Year Class	1	2785.89	97.23	<0.0001
Error	121	28.65		
Week 3				
Year Class	1	403.08	10.59	0.0017
Error	72	38.08		
Week 4				
Year Class	1	344.52	14.04	0.0004
Error	58	24.54		
Week 5				
Year Class	1	188.05	6.74	0.0248
Error	11	27.88		
Week 6				
Year Class	1	407.75	13.96	0.0022
Error	14	29.20		

Table 2.19. Analysis of variance of feeding bout steps between La Pérouse Bay adult male lesser snow geese across 1985 (“old”), and 1998 - 2000 (pooled-“new”). Males walked more during feeding in 1998, 1999, and 2000 than in 1985.

Source	df	MS	F	P
Year Class	5	204.57	5.87	<0.0001
Error	95	34.86		

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CHAPTER 3

THE FORAGING BEHAVIOR OF LESSER SNOW GEESE AND ROSS'S GEESE SHARING A DEGRADED HABITAT

INTRODUCTION

Destructive foraging behaviors by increasing numbers of lesser snow geese (*Chen caerulescens caerulescens*) on the intertidal La Pérouse Bay salt marsh have resulted in significant habitat destruction. When geese arrive in the spring they uproot roots and rhizomes of graminoid plants. In fresh-water areas, they pull shoots of sedges, eating the basal portion and discarding the remainder. During the summer months snowmelt occurs and geese graze the tips of plant stems (Abraham and Jefferies 1997). Such intensive foraging results in the loss of vegetation cover, exposure of surface sediments and increased soil salinity (Jefferies and Rockwell 2002). The increase in salinity levels then inhibits the growth and survival of plants (Srivastava and Jefferies 1996). As of 1999, extensive foraging had left less than 2% plant cover on the La Pérouse Bay intertidal salt marsh, with the remaining area consisting of bare sediment (Jefferies and Rockwell 2002).

Changes in the quality and quantity of vegetation during the breeding season can severely impact goslings' well-being. In approximately seven weeks they must increase their body weight from about 80 grams at hatch to between 1500 and 1800 grams to commence autumn migration. Decreases in food availability may lead to decreases in their structural size and weaker physical condition, increasing their susceptibility to parasites and to predation (Lazarus & Inglis 1978). Reductions in structural size and

reproductive success of snow geese breeding on La Pérouse Bay have already been documented and have been attributed to declines in biomass of preferred vegetation (Cooch et al. 1991a, Cooch et al. 1991b, Cooch et al. 2001).

For about the past 50 years, La Pérouse Bay has been used almost exclusively by lesser snow geese as a breeding habitat (Cooke et al. 1995). Recently there has been an increase in the population of breeding Ross's geese at La Pérouse Bay (Pezzanite, personal observation), an approximate four to one ratio of snow goose broods to Ross's goose broods. Although Ross's geese have been observed on the intertidal feeding flats on La Pérouse Bay in small numbers and as broodless pairs, breeding Ross's had rarely been recorded there before (Didiuk et al. 2001). And, although several Ross's goose nests have been found interspersed with snow goose nests, the location of their primary nesting area on La Pérouse Bay is unknown (Rockwell, personal communication). Given the declining condition of the marsh, and known historical reductions in snow goose growth and reproductive success of breeding snow geese on La Pérouse Bay, an important proximate question is how Ross's geese fare in relation to and in potential competition with snow geese.

The study presented here examines this by comparing the behavior of snow and Ross's geese using the degraded intertidal salt marsh in La Pérouse Bay. Variation in time-budget activities, foraging behavior, and patterns of marsh use between sexes, and within and between species, were examined in relation to changes in behavior over the course of the brood rearing period and changes in behavior related to weather conditions. Changes in brood size were analyzed, and gosling condition assessed.

METHODS

Observations were conducted on lesser snow geese and Ross's geese during the brood rearing period from June 14, 1999 - August 17, 1999, from a five-meter high observation tower on the coastal La Pérouse Bay intertidal salt marsh (58°43.29' N 93°25.71' W), approximately 1.5 km ENE of the Hudson Bay Project Research Station located in Wapusk National Park. An assistant and myself entered the tower the evening before the start of observations to allow geese to begin undisturbed normal morning activities, and remained there for approximately 1.5 consecutive days. The first day of observations began at 0500 hours and ended at 2200 hours. The second day began at 0500 hours and ended at approximately 1200 hours. Observational hours were not consistent throughout the observation period due to unavoidable circumstances including inclement weather, the presence of polar bears, bald eagles, and human disturbance, all of which scared the birds out of viewing range.

Behavioral observations were made using standard focal animal protocols and focal animal sampling on randomly selected individual pairs of geese with and without broods, as well as on lone geese (Altmann 1974, Gregoire and Ankney 1990, Williams et al. 1994, Mulder et al. 1995). This study focused on adults with broods. Therefore, families of one to five goslings only were included. Families of six goslings or more were omitted from the analyses since large family sizes may indicate intraspecific nest parasitism and/or adoption not atypical of colonially breeding waterfowl (Lank et al. 1989a, Lank et al. 1989b, Williams 1994). Because families may have been sampled more than once in scans and behavioral observations data may not be strictly independent.

Identification of gender in adult geese was based on the presence or absence of a brood patch on females (for up to approximately 4 weeks post hatch), body size (males are typically larger), or brooding (goslings typically only sit with, or under the wing of the female). Geese were videotaped with a SONY Hi-8 Handycam (Optical Zoom 18x, Digital Zoom 72X), from which forage and activity-budget observations were conducted.

Weather data were obtained from a Davis Instruments Corp. Industrial GroWeather Station, mounted 1.75 m above ground and located 100 m west of the Hudson Bay Project Research Station. Weather conditions were recorded at one-minute intervals, 24 hours, seven days a week. Principal Component analyses were conducted on air temperature, solar radiation, soil temperature, barometric pressure, and humidity to reduce potentially correlated weather variables to several independent weather indices (PC1-PC5) using the PRINCOMP procedure from SAS[®] 8.02 (SAS Institute 1999-2001). PC1 accounted for 52% of the variability in the data and were thus used as a “weather index” in correlation analyses to determine if the behavior of geese is affected by variation in weather conditions.

Loadings on this weather index for air temperature, solar radiation, and soil temperature were positive whereas barometric pressure and humidity were negative and equivalent in magnitude, but opposite in sign, to air and soil temperature (Table 3.1). For example, when air temperature is 26.1° C, with a relative humidity of 32.5%, the associated weather index is 4.62. When air temperature is -0.3 and relative humidity is 97.5%, the associated weather index is -3.24. Thus, hot/dry weather is associated with high weather index, and cold/damp weather with low weather indices.

Brood Size

Demographic data (species, goose color, sex, brood size, band information), date, time of day, and weather, were recorded on lesser snow geese and Ross's geese, both adults and goslings. Data were recorded within 100 meters of the observation tower using binoculars, and beyond 100 meters using spotting scopes. This procedure was conducted to obtain detailed information on family structure.

Daily mean brood size was first calculated for each species on June 18, June 24, June 28, July 2, July 9, July 14, and July 18, 1999. Only days with observations beginning between 0500-0600 hours and ending between 2000-2100 hours were included. Analyses were first run to determine interspecific differences in brood size using the GLM procedure from SAS[®] 8.02. Analyses were then conducted to determine changes in brood size throughout the brood rearing period by regressing mean brood size on date using the GLM procedure from SAS[®] 8.02.

Gosling Condition

Weights and measurements of banded gosling snow and Ross's geese were taken from banding data recorded on July 23, 1999, at La Pérouse Bay (see Dzubin and Cooch 1992 for methods). Goslings may or may not have been part of observations conducted for this study, however these analyses were conducted simply to estimate the general physical condition of goslings using the intertidal marsh as a foraging habitat. All measurements and weights were conducted by A. Dzubin, waterfowl biologist formerly of the Canadian Fish and Wildlife Service.

Principal component analyses were used to combine gosling measurements (culmen 1, head length, and tarsus bone) to extract a single derived variable, the first

principal component (PC1). PC1 explains most of the variance for highly correlated variables and is commonly used as an index of structural body size (Ricklefs and Travis 1980, Cooch et al. 1991a, Cooch et al. 1999). Because gosling age was unknown, 9th primary length, previously found to be a surrogate for true age, was substituted as a measure of age and used as a covariate in regression analyses (Cooch et al. 1999). To evaluate body condition, mass was then regressed on 9th primary and “structural size index.”

However, evaluations of within-season changes in gosling size must address the fact that there are differences in the age of the goslings when measured. As such, Cooch et al. (1999) showed that the length of the 9th primary could be used as a surrogate for age. The logic underlying this approach was that demands for flight south led to growth of the primary flight feathers being a constant with respect to age, a constant invariant over years. They cautioned that this assumption could be constrained under environmental stress. As such, the reasonably robust but empirically derived relation between 9th primary and age could change and the use of 9th primary as a surrogate for age should be used cautiously. Additionally, growth of 9th primary may vary depending on differential responses of individual species to environmental conditions.

Environmentally stressing conditions may also affect the body structure of species differentially. Thus, to eliminate the possibility that these covariates were confounding the results, analyses were rerun regressing mass on structural size index only, mass on 9th primary only, and mass with no covariates.

Vegetation Cover

Food availability and food change, also a measure of grazing intensity, were estimated throughout the season. One meter by one meter vegetation plots made of chicken wire and garden netting were set up on the study site before the geese arrived. Twelve exclosed plots and 12 unexclosed, control, plots were erected. Plots were situated so that vegetation in each plot was as homogeneous as possible and consisted of the preferred food of lesser snow geese, *Puccinellia phytanodes* and *Carex subspathacea* (Gadallah and Jefferies 1995). Turves of 10 cm × 10 cm were sampled from plots on June 8, June 19, July 3, July 15, July 27, and August 5, 1999. They were then returned to camp, trimmed to 7.5 cm × 7.5 cm, cut at soil or moss level, washed to remove soil remnants, collected on aquarium nets, dried to constant mass and weighed (Jefferies and Abraham, unpublished).

Means were calculated for exclosed and unexclosed plots, and vegetation cover (dry weight of above-ground biomass, g m⁻²) was regressed on date to determine changes in biomass quantity.

Marsh Use

To evaluate temporal patterns of marsh use, counts were taken of both adult and gosling snow geese and Ross's geese within 100 m of the tower on June 14, June 18, June 24, June 28, July 2, July 9, July 14, and July 18. Statistical analyses were run only on adults under the assumption that family groups feed in unison (Sedinger et al. 1995), such that goslings display the same marsh use pattern as their parents. Time of day was categorized into four time blocks: 0500 hrs - 0900 hrs, 1000 hrs -1400 hrs, 1500 hrs - 1800 hrs, 1900 hrs -2200 hrs. Because the first two time blocks were longer, and because

of missing within-day observational hours, time blocks within a given day had to be standardized. The number of adults was divided by the longest time block (i.e. 0500-0900 = 5 hours), then multiplied by the number of hours constant across time blocks.

Data for adults were summarized into a frequency distribution of the numbers of adults within 100 m of the tower (the response variable) cross-classified by time class, date, and species (the classification variables). Marsh use patterns were evaluated using log-linear models, a procedure sometimes referred to as Multidimensional Contingency analysis (Bishop et al. 1975). The dependency of the response variable on time class, date and species was generated using the CATMOD procedure from SAS[®] 8.02. Effects were evaluated statistically using the Wald statistic, and the log ratio of the unsaturated model chi-square was used to confirm the significance of the second and higher order terms (Stokes et al. 2000). Homogeneity analyses were performed on lesser snow geese and Ross's geese to examine if diurnal marsh use patterns were uniform across time blocks (Zar 1999). To avoid inflation of overall alpha error rate, Bonferroni adjustments were made.

Activity Budgets

Activity budgets were recorded to test for differences in foraging behavior in relation to brood rearing period, species and sex. Behaviors of adults and goslings were videotaped for up to 10 minutes at 10-second intervals, up to approximately 100 meters of the observation tower. Video recordings were then transferred to VHS tapes and behaviors were observed with the use of a stopwatch. Behavioral activities included: feeding, head-up and extreme head-up (Lazarus and Inglis 1978), swimming, walking,

preening, stretching, bathing, drinking, resting, and attack or threats to other geese (Williams et al. 1994).

Data for adults were summarized into a frequency distribution of behavioral activities (the response variable) cross-classified by sex and species (the classification variables). Data for goslings were summarized into a frequency distribution cross-classified by species only since gender was not known. Behavioral activities were evaluated using log-linear models. Activities were categorized as feeding (while walking and sitting), comfort (bathing, preening, stretching, resting, social), motor (running, swimming, walking and not feeding), agonistic (threats, attacks) and vigilant (head-up and extreme head-up) (Williams et al. 1994). Agonistic encounters were not common during brood rearing and so were not analyzed. Because the objective was to determine the dependency of the response variable on sex and species only second and higher order terms were included in the Results. The log-linear models used to determine dependency of the behavioral response variables on species and sex were generated using the CATMOD procedure. Effects were evaluated statistically using the Wald statistic, and the log ratio of the unsaturated model chi-square was used to confirm the significance of the second and higher order terms (Stokes et al. 2000).

The proportion of time spent in behavioral activities may change as days from hatch progress due to a variety of factors (growth of goslings, females regaining weight lost during laying and incubation, changes in daily weather conditions). Therefore, to determine if each species' behavior changed differentially over the course of the brood rearing period, or due to daily fluctuations in weather, correlation analyses on time budget behavioral variables (feeding, vigilant, comfort, motor) with date (i.e. the brood

rearing period) and weather (as represented by PC1) were conducted using the CORR procedure from SAS[®] 8.02.

Foraging Behavior

Forage observations were conducted to examine finer details of foraging behavior. Feeding was videotaped up to a maximum of five minutes, up to approximately 100 meters of the observation tower. An observation began when the individual assumed a head-down posture and took its first peck and ended either at the end of the five-minute period, if the bird went out of visual range, or if a disturbance occurred. Total observation time, number of steps taken during a feeding bout, and the number of pecks taken in 10 seconds were recorded.

Pecking rates were evaluated to determine differences in uptake rates, and steps taken during a foraging bout (as an indicator of patch size) were evaluated to determine differences in patch size between snow geese and Ross's geese. Because of differences in tarsal length between the two species, it was first necessary to scale tarsus length to adjust the number of steps taken. An average total tarsus measurement for male and female snow and Ross's geese was calculated using banding data from La Pérouse Bay. The number of feeding bout steps taken during feeding was multiplied by an arbitrary tarsal length of 90mm, then divided by the tarsal mean of that species and sex. Scaled steps were then divided by total time spent feeding. Both pecking rates and scaled feeding bout steps were evaluated using the GLM procedure. The gender of goslings was now known therefore pecking rate analyses were pooled. Analyses of goslings' steps were not performed because gosling ages were unknown and, it follows, would introduce a wide range of tarsal lengths. In addition, because families tend to travel in unison

(Sedinger et al. 1995), goslings forage the same patch area as their parents. Therefore the feeding area used by goslings would nevertheless reflect the area covered by adults.

Pecking rates and scaled steps may vary over the season due to gosling growth, changes in the seasonal phenology of plants, or daily weather fluctuations. Therefore, correlations were performed to examine any potential relationship between pecking rates and scaled feeding bout steps with date and fluctuations in the weather index.

RESULTS

Brood Size

Results from analyses of variance evaluating differences in brood size showed that at the beginning of the brood rearing period (approximately June 24th), brood sizes of snow geese and Ross's geese did not differ ($P = 0.6467$). However, as of June 28th, continuing through July 18th, Ross's goose broods were significantly larger than snow goose broods (Table 3.2). Least square means indicated a steady decline in snow goose goslings as brood rearing progressed.

Significant results from regression analyses on changes in brood size over the course of the brood rearing period confirmed that snow goose brood size declined throughout brood rearing period. No change occurred in Ross's goose brood size (Table 3.3, Figure 3.1).

Gosling Condition

PC1 explained most of the variance for highly correlated variables and was used as an index of structural body size. PC1 accounted for 96% and 83% of the variance for female snow goose and Ross's goose goslings, and 77% and 65% for male snow goose and Ross's goose goslings. The measurements contributed positively with loadings for

female snow geese and Ross's geese of 0.58 and 0.60 for head length, 0.59 and 0.54 for culmen 1, and 0.57 and 0.59 for tarsus bone. For male snow geese and Ross's geese, PC1 loadings were 0.61 and 0.66 for head length, 0.62 and 0.42 for culmen 1, and 0.50 and 0.62 for tarsus bone.

Interspecific variation in body condition was assessed first by analyzing mass corrected for structural size (structural size index) and age (9th primary) by using structural size and age as covariates. Results from this regression showed no differences in body condition between female snow and Ross's goslings (Table 3.4) or male snow and Ross's goslings (Table 3.5). Because this analysis did not take in account that environmentally stressing conditions could affect the growth of species differentially, analyses were further conducted with the use of structural size only, 9th primary only, and neither covariate to ensure that the results were not flawed by the use of the covariates.

Results analyzing body condition using only 9th primary as a covariate, structural size only as a covariate, and the final analysis with no covariate were not significant (9th primary: females $P = 0.71$, males $P = 0.70$; structural size: females $P = 0.11$, males $P = 0.65$; mass with no covariate: females $P = 0.29$, males $P = 0.35$) indicating that the use of the covariates in the original analyses (using both 9th primary and structure) did not influence the outcome of the results.

Vegetation Cover

Mean above-ground biomass for enclosed and unenclosed plots is displayed in Table 3.6. Vegetation in unenclosed plots decreased and vegetation in enclosed plots increased (Table 3.7, Figure 3.2).

Marsh Use

Results from homogeneity chi-square analyses examining diurnal marsh use patterns across time blocks were significant for both snow geese and Ross's geese indicating that within-day marsh use was not distributed uniformly (Table 3.8, Figures 3.3-3.10). For each species, the number of geese using the marsh during each time period varied diurnally, however no clear patterns were evident.

The significant third-order term (time class \times date \times species) from log-linear evaluations on diurnal marsh across days and between species indicated that marsh use patterns were dependent on a unique combination of time class \times species (Table 3.9), indicating that each species was using the marsh at different times for each observational day. This was examined further in the second-order model time class \times species. Results were significant for three of the eight days indicating that on those days lesser snow and Ross's geese used the marsh differently. On June 14, both snow and Ross's geese used the marsh more in the late evening than in the morning (Figure 3.3). On July 2nd, marsh use by both species was highest in the morning (Figure 3.7). No other clear patterns or trends could be deciphered from the results.

Activity Budgets

Adults

Results of log-linear evaluations on focal time-budget data are summarized in Table 3.10. The third-order term of adults (species \times sex \times behavior) was significant indicating that behavioral patterns depended on a unique combination of species and sex. This was examined further in the second-order models (sex \times behavior, species \times behavior). Second-order term sex \times behavior for adults indicated a significant difference

in behavior pattern between male and female snow geese. Female snow geese fed longer (79%), were less vigilant (12%), and spent less time in comfort (3.3%) and motor (5.6%) activities than did male snow geese (68%, 22%, 3.8%, and 5.9%). Similar differences in behavior were also found between male and female Ross's geese. Female Ross's fed more (79%), were less vigilant (11%), and spent more time in comfort (5%) and motor (5.5%) activities than did Ross's males (71%, 22%, 2%, and 4.5) (Table 3.11). The two-way interaction of species \times behavior was not significant between female snow geese and Ross's geese, but was significant between male snow geese and Ross's geese. Ross's goose males fed slightly longer (3.3%) than snow goose males. Both were equally vigilant.

Vigilance behaviors were negatively correlated with date for both male snow geese and Ross's geese (Table 3.12). Declines in vigilance have typically been associated with gosling growth and maturation (Lazarus and Inglis 1978). No other activity-budget activities were significantly correlated with date or weather (Tables 3.13 – 3.15).

Goslings

The significant second-order term species \times behavior indicated that behavioral pattern depended on species differences (Table 3.16). Snow geese spent less time feeding (84%) than Ross's geese (90%), and more time in comfort (6%) and motor activities (8%) than Ross's geese (5% and 3%) (Table 3.17).

Snow goose motor activities were negatively correlated with date (Table 3.18). Because movement requires energy (Wooley and Owen 1978), declines in motor activity may either be a strategy to conserve energy in light of reductions in available forage, or

may be indicative of a weakened physical state. No other significant correlations occurred (Tables 3.18 and 3.19).

Foraging Behavior

Forage observations were conducted to examine the finer details of foraging behavior. Pecking rates were evaluated to determine feeding rates, and feeding bout steps were estimated to determine if the size of feeding areas differed between geese.

Pecking Rate

Adults

Least square mean pecking rates are summarized in Table 3.20. Both female and male Ross's geese had significantly faster pecking rates than female and male snow geese (Table 3.21). Analyses comparing within species differences in pecking rate showed no differences between male and female snow geese or male and female Ross's geese (Table 3.22).

Female snow goose pecking rate was positively correlated with date, whereas female Ross's goose pecking rate was negatively correlated with date (Table 3.23). Increases in pecking rates throughout the brood rearing period may be indicative of a change in foraging tactic to accommodate declining food resources (Drent and Swierstra 1977, Riddington et al. 1997). Within-season decreases in pecking rates, on the other hand, may be in response to declines in nutritional quality of vegetation (Sedinger and Raveling 1986). Pecking rate was not significantly correlated with date for males, nor was it significantly correlated with weather for males or females of either species (Table 3.24).

Goslings

Ross's goose gosling peck rate was faster than snow goose gosling peck rate (Tables 3.25 and 3.26). Analyses of variance comparing gosling pecking rate to adults was significant for snow geese but not for Ross's geese (Table 3.27). Snow goose goslings pecked slower than snow goose adults. Ross's goose goslings pecked equally as fast as Ross's goose adults.

Peck rate for snow goose goslings and Ross's goose goslings was positively correlated with date (Table 3.28). Goslings peck rate commonly increases throughout brood rearing and may be coincident with gosling growth and development (Harwood 1974, Lessells 1987). No statistically significant correlations were found between peck rate and weather for either species.

Feeding Bout Steps

Table 3.29 summarizes mean feeding bout steps for adult snow geese and Ross's geese.

Male Ross's geese took more steps while feeding than male snow geese, and female Ross's geese took more feeding bout steps than female snow geese (Table 3.30). Feeding bout steps between male and female snow geese did not differ (Table 3.31) nor did feeding bout steps between male and female Ross's geese differ (Table 3.32).

Feeding bout steps were negatively correlated with weather for both male and female snow geese (Table 3.33). No other correlations were significant (Table 3.34).

DISCUSSION

Increases in both breeding lesser snow geese, from 1300 breeding pairs in 1968 to an estimated 44,500 breeding pairs in 1997, and staging snow geese have taken place on

La Pérouse Bay (Cooke et al. 1995, Abraham et al. 1996, unpublished aerial survey). High numbers of geese, coupled with destructive foraging methods, have virtually denuded all graminoid vegetation on intertidal areas of this salt marsh. Consequently, reductions in available food resources have had profound effects on lesser snow goose goslings. Towards the end of July, mean snow goose brood size had declined by 74%, whereas no apparent declines in mean brood size of Ross's geese occurred. Declines in both structural size and prefledging survival of goslings hatched on La Pérouse Bay have previously been documented (Cooch et al. 1991a, Cooch et al. 1991b, Cooch et al. 1993, Cooch et al. 2001).

Evaluation of the physical condition of both snow goose and Ross's goose goslings showed no differences, possibly due to early gosling death of snow geese. Given the decline in snow goose brood size throughout brood rearing this result seemed highly unusual at first, until one considers when measurements are collected. Banding occurs approximately six weeks after hatch. Because the majority of gosling deaths have been shown to occur one to five weeks post hatch (Williams et al. 1993), death of snow goose goslings weakened by food limitation during the first five weeks may have already taken place. Assuming that the observed reductions in brood size of snow goose goslings were random with respect to size, then the results imply that snow goslings are on average in as good physical condition as Ross's goose goslings. However, if smaller, weaker snow goose goslings had already died before banding they would not have been part of the sample measured. Thus, the data would have been left censored and the results indicating size equivalences would be an artifact of such a non-random sample. Previous data show that smaller goslings are less likely to survive the brood rearing

period (Rockwell, unpublished data). With no reductions in Ross's goose brood size, and the strong possibility that the smaller snow goose goslings already died prior to measurement, it may be reasonable to conclude that Ross's goose goslings were in better physical condition than all snow goose goslings but not necessarily in better condition than those snow goose surviving goslings.

Pecking rates of Ross's geese, both adults and goslings, were significantly higher than pecking rates of snow geese. Very fast pecking rates have been associated with small-billed geese (Harwood 1974). Structurally smaller birds also have smaller bills, enabling them to feed more efficiently on shorter blades of grass that may be associated with degraded vegetation (Krapu et al. 1992, Slattery 1994). Riddington et al. (1997) showed that Brant geese (*Brant bernicla bernicla*) preferred to graze on shorter swards of grass, presumably due to their higher nitrogen and lower fiber contents. Snow geese, on the other hand, have larger bills and mandibles more suited to digging and uprooting underground vegetation (Krapu et al. 1992, Slattery 1994).

Higher pecking rates may be particularly advantageous to goslings. Ross's goose goslings' pecking rates were as high as Ross's goose adults, whereas snow goose goslings' pecking rates were significantly slower than snow goose adults' rates. This may imply enhanced foraging abilities on their part. More importantly, faster pecking rates may result in an increase in food taken in per unit time (Boysen et al. 2001). It is conceivable that the higher pecking rates, suggestive of increased uptake rates, of Ross's goose goslings served to increase their fitness, contributing to the observed higher reproductive success of Ross's geese during the 1999 brood rearing period. However, bite size has been found to decrease with declining sward height, such that even the

fastest pecking rates cannot compensate for decreasing lengths of vegetation (Riddington et al. 1997). Because no measures of bite-size were taken in this study, the assumption that higher pecking rates lead to increased uptake rates can only be speculation.

Additionally, step rates of Ross's geese while feeding were higher than step rates of snow geese. Ross's geese, therefore, may be using larger feeding areas in general, spending more time in an area in search of higher quality vegetation, and moving on when the vegetation becomes too scarce. Snow geese, on the other hand, not only walked less but varied their feeding bout steps when weather conditions changed. They appeared to walk less during feeding in hotter weather, and walk more in colder weather. Decreases in steps during feeding may correspond to increased density of new plant growth enabling geese to concentrate feeding to a smaller area. However, it is more likely that rates of walking would increase as vegetation grows. McConnell River females show high rates of walking mid-season when plants were re-sprouting (Harwood 1974). In contrast, increases in rates of walking may reflect increased search times for scarce vegetation, for example early in the season when vegetation growth is still low. Notwithstanding the possible explanations for the variation in feeding bout steps of snow geese, it is more important to note that Ross's geese foraging behavior remained constant and was not affected by weather. It is this consistent behavior throughout varying environmental conditions that may contribute to Ross's geese foraging efficiency.

Lastly, adult females of both species spent a greater percentage of their time feeding than adult males, and adult males spent more time vigilant than adult females. In Arctic breeding geese, adult males typically invest more time in brood defense and vigilance behaviors than adult females, serving the dual purpose of protecting young

from predation and allowing the female to spend more time feeding to recover body reserves lost during egg laying and incubation (Harwood 1974, Lazarus and Inglis 1978, Lessells 1987, Schindler and Lamprecht 1987, Sedinger and Raveling 1990, Williams et al. 1994). Additionally, agonistic encounters occurring between adults in defense of young were rare to none, indicating that geese may have been too preoccupied with feeding to engage in aggressive encounters.

On the other hand, activity budgets of snow goose and Ross's goose goslings were found to differ. Snow geese spent less time feeding (84%) and more time in motor activities (8%) than Ross's geese (91% and 3% respectively). Additionally, gosling snow goose motor activities declined throughout the season. Although I cannot explain why snow geese spent less time feeding than Ross's geese, declines in motor activities (swimming, running, walking), and long-term declines in the proportion of time spent feeding (see chapter 2, page 22), may either reflect an attempt to conserve energy in light of inadequate amounts of available food, or more likely an overall weakened physical state due to food limitation. Given the decline in snow goose brood size during brood rearing, and long-term reductions in body measurements (see chapter 2, page 20), it would appear that snow goose goslings are not able to adapt their foraging behaviors to a degraded habitat.

Table 3.1. Principal component analysis loadings for La Pérouse Bay weather variables and proportion of variance each variable contributes.

<u>Variable</u>	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>	<u>PC4</u>	<u>PC5</u>
AT	0.57	0.07	-0.35	-0.22	0.71
SR	0.36	0.52	0.72	0.25	0.09
ST	0.38	-0.55	-0.04	0.74	-0.04
BP	-0.38	0.54	-0.43	0.58	0.22
H	-0.51	-0.36	0.41	0.05	0.66
% Variance	0.52	0.29	0.09	0.07	0.03

Abbreviations: AT - air temperature, SR - solar radiation,
ST - soil temperature, BP - barometric pressure, H - humidity

Table 3.2. Analyses of variance comparing daily means of La Pérouse Bay lesser snow goose broods to Ross's goose broods. As of June 28th, continuing through July 18th, Ross's goose broods were significantly larger than snow goose broods. Least square means indicated a steady decline in snow goose goslings as brood rearing progressed.

Source	df	MS	F	P
<u>June 24th</u>				
Species	1	0.41	0.21	0.6467
Error	254	1.93		
<u>June 28th</u>				
Species	1	12.70	8.41	0.0040
Error	283	1.51		
<u>July 2nd</u>				
Species	1	31.14	14.92	0.0002
Error	193	2.09		
<u>July 9th</u>				
Species	1	46.71	26.02	<0.0001
Error	232	1.80		
<u>July 14th</u>				
Species	1	7.75	4.43	0.0368
Error	180	1.75		
<u>July 18th</u>				
Species	1	80.55	58.79	<0.0001
Error	282	1.37		

Table 3.3. Unweighted regression analysis of brood size on date for La Pérouse Bay lesser snow geese and Ross's geese. Snow goose brood size declined throughout brood rearing period. No change occurred in Ross's goose brood size.

Source	df	MS	F	P	Slope
LSGO*					
MBS**	1	1.91	60.55	0.0006	-0.05
Error	5	0.03			
ROGO***					
MBS	1	0.07	0.61	0.48	-0.01
MSE	4	0.11			

*LSGO = Lesser snow goose

**Mean brood size

***ROGO = Ross's goose

Figure 3.1. Changes in daily mean brood sizes during the 1999 brood rearing period for La Pérouse Bay lesser snow geese and Ross's geese. Snow goose brood size declined throughout brood rearing period, whereas no change occurred in Ross's goose brood size.

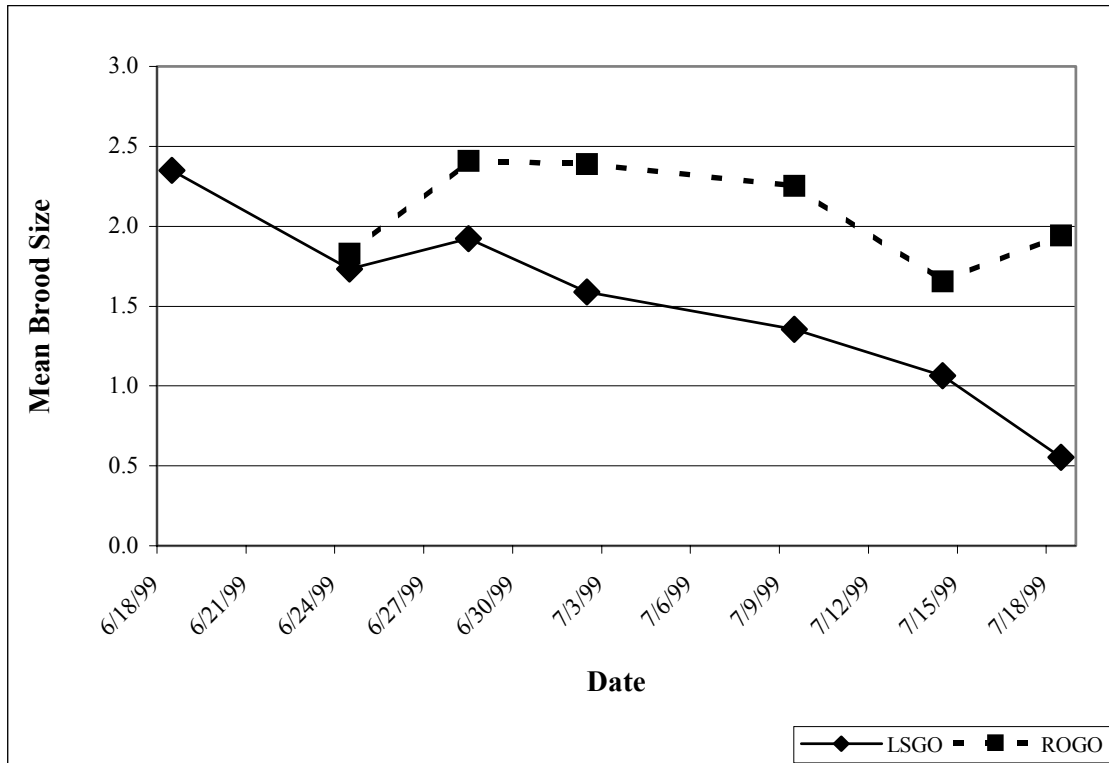


Table 3.4. Analysis of variance of condition for La Pérouse Bay female lesser snow goose and Ross's goose goslings (n = 10, 5 LSGO, 5 ROGO). Condition was estimated as mass scaled by structural size (PC1) with species as a class variable while age (primary 9) and PC1 were linear covariates. No differences in body condition between female snow and Ross's goslings were found.

Source	df	Mean Squares for Condition	F	P
Species	1	15.31	0.00	0.9649
Ninth Primary (P9)	1	153.11	0.02	0.8897
PC1	1	9.73	0.00	0.9720
P9 × Species	1	15.80	0.00	0.9643
PC1 × Species	1	11.29	0.00	0.9699
P9 × PC1	1	6.95	0.00	0.9763
P9 × PC1 × Species	1	5.35	0.00	0.9792

Table 3.5. Analysis of variance of condition for La Pérouse Bay male lesser snow goose and Ross's goose goslings (n = 20, 11 LSGO, 9 ROGO). Condition was estimated as mass scaled by structural size (PC1) with species as a class variable while age (primary 9) and PC1 were linear covariates. No differences in body condition between male snow and Ross's goslings were found.

Source	df	Mean Squares for Condition	F	P
Species	1	1209.93	0.18	0.6769
Ninth Primary (P9)	1	4359.61	0.66	0.4333
PC1	1	469.02	0.07	0.7948
P9 × Species	1	1215.13	0.18	0.6762
PC1 × Species	1	7373.52	1.11	0.3125
P9 × PC1	1	192.77	0.03	0.8675
P9 × PC1 × Species	1	8055.52	1.21	0.2921

Table 3.6. Mean La Pérouse Bay above-ground biomass (g m^{-2}) and standard errors from exclosed (E) and unexclosed (U) vegetation plots.

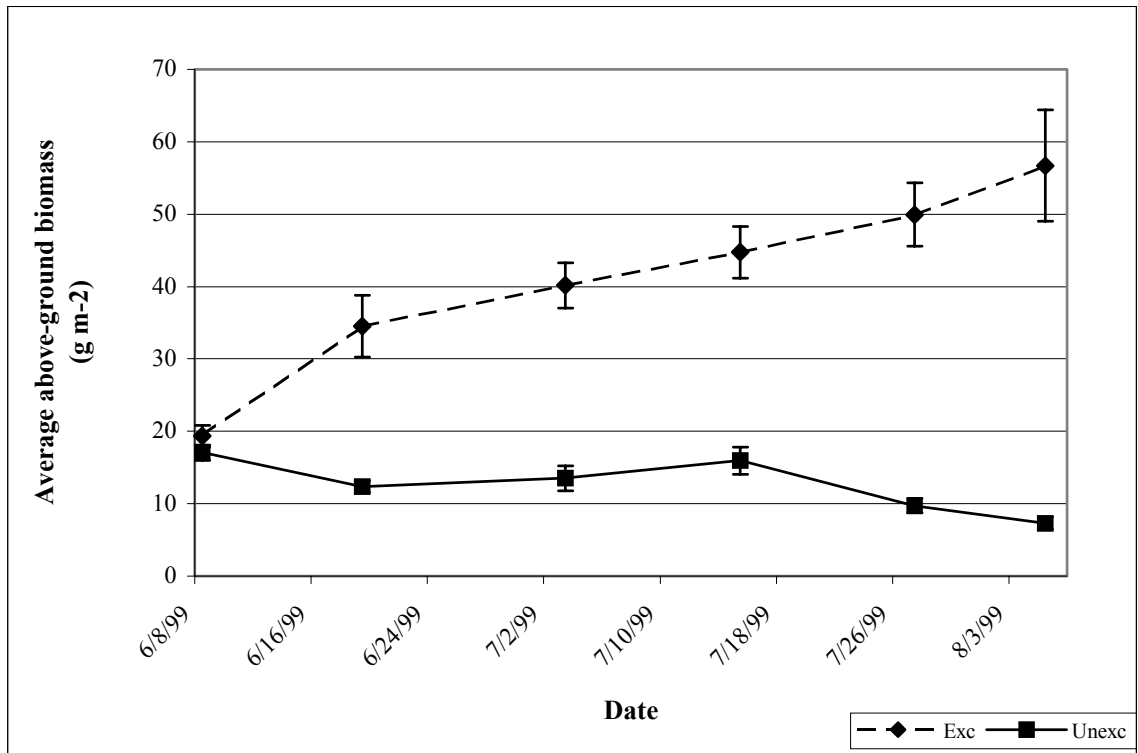
Date	N	E	Stderr	U	Stderr
June 8	12	19.3	1.5	17.0	1.1
June 19	12	34.5	4.3	12.4	0.8
July 3	12	40.2	3.1	13.5	1.7
July 15	12	44.7	3.6	15.9	1.9
July 27	12	49.9	4.4	9.7	1.0
Aug 5	12	56.7	7.7	7.3	0.8

Table 3.7. Regression analysis of above-ground biomass (g m^2) on La Pérouse Bay's intertidal salt marsh. Vegetation in unexclosed plots decreased, whereas vegetation in exclosed plots increased.

Source	df	MS	F	P	Slope
<u>Unexclosed Plots</u>					
Gm ² *	1	471.06	19.65	<0.0001	-0.125
Error	70	23.96			
<u>Exclosed Plots</u>					
Gm ²	1	9653.98	40.95	<0.0001	0.569
Error	70	235.76			

*Gm² - grams per meter squared

Figure 3.2. Graphic representation of vegetation decreasing in unexclosed vegetation plots, and increasing in exclosed plots on the La Pérouse Bay intertidal salt marsh in 1999.



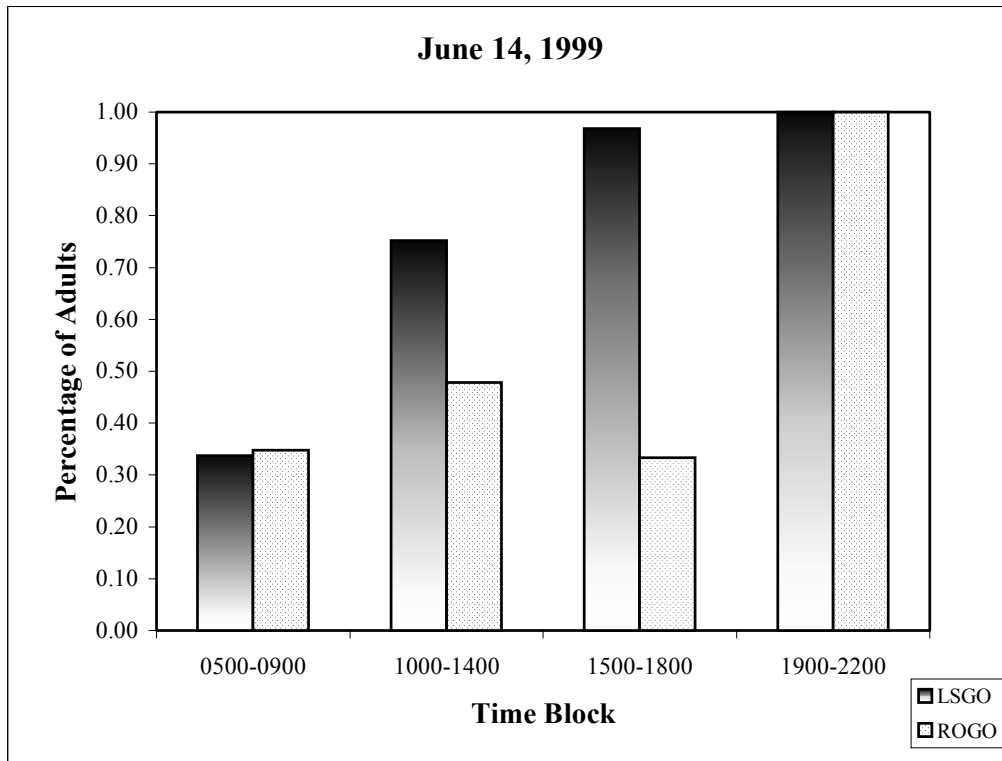
Mean above-ground biomass (g m^{-2}) and standard errors for exclosed and unexclosed vegetation plots.

Table 3.8. Results from homogeneity chi-square analysis determining marsh use patterns of La Pérouse Bay lesser snow geese and Ross's geese across time blocks. Results indicate that within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally.

Source	X^2
LSGO	398.14
ROGO	124.00

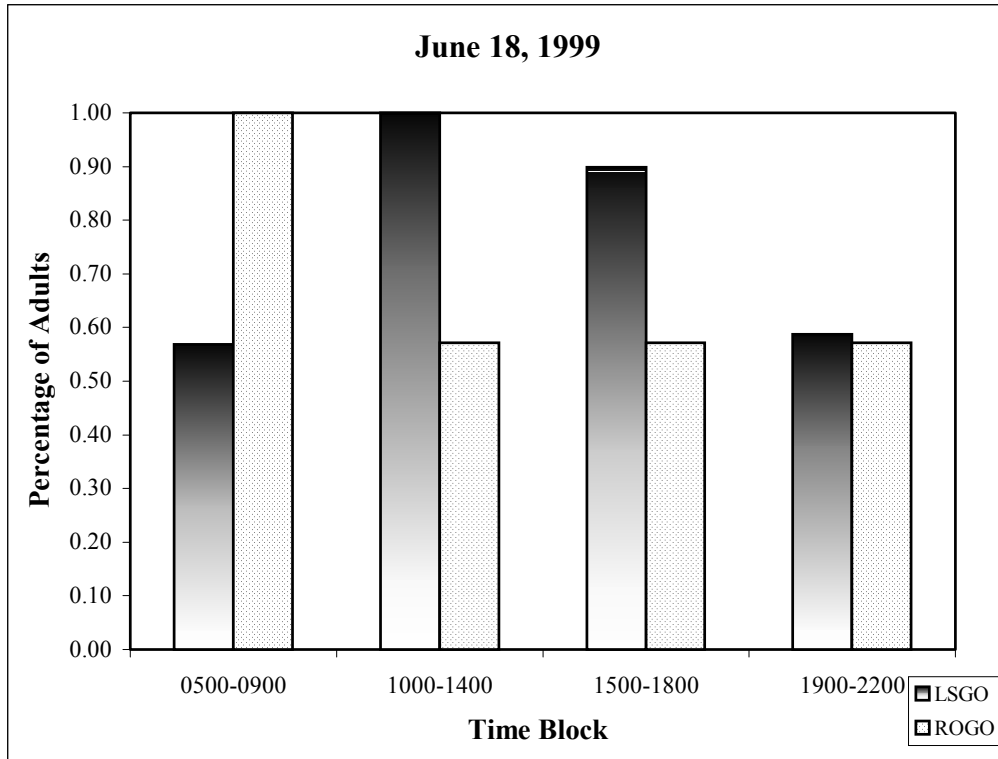
$X^2_{0.001, 24} = 16.266$

Figure 3.3. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. Both snow and Ross's geese used the marsh more in the late evening than in the morning. No other clear patterns were evident.



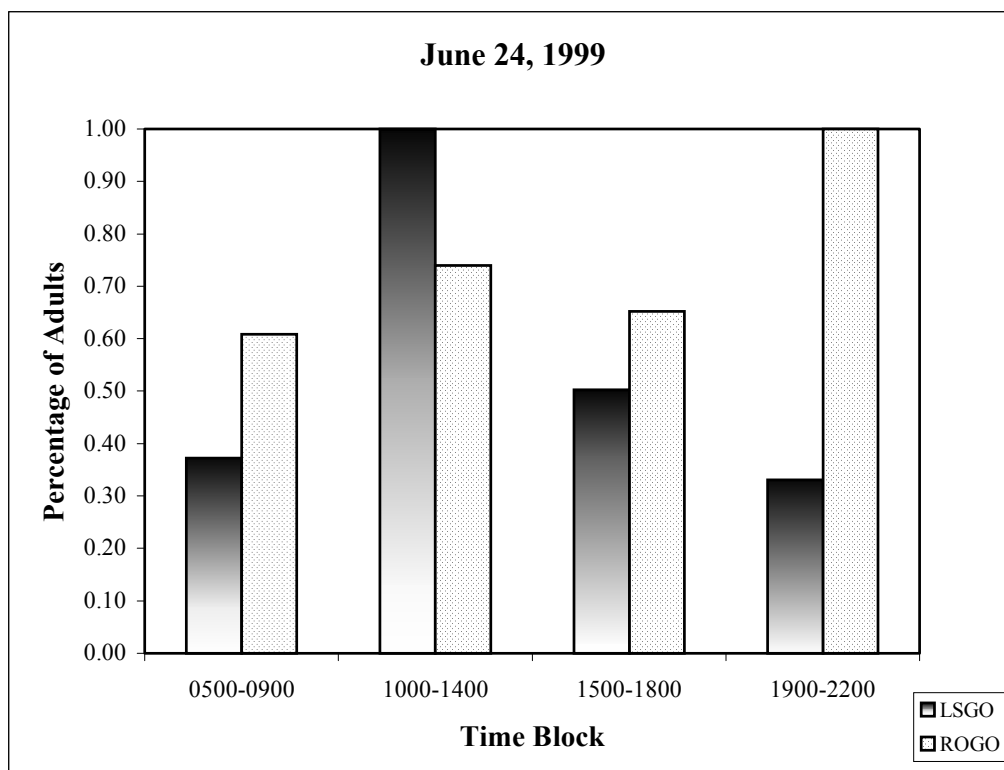
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on June 14, 1999.

Figure 3.4. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



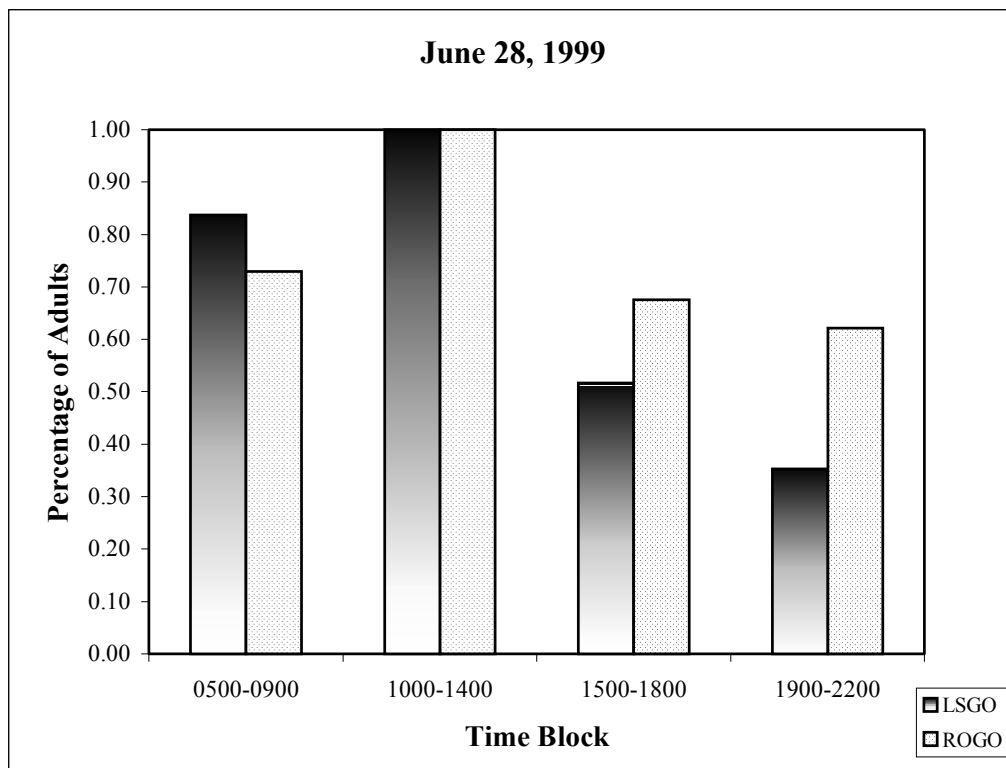
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on June 18, 1999.

Figure 3.5. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



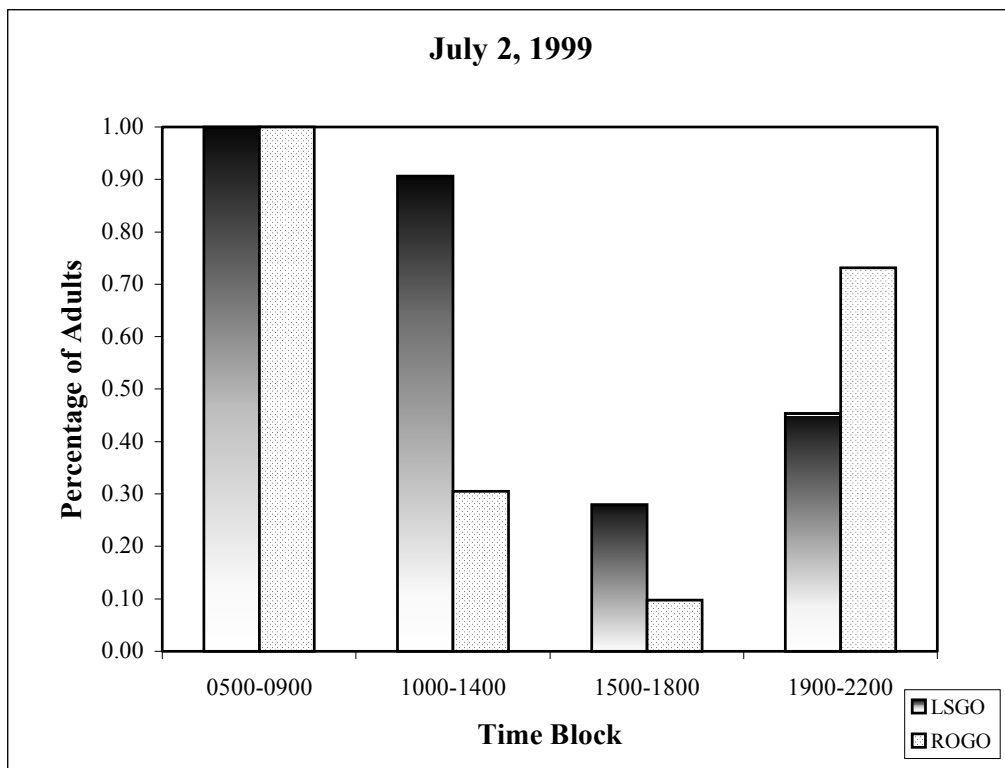
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on June 24, 1999.

Figure 3.6. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



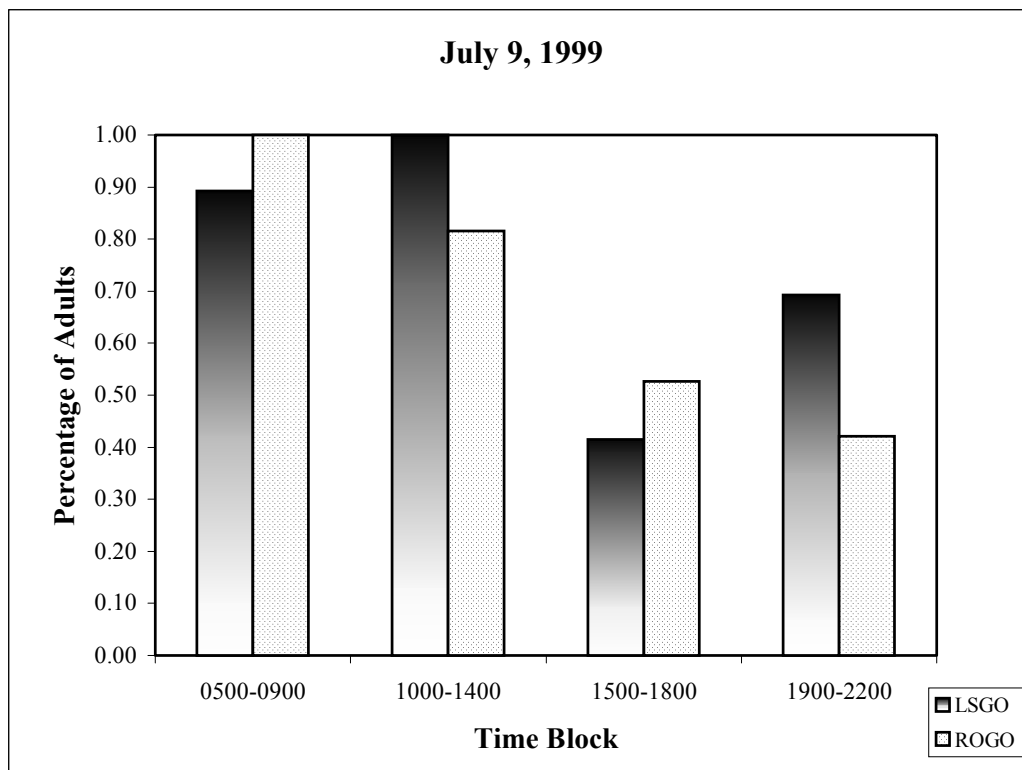
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on June 28, 1999.

Figure 3.7. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. Marsh use by both species was highest in the morning. No other clear patterns were evident.



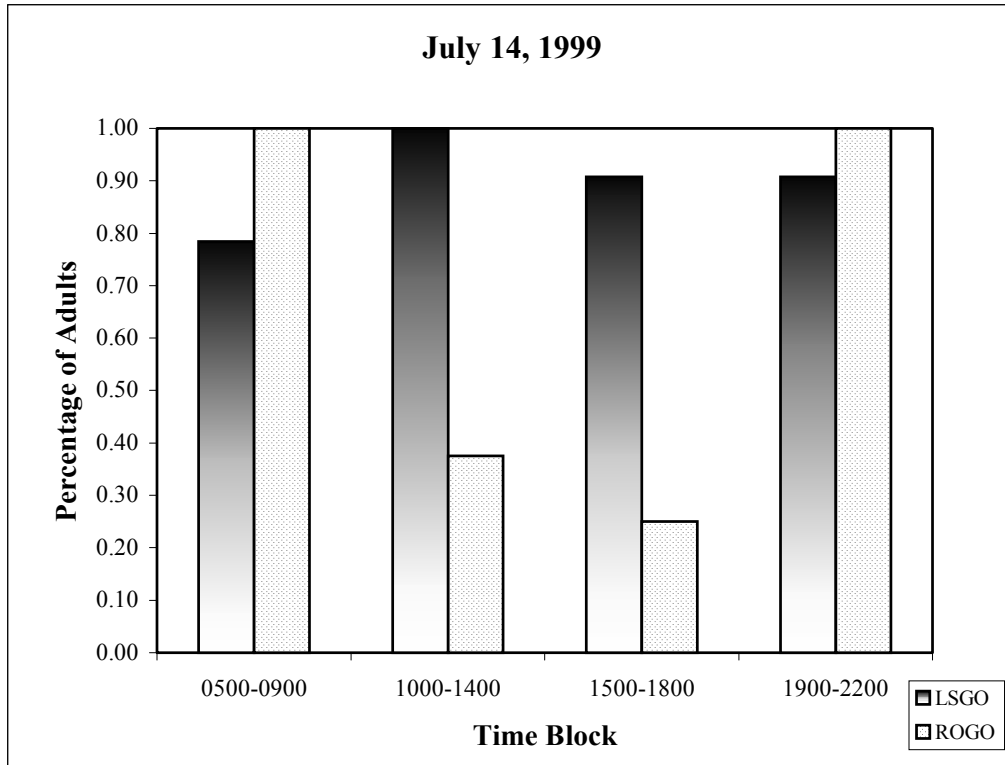
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on July 2, 1999.

Figure 3.8. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



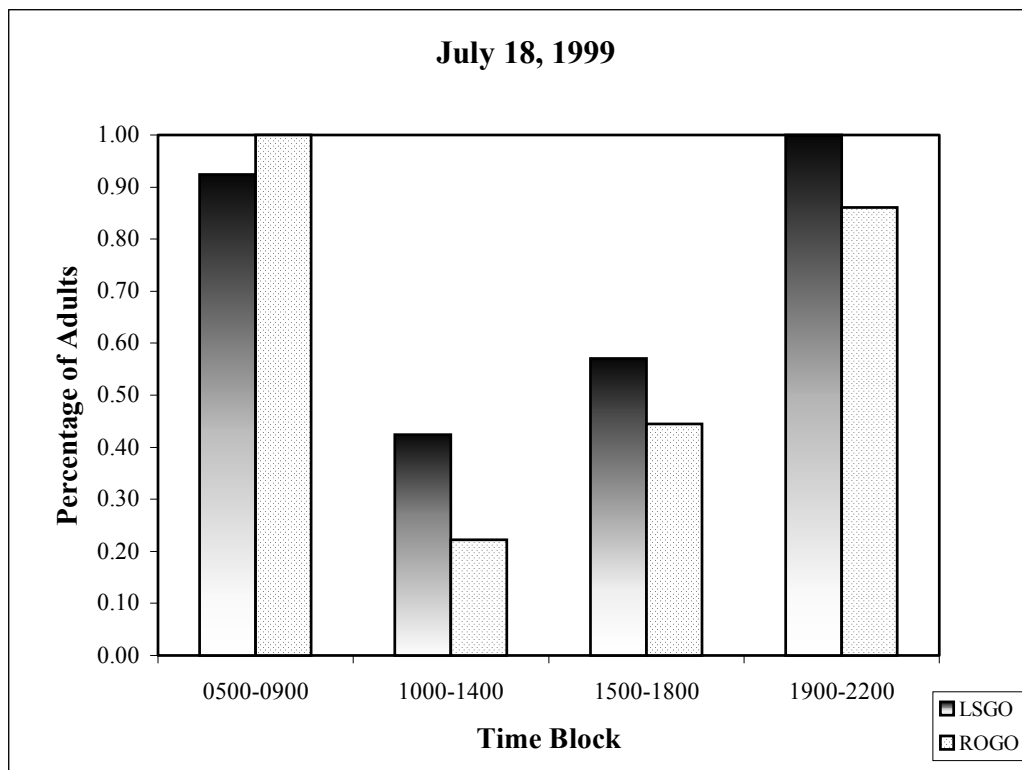
Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on July 9, 1999.

Figure 3.9. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on July 14, 1999.

Figure 3.10. Within-day marsh use was not distributed uniformly. For each species, the number of geese using the marsh during each time period varied diurnally. No clear patterns were evident.



Diurnal marsh use of La Pérouse Bay lesser snow geese and Ross's geese on July 18, 1999.

Table 3.9. Results of log-linear modeling of the cross-classified La Pérouse Bay marsh use data. The significant third-order term (time class \times date \times species) indicated that marsh use patterns were dependent on a unique combination of time class \times species, showing that each species was using the marsh at different times for each observational

Model	Source	df	Wald Statistic	P
Third-order	time class \times date \times species	22	61.23	0.0020
Second-order				
LSGO	time class \times date	24	382.96	<0.0001
ROGO	time class \times date	22	109.62	<0.0001
June 14	time class \times species	3	18.44	0.0004
June 18	time class \times species	3	4.25	0.2357
June 24	time class \times species	3	29.05	<0.0001
June 28	time class \times species	3	5.76	0.1240
July 2	time class \times species	3	30.25	<0.0001
July 9	time class \times species	3	6.59	0.0860
July 14	time class \times species	3	11.27	0.0103*
July 18	time class \times species	3	3.44	0.3284

*Not significant after Bonferroni adjustment $0.05/8 = P = 0.00625$

Table 3.10. Results of log-linear modeling of the cross-classified La Pérouse Bay lesser snow goose and Ross's goose adult activity budget data. The third-order term species \times sex \times behavior was significant indicating that behavioral patterns depended on a unique combination of species and sex. Second-order term sex \times behavior indicated a significant difference in behavior pattern between male and female snow geese. Female snow geese fed longer, were less vigilant, and spent less time in comfort and motor activities than did male snow geese. Female Ross's fed more, were less vigilant, and spent more time in comfort and motor activities than did Ross's males. The two-way interaction of species \times behavior was not significant between female snow geese and Ross's geese, but was significant between male snow geese and Ross's geese. Ross's goose males fed slightly longer than snow goose males.

Model	Source	df	Wald Statistic	P
Third-order	species \times sex \times beh	3	14.77	0.0020
Second-order				
LSGO	sex \times beh	3	131.84	<0.0001
ROGO	sex \times beh	3	25.29	<0.0001
Females	species \times beh	3	6.65	0.0839
Males	species \times beh	3	11.32	0.0101

Table 3.11. Activity budgets of La Pérouse Bay adult lesser snow geese and Ross's geese.

		<u>Percent of time spent in each activity</u>			
	<u>N</u>	<u>Feeding</u>	<u>Vigilant</u>	<u>Comfort</u>	<u>Motor</u>
Females					
LSGO	72	78.9	12.1	3.3	5.6
ROGO	9	78.6	10.6	5.3	5.5
Males					
LSGO	71	68.0	22.3	3.8	5.9
ROGO	9	71.3	22.2	1.6	4.5

Table 3.12. Pearson product-moment correlations of behavioral activities on date for La Pérouse Bay adult lesser snow goose and Ross's goose males. Vigilance behaviors were negatively correlated with date for both male snow geese and Ross's geese, indicating that vigilance declined as the brood rearing period progressed.

<u>Behavior</u>	Males					
	N	<u>LSGO</u>		<u>ROGO</u>		N
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Feeding	71	0.17	0.1531	0.52	0.1478	9
Vigilant	71	-0.24	0.0404	-0.84	0.0046	9
Comfort	71	0.03	0.7815	0.25	0.5146	9
Motor	71	0.05	0.6688	0.16	0.6784	9

Table 3.13. Pearson product-moment correlations of behavioral activities on date for La Pérouse Bay adult lesser snow goose and Ross's goose females. Behaviors were not correlated with date for either snow goose or Ross's goose females.

<u>Behavior</u>	Females					
	N	<u>LSGO</u>		<u>ROGO</u>		N
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Feeding	72	0.14	0.2572	0.13	0.7467	9
Vigilant	72	-0.21	0.0818	-0.13	0.7308	9
Comfort	72	-0.01	0.9032	0.06	0.8676	9
Motor	72	0.06	0.6231	-0.21	0.5842	9

Table 3.14. Pearson product-moment correlations of behavioral activities on weather for La Pérouse Bay adult lesser snow goose and Ross's goose males. Behaviors were not correlated with weather for either snow goose or Ross's goose males.

Males				
Behavior	<u>LSGO</u>		<u>ROGO</u>	
	N = 71		N = 9	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Feeding	-0.08	0.5118	-0.22	0.5694
Vigilant	0.15	0.1972	-0.02	0.9530
Comfort	-0.06	0.6316	-0.05	0.8954
Motor	-0.07	0.5339	0.55	0.1274

Table 3.15. Pearson product-moment correlations of behavioral activities on weather for La Pérouse Bay adult lesser snow goose and Ross's goose females. Behaviors were not correlated with weather for either snow goose or Ross's goose females.

Females				
Behavior	<u>LSGO</u>		<u>ROGO</u>	
	N = 72		N = 9	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Feeding	0.12	0.3003	-0.008	0.9826
Vigilant	0.06	0.6201	-0.03	0.9427
Comfort	-0.18	0.1249	-0.18	0.6448
Motor	-0.22	0.0627	0.31	0.4096

Table 3.16. Results of log-linear modeling of the cross-classified La Pérouse Bay lesser snow goose and Ross's goose gosling activity budget data. The significant second-order term species \times behavior indicated that behavioral pattern depended on species differences. Snow geese spent less time feeding than Ross's geese, and more time in comfort and motor activities than Ross's geese.

Model	Source	df	Wald Statistic	P
Second-order	species \times beh	3	26.99	<0.0001

Table 3.17. Activity budgets of La Pérouse Bay gosling lesser snow geese and Ross's geese.

	<u>Percent of time spent in each activity</u>				
	<u>N</u>	<u>Feeding</u>	<u>Vigilant</u>	<u>Comfort</u>	<u>Motor</u>
LSGO	172	84.4	1.4	6.2	8.0
ROGO	30	90.5	0.9	5.3	3.4

Table 3.18. Pearson product-moment correlations of behavioral activities on date for La Pérouse Bay gosling lesser snow geese and Ross's geese. Snow goose motor activities were negatively correlated with date.

Goslings				
Behavior	<u>LSGO</u>		<u>ROGO</u>	
	N = 172		N = 30	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Feeding	0.13	0.0935	0.14	0.4465
Vigilant	-0.12	0.1058	-0.34	0.0654
Comfort	0.03	0.6627	-0.21	0.2665
Motor	-0.31	<0.0001	0.28	0.1331

Table 3.19. Pearson product-moment correlations of behavioral activities on weather for La Pérouse Bay gosling lesser snow geese and Ross's geese. Behaviors were not correlated with weather for either lesser snow goose or Ross's goose goslings.

Goslings				
Behavior	<u>LSGO</u>		<u>ROGO</u>	
	N = 172		N = 30	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Feeding	-0.13	0.0918	-0.14	0.4516
Vigilant	0.13	0.0847	-0.10	0.5976
Comfort	0.14	0.0739	0.11	0.5583
Motor	-0.05	0.5495	0.20	0.2768

Table 3.20. Least square mean pecking rates (# of pecks taken in 10 seconds) and standard errors of La Pérouse Bay adult lesser snow geese and Ross's geese.

Species	Sex	N	Mean	Std Error
<u>LSGO</u>	F	76	31.7	0.475
	M	188	32.2	0.450
<u>ROGO</u>	F	8	46.0	1.464
	M	30	46.2	1.360

Table 3.21. Analysis of variance of pecking rates between La Pérouse Bay adult lesser snow geese and Ross's geese. Both female and male Ross's geese had faster pecking rates than female and male snow geese, indicative of higher uptake rates.

Source	df	MS	F	P
<u>Females</u>				
Pkrate*	1	1477.94	86.10	<0.0001
Error	82	17.17		
<u>Males</u>				
Pkrate	1	1413.83	95.54	<0.0001
Error	79	14.79		

*Pkrate = pecking rate

Table 3.22. Analysis of variance of pecking rates between La Pérouse Bay adult males and females. No differences between male and female snow geese or between male and female Ross's geese were found.

Source	df	MS	F	P
<u>LSGO</u>				
Pkrate	1	10.70	0.66	0.4181
Error	147	16.22		
<u>ROGO</u>				
Pkrate	1	0.25	0.02	0.8944
Error	14	13.68		

Table 3.23. Pearson product-moment correlations of pecking rate on weather and date for La Pérouse Bay adult female lesser snow geese and Ross's geese. Female snow goose pecking rate was positively correlated with date, indicating that they increased their rate as the brood rearing period progressed. Female Ross's goose pecking rate was negatively correlated with date, indicating that their pecking decreased as brood rearing progressed.

Females				
	<u>LSGO</u>		<u>ROGO</u>	
	N = 76		N = 8	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PC1	-0.14	0.2327	-0.17	0.6851
Date	0.27	0.0192	-0.80	0.0181

Table 3.24. Pearson product-moment correlations of pecking rate on weather and date for La Pérouse Bay adult male lesser snow geese and Ross's geese. Pecking rate was not significantly correlated with either weather or date.

Males				
	<u>LSGO</u>		<u>ROGO</u>	
	N = 73		N = 8	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PC1	0.02	0.8808	-0.12	0.7737
Date	0.09	0.4390	0.27	0.5092

Table 3.25. Analysis of variance of pecking rates between La Pérouse Bay gosling lesser snow geese and gosling Ross's geese. Ross's goose gosling pecking rate was faster than snow goose gosling peck rate.

Source	df	MS	F	P
Pkrate	1	5969.84	176.63	<0.0001
Error	216	33.80		

Table 3.26. Least square mean pecking rates (# of pecks taken in 10 seconds) and standard errors of La Pérouse Bay adult and gosling lesser snow geese and Ross's geese.

Species	N	Mean	Std Error
LSGO	73	28.4	0.424
ROGO	8	43.6	1.061

Table 3.27. Analysis of variance of pecking rates between La Pérouse Bay goslings and adults. Gosling snow geese pecked slower than adult snow geese, whereas gosling Ross's geese pecked as fast as adult Ross's geese, indicating that snow goose gosling uptake rates are slower than adult snow goose uptake rates, whereas Ross's goose gosling uptake rates are as high as Ross's goose adult rates.

Source	df	MS	F	P
<u>LSGO</u>				
Pkrate	2	533.13	20.87	<0.0001
Error	334	25.55		
<u>ROGO</u>				
Pkrate	2	33.39	1.07	0.3527
Error	43	31.27		

Table 3.28. Pearson product-moment correlations of pecking rate on weather and date for La Pérouse Bay gosling lesser snow geese and Ross's geese. Pecking rate for snow goose goslings and Ross's goose goslings was positively correlated with date, indicating that rates increased as brood rearing progressed.

Goslings				
	<u>LSGO</u>		<u>ROGO</u>	
	N = 188		N = 30	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PC1	-0.02	0.7606	0.34	0.0637
Date	0.64	<0.0001	0.69	<0.0001

Table 3.29. Mean number of scaled feeding bout steps and standard errors of La Pérouse Bay adult lesser snow geese and Ross's geese.

	N	Scaled Mean	Std Error
<u>LSGO</u>			
Females	77	21.5	1.03
Males	74	20.7	0.86
<u>ROGO</u>			
Females	9	35.4	4.30
Males	9	37.0	3.92

Table 3.30. Analysis of variance of scaled feeding bout steps between La Pérouse Bay adult lesser snow geese and Ross's geese. Male Ross's geese had higher step rates while feeding than male snow geese, and female Ross's geese had higher step rates while than female snow geese, indicative of a larger feeding area.

Source	df	MS	F	P
<u>Females</u>				
Steps	1	1559.31	17.28	<0.0001
Error	84	90.26		
<u>Males</u>				
Steps	1	2139.80	33.80	<0.0001
Error	81	63.31		

Table 3.31. Analysis of variance of scaled feeding bout steps between La Pérouse Bay adult lesser snow goose males and females. Both walked equally as fast.

Source	df	MS	F	P
Steps	1	24.11	0.35	0.5551
Error	149	68.93		

Table 3.32. Analysis of variance of scaled feeding bout steps between La Pérouse Bay adult Ross's goose males and females. Both had equal stepping rates.

Source	df	MS	F	P
Steps	1	11.81	0.08	0.7843
Error	16	152.44		

Table 3.33. Pearson product-moment correlations of scaled feeding bout steps on weather and date for La Pérouse Bay adult female lesser snow geese and Ross's geese. Feeding bout steps were negatively correlated with weather for both male and female snow geese.

Females				
	<u>LSGO</u>		<u>ROGO</u>	
	N = 77		N = 9	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PC1	-0.40	0.0003	0.25	0.5079
Date	-0.68	0.5590	0.22	0.5676

Table 3.34. Pearson product-moment correlations of scaled feeding bout steps on weather and date for La Pérouse Bay adult male lesser snow geese and Ross's geese. Feeding bout steps were not correlated with either weather or date for males of both species.

Males				
	<u>LSGO</u>		<u>ROGO</u>	
	N = 74		N = 9	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
PC1	-0.27	0.0225	0.44	0.2408
Date	-0.12	0.3069	0.07	0.8539

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CHAPTER 4

GENERAL DISCUSSION & CONCLUSIONS

Feeding “strategies” may be viewed as behavioral traits concerned with “the large scale spatio-temporal patterning of the environment”, with variations occurring across seasons (Harwood 1974). The act of grubbing upon arrival to Arctic breeding habitats is a strategic decision, remaining constant from season to season. This behavior, no doubt, was shaped by the availability of food at the time. Feeding “tactics,” on the other hand, are more concerned with moment-to-moment adjustments in feeding behavior as within-season environmental changes take place (Harwood 1974). Quantitative changes in walking or pecking rates, in response to changes in biomass, are considered tactical strategies designed to maximize intake rates. The studies in this thesis were designed to determine changes in feeding behavior, evaluating both long-term changes in feeding “strategies” and “tactics” of lesser snow geese coincident with severe destruction of the La Pérouse Bay breeding habitat (Chapter 2), and within-season variation in feeding behavior between lesser snow geese and Ross’s geese using this same habitat (Chapter 3).

Degrading environmental conditions appear to have not changed overall feeding strategies of adult lesser snow geese over time (Chapter 2). Females continue to feed more than males, and males continue to engage in vigilant behaviors twice as much as females. This strategy is in keeping with the considerable weight loss of females to that of males during egg laying and incubation (Ankney and MacInnes 1978, Ankney 1977), which allows the female to spend more time feeding to recover lost body reserves and

protects the goslings from predation (Williams et al. 1994, Sedinger and Raveling 1990, Lessells 1987, Schindler and Lamprecht 1987, Lazarus and Inglis 1978, Harwood 1974). The recovery of body reserves, in turn, strengthens the female enabling both parents to lead their young to feeding areas, increasing the survival potential of goslings. In contrast, in response to declining resources quantitative changes in pecking and walking rates of adults were made. Females increased their pecking rate in later years, thereby attempting to maximize intake per unit time. Males and females both increased their rates of walking, consistent with more time being required to search for food. Longer search times ensure that more territory will be covered and the potential to find higher quality food increased.

Snow goose goslings, on the other hand, showed decreases in the percentage of time spent feeding coincident with degrading habitat conditions. Because a tactic implies some preformed pattern of behavior, perhaps it is best to state that there has been a change in gosling behavior, not tactic, over time. Goslings at this stage of life are no doubt driven by the need to maximize growth rate (Sedinger et al. 1995), achieved best by maximizing feeding rates. Recorded declines in growth and pre fledging survival (Cooch et al. 2001) demonstrate that goslings are not able to feed at optimal levels.

Snow goose and Ross's goose foraging behavior was compared in Chapter 3. Because brood rearing Ross's geese were new to the La Pérouse Bay intertidal feeding flats, little was known on their foraging behavior and how they would interact with snow geese on this habitat, especially in light of current degradation levels.

Examination of activity budgets showed no variation in behavioral strategies between adult snow geese and Ross's geese. Adult females of both species spent more

time feeding than males, and males spent close to twice as much time in vigilance behaviors than females. Female Ross's geese, like female snow geese, also lose considerable amounts of weight during egg laying and incubation (Hobson et al. 1993). Thus, heightened vigilance by males of both species allows for weight gain by females, and protection of goslings. This dichotomous pattern of behavior is common amongst many species of Arctic breeding geese (Fowler et al. 1997, Sedinger et al. 1995, William et al. 1994, Sedinger and Raveling 1990, Lazarus and Inglis 1978, Harwood 1974) and must therefore represent an optimal behavioral strategy.

The higher rates of pecking and walking of Ross's geese are representative of tactical differences in behavior. Although the pecking rates of snow geese were higher in the latter part of the study, indicative of a change in behavior designed to increase nutrient uptake, their rates were nevertheless slower than those of Ross's geese. Very high pecking rates on degraded vegetation may be advantageous, leading to high uptake rates. High uptake rates, together with larger feeding areas which increase the chance of encountering higher quality vegetation, may therefore maximize feeding (Boysen 2001). Care must be taken, nevertheless, when interpreting these results. Higher pecking rates of birds with smaller bill morphologies have been documented (Harwood 1974). Therefore variation in behavior may not just correspond to differential responses to environmental conditions. Furthermore, because bite size was not measured, it cannot be shown that more food was ingested per unit time.

The greatest difference in behavior occurred between goslings: snow goose goslings fed considerably less than Ross's goose goslings. Perhaps the only way to interpret this difference is in view of tactical differences. Gosling Ross's goose rates of

pecking were higher than those of gosling snow geese. More importantly Ross's goose goslings' pecking rates mirrored those of adult Ross's geese whose rates, as previously discussed, were higher than those of snow goose adults. Given the similarities in age at the time observations were conducted, differences in bill size were no doubt slight ruling out morphology as a probable cause for variation in pecking rate. Goslings feed close to their parents, likely mimicking parental behavior. Their high pecking rate may in fact be a result of imitative learning (Harwood 1974). Why snow goose goslings' pecking rates did not mimic those of their parents is unknown. It may be appropriate to conclude, then, that Ross's goslings' uptake rates were higher than those of snow goose goslings', thereby increasing their energy levels which would then enable them to feed for longer periods of time. In contrast, the lower pecking rates of snow goose goslings may have resulted in a decrease in food uptake, leaving them weak and unable to feed for longer periods of time. Again, without any measure of bite size this can only be speculation.

It must be noted that behavioral differences between snow goose and Ross's goose goslings may not be the only reason for why Ross's goose goslings appeared to have higher survival rates on La Pérouse Bay. It has been determined that Ross's goose goslings have faster growth rates than snow goose goslings (MacInnes et al. 1989). At hatch, Ross's goose goslings are more functionally mature than snow geese: they have larger protein reserves and less growth required to achieve adult size (Slattery et al. 1995). Measurements on one-day old Ross's goose goslings showed their gizzards to be proportionately larger than lesser snow goose goslings' gizzards, which may make them more efficient at processing food (Slattery 1994). By 35 days of age snow goose goslings have only grown to approximately 60-65% of adult size whereas by 3 weeks post hatch

Ross's goslings have reached approximately 80% of adult size (Mowbray et al. 2000, Ryder and Alisauskas 1995). Perhaps Ross's goose goslings' rapid growth rate, and subsequent larger size earlier in the season, reduces their risk of predation by herring gulls (*Larus argentatus*).

In sum, degraded habitat conditions on the intertidal feeding flats of La Pérouse Bay have resulted in declines in local reproductive success of snow goose adults, and reductions in growth rates of snow goose goslings. Although feeding behaviors of adults seem to change in consort with reductions in food availability, such modifications in feeding behaviors by goslings are not evident. In most years, 80% to 90% of snow goose goslings do not survive to fledging (Rockwell, personal communication). As the intertidal marsh continued to degrade, the number of brood rearing snow geese declined, due to dispersion, and the number of breeding Ross's geese increased. Of more significance, however, was the reproductive success experienced by these newly arrived Ross's geese to an already degraded habitat. And, as of 2001, breeding Ross's geese were the dominant species on this intertidal marsh, replacing snow geese.

Evidently, high gosling survival rates demonstrated that Ross's geese were able to profit from La Pérouse Bay's habitat in its degraded state. Their presence, however, appeared to further the degradation initiated by snow geese to a point where, unless they too disperse, vegetation on the intertidal feeding area may never recover. To use an analogy, Ross's geese may become the "sheep" of the tundra, eating all remaining vegetation already grazed by snow geese, the tundra "cattle". And, if Ross's geese do begin to disperse and follow in the path of snow geese, other ecosystems may be in jeopardy of irrecoverable damage. Therefore, when formulating plans to reverse the

habitat damage initiated by snow geese, management must now include the potential role of Ross's geese in the continued destruction of an ecosystem.

In conclusion, the integration of behavioral research with conservation studies is long overdue. Behavioral studies are designed to determine the underlying mechanisms that may explain why certain individuals or populations are selected to respond to divergent conditions, or to explain why different strategies exist under specific conditions. As such, animal behavior research can enhance the predictive value in conservation studies. In the absence of behavioral studies, research programs may fail because the ecological or behavioral requirements of the animals are not known (Martin 1998). For example, an attempt to increase the population of sage grouse (*Centrocercus urophasianus*) in southeastern Utah by introducing sage grouse from southwestern Colorado failed because behavioral work had not been conducted beforehand. Had observations been conducted, it would have been known that the introduced grouse set up different mating grounds and did not mix with the local population. Additionally, a later study showed that these species were behaviorally and morphologically distinct from each other. At present, the sage grouse in southeastern Utah are almost completely extirpated (Hupp and Braun 1991, Young et al. 1994).

In another reintroduction project of ibex (*Capra ibex*), had behavioral research been conducted prior to the reintroduction attempt knowledge of its mating system would have been available and the project may have succeeded. After the extirpation of ibex from the Tartra Mountains in Slovakia, reintroductions were attempted using ibex from Austria, Turkey, and the Sinai. Because these individuals represented 3 different subspecies, the offspring from the crosses mated in the fall instead of winter as did the

local and Austrian ibex populations. Consequently, the young were born in winter and died, and the reintroduction failed (Turcek 1951).

Previous research on snow goose foraging, as well as research conducted in this dissertation, demonstrates the necessity to integrate behavioral studies with conservation and wildlife management. The initial destruction of snow goose wintering habitats may have led conservationists to predict an imminent decline in snow goose population size. However, observations of dispersal patterns and foraging behaviors of these geese revealed their ability to adapt their diet from salt marsh feeders, eating grasses and sedges, to generalist herbivores, eating agricultural by-products. Destruction of traditional feeding habitats, in turn, was beneficial to snow geese as evidenced by the extent to which their population size exploded. Knowledge of this diet shift could only have been obtained via behavioral techniques.

The studies in this dissertation revealed the differential effects of habitat change on the local viability of lesser snow geese and Ross's geese. At La Pérouse Bay, current habitat degradation has led to declines in snow goose gosling survival. Observations of changes in the foraging behavior of snow goose adults and goslings, and dispersal of adults to inland sites with more abundant vegetation, have contributed to understanding why local snow goose adult population is not declining in a typical density dependent fashion, and why snow goose gosling survival, in contrast, is declining. To the contrary, observations of Ross's geese using this same habitat have revealed that Ross's geese are able to forage more efficiently on this degraded habitat, as evidenced by high Ross's goose gosling survival. Without these behavioral studies, this knowledge would not be available. As such, data from this research can now be used by conservationists in

monitoring the local population dynamics of both of these species, as well as their potential impact on adjacent ecosystems.

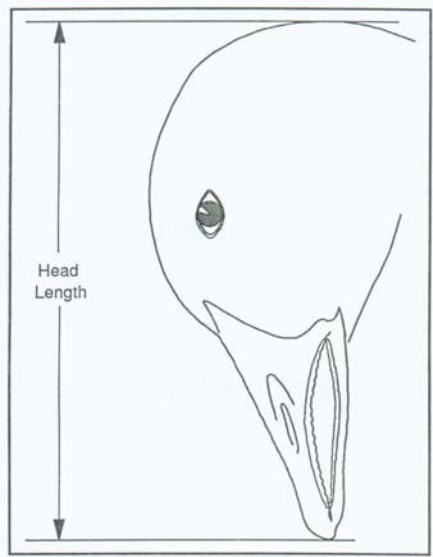
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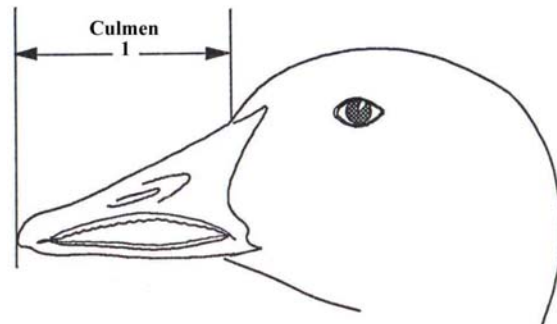
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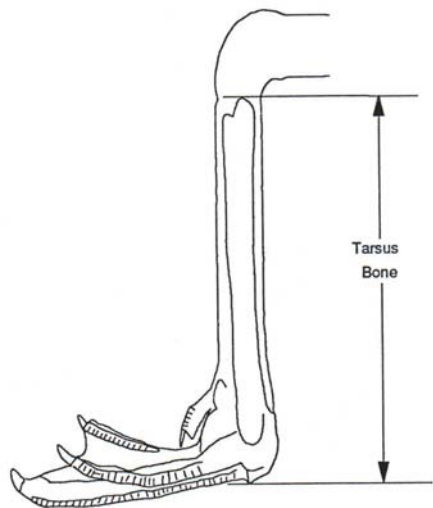
APPENDIX A



Head length



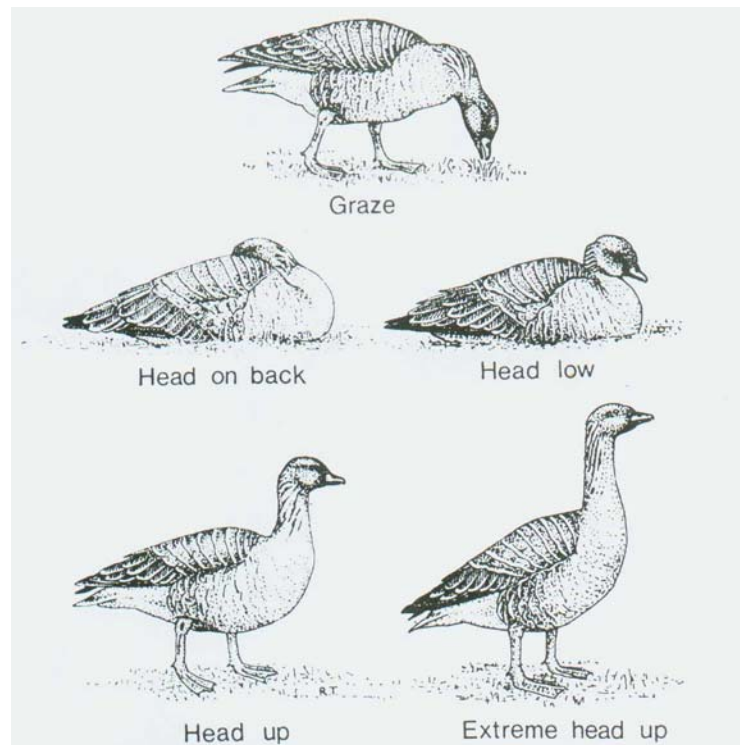
Culmen 1



Tarsus Bone

Ninth Primary

The 4 anatomical structures of geese analyzed in this thesis. From: Dzubin, A., and E. Cooch. 1992. Measurements of geese. General field methods. California Waterfowl Association, Sacramento, California.

APPENDIX B

Diagrams of common goose postures (illustrated by Rebecca Torrance). From: Inglis, I.R. 1977. The Breeding Behavior of the Pink-Footed Goose: Behavioural Correlates of Nesting Success. *Animal Behavior* 25: 747-764.

CHAPTER 5

ANNOTATED BIBLIOGRAPY

This bibliography contains 51 published references relevant to the lesser snow goose (*Chen caerulescens caerulescens*) and Ross's goose (*Chen rossii*). The referenced works date from 1928 to 2002.

Key Words: lesser snow goose, *Chen caerulescens caerulescens*, Ross's goose *Chen rossii*, La Pérouse Bay.

The objective of the literature review was to identify variation in body size, and potential differences in feeding habits and behavior of both snow geese and Ross's geese that might contribute to differential feeding efficiency and reproductive success.

Additionally, I will call attention to contradictory studies on which I will opine.

The lesser snow goose (*Chen caerulescens caerulescens*) until circa the 1950s was considered two different species based on its plumage coloration: one being blue, the other white. Adult blue-phased geese have a white head and neck, brown back, variable amounts of white ventrally, black primaries and secondaries, and bluish-gray wing coverts. Adult white phased geese are white with black primaries (Owen 1980). Each had originally been assigned different Latin classifications, the "blue" goose called *Chen caerulescens* and the "white" *Chen hyporborea* (Cooke and Cooch 1967). Departing from the formal Latin *classifications* to more informal *designations* representative of snow goose characteristics, they were given names by the native people denoting onomatopoeic words: the first syllable representing the auditory display of the snow

goose warning cry. To the Alaskan and Mackenzie Eskimos, the “white” snow goose was known as *kangok*, *kanguk*, *kuno*, and *kagnok*; to the Aivilikmiut and Okomiut Eskimos it was *khanguk*. The “blue” snow goose was known as *kungovik* on Baffin Island and *khavik* on Southampton Island (Johnsgard 1974).

The blue and white-phased geese were not only distinguished by their color differences and characteristic warning cries, but also by their winter distribution. The white geese were typically abundant in western regions of the United States, and the blue in eastern regions (Cooke et al. 1988). As a result of commercial development in the 1940’s, their traditional salt marsh habitat along the Gulf Coasts was lost or degraded. Consequently snow geese expanded their foraging areas to include newly developed agricultural crops (rice prairies) adjacent to the coastal marshes. They also began wintering further north, feeding on corn, wheat and other cereal grains. Changing their winter foraging areas from marshland to cropland not only caused a mixing and interbreeding of the two color phases, but also an increase in the over-wintering population (Abraham et al. 1996). Originally, over-winter survival was limited by the amount of forage in the coastal marsh, and the subsequent degradation of that vegetation due to their feeding behaviors. The effect of increased feeding on agricultural crops led to an increase in over-winter survival. Consequently, there were more geese migrating to the breeding grounds in the sub-Arctic tundra, where only a limited amount of food was available. As a result, food resources in the Arctic became depleted. Nesting and brood rearing areas, such as La Pérouse Bay, have been either severely degraded or destroyed beyond any foreseeable recovery (Jefferies and Rockwell 2002, Abraham and Jefferies 1997, Rockwell et al. 1996, Rockwell et al. 1997a). Coincident with this degradation, reductions in snow goose body size (Cooch et al. 1991a, Cooch et al. 1991b) and a decline in reproductive success (Cooch et al. 1993, Cooch et al. 2001, Francis et al. 1992,

Williams et al. 1993) have occurred. To what extent this will continue is unknown, especially in light of increased grazing pressure on the marsh with the arrival of breeding Ross's geese (*Chen rossii*) to La Pérouse Bay.

The Ross's goose is closely related to the snow geese morphologically. Its plumage is dimorphic: one being white and most common, the other being blue and more rare. It can be distinguished from snow geese by their smaller size, two-thirds that of snow geese, their short neck, small bill lacking the "grinning patch" characteristic the snow geese, and "caruncles," or wart-like protuberances, on the maxilla typical of older males (Ryder and Alisauskas 1995).

Early in the century Ross's geese were considered to be a rare species, possibly due to over hunting. However once legislation was passed to prohibit the hunting of Ross's geese, their numbers increased from approximately 2,000 nesting birds in the 1950's to over an estimated 188,000 nesting birds in 1988 (Ryder and Alisauskas 1995). As of 1995, that number had almost doubled (Abraham and Jefferies 1997).

The majority of Ross's geese breed in the Central Canadian Arctic, at Queen Maud Gulf Migratory Bird Sanctuary (Ryder and Alisauskas 1995). Recently, however, there has been an increase in the population of breeding Ross's geese at La Pérouse Bay (Pezzanite, personal observation). They have been observed there before, but only in small numbers and as broodless pairs (Didiuk et al. 2001). Their food habits are similar to those of snow geese: they are strict vegetarians feeding on roots of sedges and grasses.

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The effects of increasing numbers of snow geese on their own well-being, other fauna, and vegetation on their breeding habitat were discussed, as well as their population dynamics, migration routes, breeding and wintering colonies, food resources, and feeding behavior.

2. Alisaukas, R.T. 2002. Arctic climate, spring nutrition, and recruitment in mid-continent lesser snow geese. *Journal of Wildlife Management* 66 (1): 181-193.

Fall age-ratios of mid-continent snow geese shot by hunters and spring nutrient reserves were examined. Age ratios were inversely related to severity of Arctic weather, and declined in immatures and adults. Body size declined annually, body mass, fat, protein, and mineral reserves varied annually, and mass and body fat increased during spring staging. Findings from this study provide further evidence of annual declines in body mass and size found in chapter 2 of this dissertation.

3. Alisaukas, R.T., and C.D. Ankney. 1992. Spring habitat use and diets of midcontinent adult lesser snow geese. *Journal of Wildlife Management* 56(1): 43-54.

Esophageal contents, activity patterns and feeding behavior of adult lesser snow geese were examined from Oklahoma (in March) to Hudson Bay (in May), 1983-1984. As they migrated north, they changed from herbivory (Oklahoma & Nebraska) to granivory (Southern Manitoba). Corn was most eaten during migration, and foraging rates were greater in corn stubble in Manitoba than in South Dakota. Geese foraged at higher rates in plowed fields in South Dakota than in Manitoba. Foraging time increased as migration proceeded. Spring feeding of lesser snow geese migrating through agricultural areas of North America consisted of grasses and seeds on southern prairies, with increasing carbohydrate consumption as birds moved north. In Manitoba, high carbohydrate foods (e.g. corn, rhizomes) were eaten, increasing fat reserves. No grasses were consumed. Upon arrival at Hudson Bay, they reverted to a diet of green vegetation (roots and rhizomes). It is believed that the increased consumption of agricultural foods has reduced the annual variation in the ability of snow geese to acquire fat reserves on the prairies as compared to pre-agricultural times.

4. Alisaukas, R.T., C.D. Ankney, and E.E. Klaas. 1988. Winter diets and nutrition of midcontinental lesser snow geese. *Journal of Wildlife Management* 52(3): 403-414.

The diets of lesser snow geese wintering in 3 habitats were determined based on esophageal contents and habitat use.

Diurnal habitat use (% of observation scans) of snow geese wintering on the Garwood Prairie, Texas

Field	1983		1984	
	Jan-Feb	Feb-March	Jan-Feb	Feb-Mar
Rice stubble	56	49	44	49
Plowed field	23	13	9	31
Fallow (various plants)	0	33	47	10
Improved pasture	20	5	0	10
No. Scans	467	348	277	394

Most frequently consumed foods and foraging method

Location/Field	Mo(s)	Year	Food Eaten	Foraging Behavior
Rockefeller Wildlife Refuge, LO - brackish marsh	Jan Feb	1983 1984	bulrush tubers & rhizomes (marshhay cordgrass, seashore saltgrass)	grubbing
Garwood Prairie - rice stubble	Jan Mar Mar	1983 1983 1984	green veg (graminoids, forbs)	grazing
Garwood Prairie - rice stubble	Feb	1983	subterranean parts of plants	grazing
Garwood Prairie – fallow fields	Jan Feb	1984 1984	weed seeds	
Riverton, Iowa -corn stubble	Jan Feb	1983 1984	corn	pecking
Other cropland: Kansas Missouri	Feb Jan	1983 1984	green shoots of winter wheat and milo grains	

Nutritional composition of food items

Food Item	Nutrient Composition
seeds and subterranean parts	carbohydrates & rhizomes also high crude fiber
green shoots	protein, less digestible carbohydrate
Corn	deficient in lysine, tryptophan, methionine

Nutritional characteristics in winter habitats (midcontinental US 1983-1984):

	Protein (g)	Mineral (g)
Marsh	7.1	5.3
Rice	22.3	9.1
Corn	8.1	2.0

Additional notes:

Marsh geese had heavier gizzards than rice or corn geese (presumably from the high fiber content of the marsh diet).

By 1950, snow geese were using agricultural areas contiguous to the coastal marshes of Louisiana. By 1970, 60% snow geese wintering in Louisiana were associated with agricultural areas. By 1960, geese were seen feeding and roosting in Texas rice fields, 150 km inland from coast. In December 1980, rice prairies contained 52% of the snow geese wintering in Texas.

- Ankney, C.D. 1977. The use of nutrient reserves by breeding male lesser snow geese. *Chen caerulescens caerulescens*. Canadian Journal of Zoology 55: 1984-1987.

Nutrient reserve loss in male lesser snow geese was examined. Mean body weight was highest at arrival and decreased significantly during the nesting period (20% loss from arrival through late incubation). Fat reserves decreased significantly and were depleted by the middle of post hatch. Significant changes in protein reserves occurred between early and late incubation (a decrease of 14%). Nutrient reserves are primarily expended in territory defense and existence energy.

- Ankney, C.D., and C.D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95: 459-471.

The importance of nutrient reserves to females' clutch size, and successful incubation, was examined. Protein, calcium and fat reserves were measured in lesser snow geese at the McConnell River, NWT. Females with greater fat, protein and calcium had larger potential clutch sizes. Arriving females that were heavier and had greater nutrient reserves had more large developing follicles

(larger potential clutch) than females arriving with less nutrient reserves. These results contradict Davies et al. 1988 study where no relationship was found between body size and clutch size. The difference may be attributed to the fact that McConnell River snow goose females have a longer distance to travel to reach their breeding habitat and have fewer opportunities to feed during migration. The migration distance from the wintering ground to La Pérouse Bay is shorter, and females have more feeding opportunities. Additionally, La Pérouse Bay geese may return back south if weather conditions in the region are poor. McConnell River geese do not have this option in light of the long journey north, and high nutrient expenditure.

7. Aubin, A.E., A. Dzubin, E.H. Dunn, and C.D. MacInnes. 1993. Effects of feeding area on gosling growth in Snow Geese. *Ornis Scandinavica* 24: 225-260.

Variation in relative growth rates among groups of gosling snow geese breeding several kilometers apart was assessed. Ninth primary length showed the greatest variation between sites. The variation was believed to be due to nutritional differences between sites.

8. Bolen, E.G., and M.K. Rylander. 1978. Feeding adaptations in the lesser snow goose (*Anser caerulescens*). *Southwestern Naturalist* 23: 158-161.

This study was undertaken to determine if distinct anatomical features associated between species that grub and species that graze. These features would represent anatomical adaptations reflecting straining habits since, in grubbing, food is sorted from other material in the buccal cavity. The feeding apparatus of the lesser snow geese was examined. The grubbers were found to have stouter maxillary and mandibular serrations than the typical grazers, but these differences were minimal in comparison to certain other grazers (e.g. the white-fronted goose). They contain a larger number of lamellae per tomium length, which is suggestive of a straining function associated with grubbing. Perhaps, then, the less stout and diminutive bill of Ross's geese enabled them to feed more efficiently on the degraded La Pérouse Bay marsh as opposed to snow geese with their stouter bill structure.

9. Burton, B.A., R.J. Hudson, and D.D. Bragg. 1979. Efficiency of utilization of bulrush by lesser snow geese. *Journal of Wildlife Management* 43(3): 728-735.

Metabolizable energy (ME) content of rhizomes was determined to assess its rate of passage through the digestive tract. Changes occurring in the size and capacity of the digestive tract were recorded. ME content of rhizomes was lower than that of most cultivated grains, and the mean length of time rhizomes were retained in the alimentary tract was 2 hours. The rate of passage for a single type of food is relatively constant and is not influenced significantly by the quantity of food. The maximum passage rate for resting snow geese on a diet of *Scirpus americanus* rhizomes was 58 minutes. The rapid passage of food through the

alimentary tract reduces the opportunity for cellulolytic activity. Cellulose, therefore, is probably not of much nutritional benefit to geese. No increase in caecal volume occurred from the increase in levels of crude fiber during the winter. Increases in small intestine (15.4g to over 27.0g) and gizzard size may have been mechanical adaptations to a reduction in diet quality rather than a physiological response to increased microbial populations. The increase in small intestine size may serve to retard the passage rate, permitting improved digestion of the food consumed. Larger gizzard size may increase the rate of food processing. The purpose of these morphological changes may be to improve the utilization efficiency of a food source high in crude fiber.

10. Burton, B.A., and R.J. Hudson. 1978. Activity budgets of Lesser Snow Geese wintering on the Fraser River Estuary, British Columbia. *Wildfowl* 29: 111-117.

Diurnal activity budgets from late August to early spring were recorded to determine the important factors affecting feeding and sleeping. Food availability, dependent on changes in tidal fluctuations and flock location, was the major factor in feeding and sleeping periodicity. 83% of all feeding activity took place between 2.0m -3.7m tide levels. They ate *Scirpus americanus* and *S. paludosus*, which grow between 2.1m and 3.5m. They fed an average of 7.2 hours each day, amounting to only 52% of the total activity budget even during periods of optimal food accessibility. This is indicative of efficient feeding techniques and a nutritious diet. Geese rested when tide levels were below 2.1m or above 3.4m, preened when the water depth was 3.7m, and became increasingly alert as the tide height reached a maximum of 4.0m. Nocturnal feeding occurred both in and out of hunting season, indicating that fluctuating food availability (due to changing tide levels) is more important than hunter pressure.

11. Cargill, S.M., and R.L. Jefferies. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology* 21: 669-686.

The effects of goose grazing on net primary production and nutritional quality of forage at the salt marsh on La Pérouse Bay was analyzed. Grazing increased net above-ground primary production and nitrogen concentrations. Grazing was thought to stimulate primary production by accelerating nitrogen cycling. Grazing may still be beneficial to plant growth at La Pérouse Bay if extensive spring grubbing by increased numbers of geese did not precede summer grazing (see Kerbes 1990 for explanation of grubbing).

12. Cooch, E.G., R.L. Jefferies, R.F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia* 93: 128-138.

Dispersal from traditional foraging areas may be an adaptive strategy under conditions of temporal environmental change. Patterns of gosling growth and

survival among broods remaining philopatric to the traditional foraging area at La Pérouse Bay were compared to growth patterns of goslings that had dispersed to surrounding areas. Goslings from dispersed broods were significantly greater in mass and structural size, and have a higher survival rate than goslings from broods remaining. These differences appear to be due to differences in the higher quality and quantity of forage plants eaten by dispersed broods.

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

This study examines the pattern of annual variation in body size of gosling female lesser snow geese at La Pérouse Bay due to an increase in the numbers of snow geese using the marsh, and concurrent declines in available food resources. Body mass and structural size were examined. Results from data from 1969-1986 showed the following: a long-term decline in gosling body mass (15%), tarsus (4%), and culmen length (2%), a decrease in gosling tarsus and culmen length with later mean hatch date, and reduced growth rates in body mass, tarsus, and culmen length. Results from analyses on long-term declines in body mass, tarsus, and culmen from chapter 2 in this dissertation support Cooch et al. findings. All declines were found to be due to environmental factors (late hatch date, cold, wet weather, reduction in food availability), rather than genetic factors.

14. Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* 72(2): 503-512.

The influence of timing of reproduction and brood size on gosling growth rates were examined. Growth rates declined during the season. Goslings with later hatch dates, and from smaller brood sizes, grew more slowly resulting in smaller adults. It is believed that environmental conditions during brood-rearing have a great effect on final adult body size. Goslings from larger broods grew faster possibly due to behavioral interactions between broods.

15. Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. *The Snow Geese of La Perouse Bay. Natural Selection in the Wild.* Oxford University Press, Oxford.

All aspects of the lesser snow goose of La Pérouse Bay are discussed at length.

16. Davis, S.E., E.E. Klaas, and K.J. Koehler. 1989. Diurnal time-activity budgets and habitat use of Lesser Snow Geese *Anser caerulescens* in the middle Missouri River valley during winter and spring. *Wildfowl* 40: 45-54.

In late December to March 1983 and 1984, lesser snow geese mainly fed on corn stubble. They also fed on winter wheat and brome grass, especially during spring. The availability of waste corn in the middle Missouri River valley may influence

winter distribution of lesser snow geese. Corn is a high-energy food, and as such lesser snow geese can winter north of their traditional wintering ground despite more severe weather. They spend less time and energy obtaining food than geese feeding on grass and rhizomes in rice fields and salt marshes along the Gulf Coast. Geese mostly loafed and slept on land and on water, especially during winter. Feeding occurred on land more frequently during migration. Alert behaviors occurred both on land and on water most frequently during early migration.

17. Davies, C.J., R.F. Rockwell, and F. Cooke. 1988. Body-size variation and fitness components in lesser snow geese (*Chen caerulescens caerulescens*). *Auk* 105: 639-648.

Genetic variation and fitness associated with adult body size in lesser snow geese at La Pérouse Bay was examined. There is a heritable component to body size variation derived from the transmission and segregation of genes with additive effects on body size. A fitness differential is associated with this body-size variation. Smaller birds bred earlier with no reduction in viability and may have a longer lifespan than larger birds. As such, the authors believe that smaller birds may have higher fitness than larger birds. No relationship was found between body size and the number of eggs laid, the number of eggs surviving predation, the number of goslings leaving the nest, and the number of goslings fledging. This study should engender further research on the fitness differential between the larger snow goose and Ross's goose to determine if Ross's geese have higher fitness as compared to snow geese.

18. Flickinger, E.L., and E.G. Bolen. 1979. Weights of lesser snow geese taken on their winter range. *Journal of Wildlife Management* 43(2): 531-533.

Weights of lesser snow geese from the Garwood Prairie in Colorado County, Texas, were taken to determine if weights increased before northward migration. During pre-spring migration adult males, females, and immature females weighed less than in the post-fall migration period. In May 1971 and 1972 in the Northwest Territories, males and females weighed more than in March and April. The weights of adult male and females and the amount of fat on them on the Garwood Prairie in March were similar to late incubation period measurements of geese at the McConnell River in late June.

19. Frederick, R.B., and E.E. Klaas. 1982. Resource use and behavior of migrating snow geese. *Journal of Wildlife Management* 46(3): 601-614.

Frederick and Klaas observed lesser snow geese at the DeSoto National Wildlife Refuge in 1976-1977. They spent a greater proportion of time feeding in corn stubble fields (off the refuge) than in refuge wheat fields. They used wheat fields primarily for loafing and sleeping.

20. Gadallah, F.L., and R.L. Jefferies. 1995. Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. *Journal of Applied Ecology* 32: 276-287.

A decline in gosling weight over the last 10 years can be attributed to decreases in preferred nutrient-rich salt marsh vegetation and the alternative use of nutrient-poor inland forage, which explains the results in chapter 2 on the long-term declining body mass of snow goose goslings. Experimental feeding trials were performed on captive goslings to determine their ability to utilize different types of forage (saltmarsh - *Puccinellia phryganodes* and *Carex subspathacea*; inland - *Festuca rubra*, *Carex x flavicans*, *Carex aquatilis*). Birds gained or maintained weight on the salt marsh diet, and either maintained or lost weight on the inland diet. Salt marsh vegetation has a higher nutrient content and lower fiber and silica versus inland vegetation that is lower in nutrients and higher in fiber and silica.

21. Ganter, B., and F. Cooke. 1996. Pre-incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity? *Oecologia* 106: 153-165.

The contribution of early spring feeding on lesser snow goose clutch size variation was examined. Energy budgets of prelaying and laying females were estimated via a combination of behavioral observations and energetic analyses of food. Food intake from arrival on the breeding ground to incubation was high, with energy gained during this period possibly contributing to the addition of one or several eggs. They conclude that the prelaying period on the breeding ground can be energetically beneficial. However, given declines in body mass, structural measurements, and survival of goslings, the beneficial effect of early spring feeding appears negated by the lack of good quality resources throughout brood rearing.

22. Gawlik, D.E., and R.D. Slack. 1996. Comparative foraging behavior of sympatric Snow Geese, Greater White-fronted Geese, and Canada Geese during the non-breeding season. *The Wilson Bulletin* 108(1): 154-159.

Focal time-budgets were performed on flocks of three species of geese (Lesser Snow, Greater White-fronted, and Canada) from November 1991 to February 1992, and October 1992 to February 1993 on agricultural fields in Colorado and Wharton counties. All three species spent most of their time feeding or in alert behaviors. Time spent feeding, resting, and alert did not differ interspecifically. Canada geese spent more time feeding while walking and less time feeding while stationary than did snow and Greater White-fronted geese. These differences corresponded to differences in diet and morphology. Canada geese spent more time grazing exposed portions of plants, whereas snow and Greater White-fronted geese grubbed.

23. Gloutney, M.L., R.T. Alisauskas, A.D. Afton, and S.M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and Lesser Snow Geese. *Oecologia* 127: 78-86.

Foraging time and food mass consumption of breeding female Ross's and lesser snow geese were compared at Karrak Lake, N.W.T., Canada. Female Ross's spent more time foraging (mean % \pm SE=28.4 \pm 1.3%; P=0.0002) than female snow geese (21.5 \pm 1.4%). Females of both species spent more time foraging during prelaying and laying than during incubation. Ross's foraged longer during incubation recesses than snow geese. Consumption of organic matter averaged 9.6 \pm 4.0g and 12.4 \pm 4.6g (mean \pm SE) dry/mass/day before incubation and 5.9 \pm 2.0g and 5.7 \pm 2.1g for lesser snow and Ross's respectively. Diets consisted of mosses (bryophytes), Chickweed (*Stellaria* spp.) and sedges (*Carex* spp.). Eggshell consumption was 4.3 \pm 3.2g and 0.4 \pm 0.3g dry/mass/day for lesser snow geese and Ross's before incubation. Neither ate eggshells during incubation. They concluded that eggshell consumption is an important source of dietary calcium meeting mineral demands of eggshell formation. One may conclude then that Ross's goose females commence brood rearing in better physical condition than snow goose females, and are better able to care for young. However, this appears unlikely given that consumption of plant matter by both species was minimal, and the major plant consumed was moss that is low in nutritional value.

24. Gloutney, M.L., R.T. Alisauskas, K.A. Hobson, and A.D. Afton. 1999. Use of supplemental food by breeding Ross's geese and lesser snow geese: Evidence for variable anorexia. *Auk* 116: 97-108.

The importance of exogenous resources to reproduction was investigated. Food supplementation experiments were conducted on breeding female Ross's geese and lesser snow geese during egg laying and incubation to evaluate: if females consumed supplemental food, how food consumption influences mass dynamics of somatic tissues, whether patterns of mass loss were consistent with fasting adaptations, and whether the smaller Ross's goose would eat more food relative to its body size than the larger snow goose. The quantity of food eaten was found to be highly variable. Treated Ross's goose females completed egg laying heavier and with more abdominal fat than untreated Ross's geese. Treated snow goose females completed egg laying with heavier breast muscles and hearts. Overall body composition did not differ between treatment and control geese at the end of incubation, but treatment geese had heavier hearts than control geese suggesting that treatment geese did not rely to the same extent on metabolic adaptations associated with fasting to meet energetic costs of incubation as did controls. Ross's geese consumed 30% less mass-specific food than snow geese during egg laying, and 48% more mass-specific food than snow geese during incubation.

25. Gregoire, P.E., and C.D. Ankney. 1990. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk* 107: 550-560.

Dominance and aggression among family and nonfamily groups in salt marshes and rice fields in Louisiana were examined during winter and spring migration periods. Large families dominated over small families, which dominated over pairs (no brood), lone adults, and lone juveniles. Adults of single-parent families were involved in a greater proportion of encounters than were adults of two-parent family groups, won most of the interactions over broodless pairs, and lost most interactions with two-parent families. Most aggressive interactions occurred in salt marshes and cornfields and were food related. Aggressive interactions were 3 times more frequent in cornfields than in other habitats. Family groups initiated most interactions, with larger families tending to initiate more interactions than smaller families. Any group initiating an interaction was more likely to win. Juveniles in families fought less than lone juveniles. Parents took part in more interactions than their offspring (most encounters involved only one adult). As family size increased, involvement in interactions decreased. Part of the study on snow goose and Ross's goose foraging in chapter 3 was to determine the extent of agonistic encounters between the two species due to increased competition for resources. Unexpectedly, very few were observed. I concluded that given the severity of the degradation, geese needed to expend energy to feed, not fight.

26. Harrold, C.G. 1928. Notes on the lesser snow and blue geese observed at Whitewater Lake, Manitoba. *Auk* 45: 290-291.

Observations performed April 11-May 9, 1926 showed that geese preferred barley to any other variety of grain.

27. Harwood, J. 1977. Summer feeding ecology of lesser snow geese. *Journal of Wildlife Management* 41(1): 48-55.

Variations in feeding behavior during the summer of 1973, based on changes in the characteristics of vegetation, were measured at the McConnell River, NWT. Standing crop of green monocotyledons attained its maximum value in the first week of August then declined. Variation in feeding bout length of males and females showed a similar pattern to variations in vegetation standing crop, with maximum bout lengths reached the first week of August. Pecking rates reached peak values in mid-July then declined in August, corresponding to crude protein content of ungrazed monocotyledons. Crude protein content of grazed monocotyledons had a maximum crude protein content in late July, with little decline in August. In contrast to both studies in my thesis, no variation in the feeding bout length occurred. It may be that vegetation values were relatively constant throughout the season due to the initial high level of degradation.

28. Hik, D.S., R.L. Jefferies, and A.R.E. Sinclair. 1992. Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology* 80: 395-406.

The effects of grazing by lesser snow geese on above-ground biomass and species composition of vegetation were examined at La Pérouse Bay. Cessation of grazing leads to changes in species composition including declines in the frequency of *Puccinellia phryganodes*, and increases in dicotyledonous plants and *Calamagrostis deschampsiodies* and *Festuca rubra*. In turn, there is an increase in amounts of litter deposited on the surface of the sediment. This results in a decrease in surface temperatures leading to lower rates of evapotranspiration and corresponding reductions in the salinity of surface sediments.

29. Hobaugh, W.C. 1984. Habitat use of snow geese wintering in Southeast Texas. *Journal of Wildlife Management* 48 (4): 1085-1096.

Observations of 1.6 million snow geese were taken. 60% of geese were seen in rice-stubble fields and rice fields were the most intensively used habitat type. Geese shifted to soybean and plowed fields once rice was depleted.

30. Hobaugh, W.C. 1985. Body condition and nutrition of snow geese wintering in southeastern Texas. *Journal of Wildlife Management* 49(4): 1028-1037.

Body conditions of 703 snow geese were examined from October - March 1978-1979 and 1979-1980. Esophageal contents consisted exclusively of rice kernels in October and November, new plant growth in January, and green vegetation in February and March. Nutritional analysis showed high concentrations of soluble carbohydrates (nitrogen-free extract) and energy, moderate levels of protein in October and November, and higher protein levels and lower concentrations of soluble carbohydrates and energy in January and February through March.

31. Jefferies, R.L., and R.F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5: 7-16.

Long-term changes in vegetation on the intertidal salt marsh at La Pérouse Bay were examined. Due to intensive goose grazing, in 1999 above-ground biomass estimates of *Puccinellia phryganodes* and *Carex subspathecea* fell to between 20 and 30 g m⁻² from estimates of 40 - 60 g m⁻² in 1979. Plant cover is now estimated at less than 2%, with the remaining area composed of bare sediment. It must be noted that destructive spring grubbing preceded summer grazing, which is what initiated the damage. Otherwise, grazing is beneficial to plant growth (see Cargill et al. 1984).

32. Kerbes, R.H., P.M. Kotanen, and R.L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27: 242-258.

The affect of the lesser snow geese foraging on the plant community along the west coast of Hudson Bay was described. Spring grubbing by geese on roots and rhizomes of graminoid plants creates bare areas of peat and sediment. The increased numbers of birds have increased the scale of disturbance, especially around the McConnell River. It is believed to be unlikely that the vegetation that re-establishes will closely resemble the original.

33. Kotanen, P., and R.L. Jefferies. 1997. Long-term destruction of wetland vegetation by lesser snow geese. *Ecoscience* 4: 1895-1898.

Foraging by geese, specifically shoot pulling of sedges, was shown to have deleterious effects on shoot densities, and ultimately on species composition of plant assemblages.

34. Lessells, C.M. 1987. Parental investment, brood size and time budgets: behaviour of lesser snow goose families. *Ardea* 75: 189-203.

The extent to which parental care can limit optimal clutch size was examined by investigating adult and gosling lesser snow goose behavior in relation to brood size. Feeding rates of both adults and goslings, and time budgets of goslings, did not vary with brood size. With increasing brood size, the amount of sitting by parents declined, and adult-gosling minimum distance decreased and maximum adult-gosling distance increased. Non-breeders stood and fed more, sat and used the extreme head-up posture less. Females fed proportionately more than males.

35. MacInnes, C.D., R.K. Misra, and J.P. Pevett. 1989. Differences in growth parameters of Ross' geese and snow geese: evidence from hybrids.

Growth parameters of Ross's and lesser snow goose goslings were subjected to genetic analysis and evaluated to determine if differences were related to breeding environment. Ross's had more genes contributing to faster growth rate. It is thought that this faster growth rate is due to the short plant growth season and severe weather conditions associated with breeding in the high Arctic. This may have contributed to the high reproductive success of Ross's geese versus snow geese observed on La Pérouse Bay in chapter 3.

36. McCracken, K.G., A.D. Afton, and R.T. Alisauskas. 1997. Nest morphology and body size of Ross' geese and lesser snow geese. *The Auk* 114(4): 610-618.

Nest size, representative of nest insulation, of Ross's and lesser snow geese in 4 different habitats at Karrak Lake was compared. Ross's geese constructed relatively larger, more insulated nests than snow geese. This may increase

embryonic development, minimize energy expenditure during incubation, and minimize embryonic cooling during incubation recesses. The difference in nest size may reflect greater selection for efficient nest insulation by Ross's geese because of their small size, higher mass-metabolic rate, and lower incubation constancy. Differential nest construction between snow geese and Ross's geese should be examined at La Pérouse Bay to determine differences in nest construction could have contributed to the high local reproductive success of Ross's geese versus snow geese. However this is a difficult proposition given that the primary nesting area of Ross's geese on La Pérouse Bay has yet to be located.

37. McIlhenny, E.A. 1932. The blue goose in its winter home. *Auk* 49(3): 279-306.

McIlhenny gives detailed observations of fall and spring migration patterns, distribution of geese, food and feeding behaviors, plumage coloration, goose calls, and known predators of the blue goose wintering on Avery Island, Louisiana. He observed that blue geese never fed or slept more than 8 miles back in the marshes from the salt beaches, and primarily grubbed (roots during the day), not grazed in winter. Upon first arrival in October and early November, they fed on seeds of feather grass (*Leptochloa fascicularis*) and wild millet (*Echinochloa crus-galli longiaristata*). When these became depleted, they ate roots of 3 cornered grasses (*Scirpus robustus* and *Scirpus americanus* - their staple food) and roots of paille salle (*Spartina patens*). They also ate tubers and roots of Delta duck potato (*Sagittaria platyphylla*) and occasionally nibbled on young grass and other roots. At times they fed exclusively on one root or the other (3-cornered grasses and paille seed), and preferred sections freshly burned over. Grass that had been burned and re-sprouted green shoots were not desirable. In early fall, when no fires were set, they settled on grass 4-5 feet high beating it flat with their wings (done in 3-cornered grass only where stems are soft). They discarded the fibrous roots and ate the rhizomes. Sand (grit) was eaten every second or third day. During pre-migration gathering, they became lazy, fed little, got very noisy, fought, took flight, circled, then returned.

38. Mobrawy, T.B, F. Cooke, and B. Ganter. 2000. Snow Goose *Chen caerulescens*. *The Birds of North America* 514: 1-40.

Snow goose biology, morphometrics, systematics, behavior, food habits and nutrition, migration routes, winter and breeding habitats and ecology, disease, population dynamics, and conservation and management are discussed in detail.

39. Mulder, R.S., T.D. Williams, and F. Cooke. 1994. Dominance, brood size and foraging behavior during brood-rearing in the lesser snow goose: an experimental study. *Condor* 97: 99-106.

The relationship between brood size and social dominance during brood rearing was examined. It was found that families (pairs with one or more goslings) were always dominant over pairs without goslings. Individual aggressiveness and

successful interactions varied with brood size therefore it was concluded that dominance ranking is determined more by individual aggressiveness of the parent rather than by brood size. Gregoire et al. 1990 drew the same conclusions from their study of wintering geese. Aggressiveness was rare on La Pérouse Bay during my years of study (1998-2001), therefore it was difficult to determine social dominance.

40. Owen, M. 1980. Wild Geese of the World: Their life history and ecology. B.T. Batsford, Ltd., London. 236pp.

Owen provides a detailed description of the a variety of geese species as well as their geographical variation, population numbers and distribution, breeding and winter biology, and their exploitation by man over the years.

41. Prevett, J.P., I.F. Marshall, and V.G. Thomas. 1979. Fall foods of lesser snow geese in the James Bay Region. *Journal of Wildlife Management* 43(3): 736-742.

9 species of plants from the following made up 90% of foods eaten: sedges (Cyperaceae), arrow grasses (Juncaginaceae), horsetails (Equisetaceae), and grasses (Graminaea).

1975: On Winsk geese ate *Equisetum variegatum* (shoots -90%)

1976: On Southern James Bay geese ate various sedges with carex species dominant, and *Puccinellia langeana*. The arrowgrass *Triglochin palustris* was the most important food; its bulbs are a good source of crude protein, carbohydrates and minerals. Parts of plants eaten were roots, seeds, and bulbs of *T. palustris* (just over 10%), fibrous roots of sedges and grasses, and seeds of sedges (especially Carex-13%).

42. Ryder, J.P. 1967. The breeding biology of Ross' goose in the Perry River region, Northwest Territories. Canadian Wildlife Service Report Series No. 3. Ottawa.

Extensive details are given on the breeding distribution, reproductive and post-breeding biology, nesting ecology, and breeding behavior of Ross's geese.

43. Ryder, J.P., and R.T. Alisauskas. Ross' Goose. 1995. *The Birds of North America* 162: 1-28.

Ross's goose biology, morphometrics, systematics, behavior, food habits and nutrition, migration routes, winter and breeding habitats and ecology, disease, population dynamics, and conservation and management are discussed in detail.

44. Slattery, M., and R.T. Alisauskas. 1995. Egg characteristics and body reserves of neonate Ross' and lesser snow geese. *The Condor* 97: 970-984.

The effects of species, timing of nesting, and egg size on composition of eggs and goslings were examined. Snow goose eggs are larger and have heavier constituent components than Ross's goose eggs. However when controlled for egg size there was no difference in components between species. Correcting for differences in egg size, Ross's eggs had more protein than snow goose eggs. Structural measurements were larger in snow goslings than Ross's except for pectoralis muscle that was larger in Ross's. Ross's goslings had less water per gram of dry skeletal tissue mass than snow goslings indicative of more functional maturity of Ross's neonate tissue. Larger gizzard size and enhanced functional maturity of the Ross's gosling may represent adaptations to metabolic constraints associated with smaller body size. These enhanced features may have contributed to their high survival rates on La Pérouse Bay in 1999. Further studies on survival rates of snow goose and Ross's goose goslings breeding sympatrically in other habitats could prove useful in determining the effects if faster growth rates affect survival rates.

45. Slattery, S.M., G. Samelius, R.T. Alisauskas, J.R. Danielson, and F.P Moore. 1998. For whom the geese toll: aberrant or adaptive behaviour in Ross's *Chen rossii* and lesser snow geese *Chen caerulescens caerulescens*? *Wildfowl* 49: 242-244.

Tolling -the response of approaching or following terrestrial predators or novel moving objects - by geese during nesting was studied. Tolling may be an adaptive mobbing response to predators. Long-distance tolling may be a type of inspection behavior that serves as learning function, informing geese of the identity and behavior of potential predators.

46. Soper, J.D. 1942. Life history of the Blue Goose *Chen caerulescens* (Linnaeus). *Proceedings of the Boston Society of Natural History* 42(2): 121-225.

Soper provides a detailed description of various aspects of the Blue Goose, including a description of the goose, its geographical distribution, breeding and wintering areas, fall and spring migration ranges, and food and feeding patterns. He outlined the foods grubbed on Baffin Island in order of most consumed. Those included: the common tundra grass (*Carex stans*), roots of *Carex membranopacta*, Arctic meadow grass (*Poa arctica*), foxtail grass (*Alopecurus alpinus*), and Arctic cotton grasses (*Eriophorum Scheuchzeri* and *E. callithrix*).

47. Sprunt, A. 1936. The blue goose again in Coastal S. Carolina. *Auk* 53: 75-76.

Observations performed on November 7, 1935 at Summerhouse Pond on Bull's Island (part of the Cape Romain Federal Bird Refuge) showed that birds remained there for one week. The pond contained widgeon grass, sago, pond-weed, and banana water lily. Exactly what the geese ate was not determined.

48. Trauger, D.L., A. Dzubin, and J.P. Ryder. 1971. White geese intermediate between Ross's geese and lesser snow geese. *Auk* 88: 856-875.

Various morphometric measurements of white geese with characteristics intermediate between lesser snow and Ross's geese were taken between 1961-1968 in Saskatchewan, the central and eastern Canadian Arctic, Louisiana, Missouri, Iowa, Nebraska, and South Dakota. Head and bill measurements provided the most obvious evidence that the geese were lesser snow and Ross's goose hybrids. The occurrence of Ross's geese outside the traditional wintering range may have contributed to the breakdown of isolating mechanisms caused by a shortage of conspecific mates in large concentrations of lesser snow and blue geese in the Mississippi and Central Flyways. Competition for nesting sites where lesser snow and Ross's geese are sympatric has resulted in mixed clutches, most notably in late springs. It is thought that young from these nests may become imprinted to the wrong species-specific characteristics inducing hybridization.

49. Williams, T.D. 1994. Adoption in a precocial species, the lesser snow goose: intergenerational conflict, altruism or a mutually beneficial strategy? *Animal Behavior* 47: 101-107.

This study focused on whether adoption represents intergenerational conflict, altruism, or some mutual benefit to both goslings and adults. If adoption represents an intergenerational conflict than adults should be selected to reject genetically unrelated goslings. Selection should exist for traits that allow young to solicit parental care from non-genetically related adults, and costs should be incurred by adopting adults (reduced fitness and survival). Of 982 broods sighted, 131 (13.3%) adopted one or more goslings, 264 (26.9%) lost one or more goslings, and 587 (59.8%) showed no change in brood size. Daily probability of adoption was greater between days 25 and 30 post hatch. Of 96 broods, 91 (94.8%) adopted goslings the same color as the original brood, and 5 (5.2%) of adopted goslings were a different color. Results show that adoption does not represent intergenerational conflict and altruism. In fact, adoption appears to be beneficial to both adults and goslings. Goslings of larger broods may grow faster than goslings of smaller broods. Additionally, the family unit may gain a higher dominance ranking on the wintering grounds allowing them increased access to resources, resulting in increased overwinter survival. Return rates to the breeding grounds were also higher in adopting versus non-adopting adults.

50. Williams, T.D., M.J.J.E. Loonen, and F. Cooke. 1994. Fitness consequences of parental behavior in relation to offspring number in a precocial species: the lesser snow goose. *Auk* 111(3): 563-572.

Analyses were conducted on the relationship between parental behavior and brood size, the effect of parental age on parental care and the number of offspring reared, and the relationship between the number of offspring reared and five measures of parental fitness including: (1) timing of molt and body mass at molt in the brood rearing year, and (2) the probability of return, timing of breeding, and clutch size in the year following brood rearing. The percentage of time spent feeding by parental birds decreased with increasing brood size (90% for 0 goslings to 80% for 7-8 goslings). Alert postures increased with increasing brood sizes from 1-5, then decreased for brood sizes over 5. Males spent more time in alert behaviors and less time feeding than females. Ninth primary length decreased significantly in males with increasing brood size (an average of 3.96 mm for each additional gosling) such that males with larger broods molted significantly later in the season. Ninth primary length increased significantly with increased brood loss in males with broods of ≥ 4 (4.01 mm per gosling lost). Birds with the largest decrease in brood size molted significantly earlier. It was concluded that parental fitness does not decrease with larger brood sizes.

51. Wypkema, R.C.P., and C.D. Ankney. 1979. Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. *Canadian Journal of Zoology* 57: 213-219.

Observations were performed at James Bay during spring migration and fall migration. The objective was to determine if adult geese use James Bay in the spring to accumulate nutrient reserves for breeding and gonadal development, and in the fall for post-breeding weight loss recovery and structural growth in juveniles. In spring, adult body weight and protein reserves in females increased. There were no changes in fat reserves in males or females. Ovary weight was positively correlated with body weight, protein and fat reserves. During fall, fat reserves increased in males, females and juveniles. Tarsus length in male and female juveniles increased, but protein reserves could not be evaluated.