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THE IMPLICATIONS OF AGRICULTURE IN INTERIOR ALASKA FOR POPULATION DYNAMICS OF CANADA GEESE

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Michael William Eichholz, B.S. M.S.

Fairbanks, Alaska

December 2001

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THE IMPLICATIONS OF AGRICULTURE IN INTERIOR ALASKA FOR POPULATION DYNAMICS OF CANADA GEESE

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ABSTRACT

Understanding how environmental change affects demography is essential for understanding and managing populations. An anthropogenic change in the environment that has affected wildlife populations is widespread agricultural development. Agriculture has both negatively and positively impacted abundance of species by affecting a variety of vital rates that influence population abundance. In this study, I describe the migration ecology of Canada geese (*Branta canadensis*) that nest and stage in Interior Alaska. I also describe how the introduction of agriculture has potentially positively impacted population dynamics of Canada geese by increasing nutrient acquisition, thereby improving their fecundity and survival. Two subspecies of Canada geese used Interior Alaska for staging and at least partially segregated themselves during spring and fall staging. I documented a difference in survival between two age classes of Canada geese, primarily lesser Canada geese (*B. c. parvipes*), and attributed it to the higher susceptibility to harvest of hatch-year (HY) geese. Estimates of annual survival of Canada geese in this study are among the lowest, and estimates of recovery rates are among the highest, for a migratory population of geese, likely due to behavioral traits and habitat selection that make lesser Canada geese more susceptibility to harvest. Survival of after-hatch-year (AHY) female Canada geese was positively associated with the amount of endogenous nutrient reserves females had at the time of banding in fall. An experimental manipulation of nutrient reserves, however, suggested that the association between nutrient reserves and survival results from variation in individual quality (not measured), not a direct relationship between nutrient reserves and survival.

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Female geese in our study gained fat and minerals, but not protein, during spring staging. Fall staging geese had fat levels greater than or equal to spring staging geese, suggesting fat reserves are important during early fall staging in this population of geese. Although I concluded that the introduction of agriculture has likely increased fecundity and decreased natural mortality in Canada geese that stage and breed in Interior Alaska, I also concluded that mortality due to harvest is sufficient to offset those changes, preventing an increase in the population.

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No one completes a graduate degree without the help and support of numerous friends and colleagues. Unfortunately, often the only opportunity we are given to publicly acknowledge and thank these people is at the completion of our degree. Although these few words understate the gratitude I have for these people, I hope they give them some insight into the way I feel.

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Although this is a single-authored thesis, each chapter is written as a manuscript for publication and co-authored. Thus, the "we" in each chapter refers to the authors and others who assisted in collecting and analyzing data.

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INTRODUCTION

Two of the key components of the dynamics of a population are fecundity and mortality. These two demographic parameters are often influenced directly by environmental conditions. Thus, the influence of these two parameters is dependent on environmental conditions experienced by the individual. A change in the balance between average fecundity and mortality will lead to a change in the population trajectory. For example, a change in the environment, allowing fecundity to increase, without a balancing increase in mortality, will bring about an increase in the population growth rate (Wakeley 1982). Environmental factors that are known to influence population dynamics include weather (Francis 1970), predation (Mosby 1969), and inter- and intraspecific competition (Orians and Willson 1964, Anderson 1977 Sedinger et al. 1998).

Understanding how environmental change affects the demographic parameters that determine population dynamics is essential for understanding and managing populations (Wakeley 1982). An anthropogenic change in the environment that has affected numerous wildlife populations is widespread agricultural development. Agricultural development has both positively and negatively impacted abundance of numerous species by affecting a variety of life history traits that influence population abundance (Yeater 1963, Gates and Gysel 1978, Oehler and Litvaitis 1996, Heske 1999). For example, agricultural practices have been detrimental to duck populations nesting in the mid continent prairies (Beauchamp et al. 1996). Numerous goose populations, in contrast, have increased in response to agricultural development; most dramatically are lesser snow (*Chen caerulescens caerulescens*) and Ross' geese (*C.*

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rossii) (Abraham et al 1996). The change in abundance of lesser snow and Ross' geese is likely a result of modern agricultural practices, which has increased food availability during winter and spring migration, decreasing competition, leading to an increase in both fecundity and survival (Abraham et al. 1996).

Arctic-nesting and to a lesser extent subarctic-nesting geese are dependent on nutrient reserves for most of their reproductive nutrients (Ankney and MacInnes 1978, Raveling 1979, Gates et al. 1998). Geese acquire these nutrient reserves during late winter or during spring migration (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979, Alisauskas and Ankney 1992). An increase in nutrient availability from agricultural cropland has likely increased the nutrient reserves that geese carry to the breeding grounds, thereby increasing their fecundity (Abraham et al 1996). The introduction of modern agriculture, in conjunction with safety provided by wildlife refuges, also has increased the survival of lesser snow and Ross' geese (Francis and Cooke 1992, Abraham et al 1996). Agricultural development in the Canadian prairies has increased food availability, which is also an important determinant of a successful fall migration (Wypkema and Ankney 1979, Sedinger and Bollinger 1987). Furthermore, agricultural development on the wintering grounds has extended wintering habitat availability (Alisauskas 1998). Before the introduction of rice (*Oryza sativa*) in Texas and Louisiana, lesser snow geese were restricted to coastal salt marsh habitat for winter-feeding (Alisauskas 1998). The introduction of rice inland from the coast has provided an additional source of food, allowing lesser snow geese to expand their range into the rice fields, decreasing intraspecific competition on their winter range.

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Development of grain agriculture in Interior Alaska in the 1960's - 1980's created spring and fall staging habitat for geese nesting in and migrating through this region. About 44,000 ha of boreal forest were cleared near Delta Junction in 1978 - 1983, and barley (*Hordeum murinum*) has been grown there. Geese also are attracted to a warm water lake in the area, which provides open-water roost sites in spring when other bodies of water are still frozen. Barley also is grown in two locations in Fairbanks, Creamers Field Migratory Bird Refuge, and the University of Alaska experimental agricultural fields. All of these areas are used by Canada geese (*Brant canadensis*) and greater white-fronted geese (*Anser albifrons frontalis*) during spring and fall. Availability of sources of food within 100 km of breeding areas of geese nesting in the subarctic has the potential to dramatically influence dynamics of these goose populations.

Little is known about the Canada geese that use these areas for spring or fall staging or how the introduction of agriculture to Interior Alaska has affected them. Canada geese staging in Interior Alaska are thought to be primarily lesser Canada geese (*B. c. parvipes*) and Taverner's Canada geese (B. c. *taverneri*) (King and Hodges 1979).

Lesser Canada geese are thought to nest from Upper Cook Inlet to the southern edge of the Brooks Range, west to the transition zone between forest and coastal tundra, and east into the Yukon River basin in Yukon Territory, Canada (Johnson et al. 1979, Fig. 1.1). Taverner's Canada geese nest on coastal tundra of the north and west coast of Alaska (Johnson et al. 1979). Although these two subspecies are similar in body size (Johnson et al. 1979), Quinn et al. (1991) suggested lesser Canada geese, the smallest of the large-bodied races, and Taverner's Canada geese, the largest of the small-bodied

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races, last shared a common ancestor approximately 1 million years ago.

Numerous molting lesser and Taverner's Canada geese have been banded since 1941 near Teshekpuk Lake on the North Slope of Alaska (King and Hodges 1979, Fig. 1.1). Because of difficulties in distinguishing between lesser and Taverner's Canada geese (King and Hodges 1979, Johnson et al. 1979), however, our understanding of nay differences in migration routes, staging, and wintering areas is poor.

In this study, I describe migration and wintering characteristics of Canada geese staging in Fairbanks and lesser and Taverner's Canada geese staging in Delta Junction Alaska. I also estimate annual survival of Canada geese trapped during early fall staging in Fairbanks Alaska, which, based on morphology and winter distribution, are primarily lesser Canada geese. I test for age class- and sex-specific survival and recovery rates, and discuss how and when different age class- and sex-specific adult survival and recovery might occur. I also compare survival and recovery estimates of Canada geese staging in Interior Alaska with those for other subspecies of Canada geese, and discuss management implications of my results. I report on the potential impact on this subspecies of Canada geese of introducing agriculture to Alaska by describing nutrient dynamics of Canada geese during spring and fall staging and comparing my results with those from studies of goose populations foraging on natural vegetation. I also investigate the potential impacts of introducing agriculture to Interior Alaska by testing the hypothesis that geese in better body condition in early fall staging survive at a higher rate than geese in poorer condition. I then use a manipulative experiment to test whether the association between body condition and survival is a direct relationship, or a result of

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confounding among body condition, individual quality, and survival. Finally, I test for a relationship between body size and survival, independent of condition, because body size has been found to be positively related to other life history traits (Ankney and MacInnes 1978, Sedinger et al. 1995, Eichholz and Sedinger 1999).

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CHAPTER 1

STAGING, MIGRATION, AND WINTER DISTRIBUTION OF CANADA GEESE BANDED ON STAGING GROUNDS IN INTERIOR ALASKA

Eichholz, M. W. and J. S. Sedinger. Staging, migration, and winter distribution of Canada geese banded on staging grounds in Interior Alaska. Prepared for submission to the Journal of Field Ornithology.

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ABSTRACT

Currently, our understanding of the subspecific composition and ecology of Canada geese staging in Interior Alaska is poor. Here, we describe staging, migration, and wintering distribution of neck-collared Canada geese that migrate through and stage in Fairbanks and Delta Junction, Alaska. We also report results of weekly aerial and ground based surveys in Delta Junction and opportunistic ground based surveys in Fairbanks to estimate the staging chronology and number of geese using the area. Finally, we measured exposed culmen, flattened wing chord, total tarsus, and body length of geese staging in Interior Alaska to assist with determination of subspecific status. During spring in all years, the number of geese gradually increased in the Delta Junction staging area from early to mid-April until 3,000 - 6,000 were present, then a large influx of 8,000 - 12,000 geese occurred over a 2-day period, with another gradual increase until a peak of about 18,000 geese occurred. Geese then departed *en mass* in a 2-day period at the end of April. The first principal component, as well as univariate measurements of total tarsus and exposed culmen, indicated geese trapped in Fairbanks in the fall were larger than geese trapped in Delta Junction in either spring or fall. Most banded geese detected in winter were observed or recovered in central Washington and north-central Oregon, east of the Cascade Mountain range, with relatively few sightings in western Washington and Oregon. We found no evidence of movement between wintering areas on the east and west sides of the Cascade Mountain Range. Geese trapped during spring staging in Delta Junction were more likely to be observed on the west side of the Cascade Mountain Range than were geese trapped during fall staging in

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Fairbanks. However, nearly all (92 %) geese trapped during fall staging in both Fairbanks and Delta Junction wintered east of the Cascades. Finally, we found that after-hatch-year (AHY) geese observed on the west side of the Cascade Mountains were structurally smaller on average than AHY geese observed on the east side of the Cascade Mountain Range. Our results indicate that fall staging Canada geese in Fairbanks are predominantly lesser Canada geese (Branta canadensis parvipes), while fall and spring staging Canada geese in Delta Junction are both lesser Canada geese and Taverner's Canada geese (B. c. taverneri).

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INTRODUCTION

Seven of the 11 recognized subspecies of Canada geese (*Branta canadensis*) nest or stage in Alaska. Five of the seven subspecies: Richardson's Canada geese (*B c. huchinsii*), cackling Canada geese (*B. c. minima*), Aleutian Canada geese (*B. c. leucopareia*), Vancouver Canada geese (*B. c. fulva*), and Dusky Canada geese (*B. c. occidentalis*) are relatively well studied (Chapman 1967, MacInnes et al. 1974, Yparraguirre 1982, Lebeda and Ratti 1983, Sedinger and Raveling 1990); however, little research has been conducted on lesser Canada geese (*B. c. parvipes*) or Taverner's Canada geese (*B. c. taverneri*). Lesser Canada geese are thought to nest from Upper Cook Inlet to the southern edge of the Brooks Range, west to the transition zone from boreal forest to coastal tundra, and east into the Yukon River tributaries in Yukon Territory, Canada (Johnson et al. 1979, Fig. 1.1). Taverner's Canada geese nest beyond the range of lesser Canada geese on coastal tundra of the north and west coasts of Alaska (Johnson et al. 1979). Although these two subspecies are similar in body size (Johnson et al. 1979), Quinn et al. (1991) suggested that lesser Canada geese, the smallest of the large-bodied subspecies, and Taverner's Canada geese, the largest of the small-bodied subspecies, last shared a common ancestor approximately 1 million years ago and, therefore, differ genetically more than some subspecies differing markedly in body size.

Fecundity is often correlated positively with body size across subspecies of Canada geese (Dunn and MacInnes 1987); however, climate, predation, and habitat also likely influence reproductive success (Richner 1989, Rhymer 1992). Thus, any of several environmental differences experienced by these two subspecies on breeding areas

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may cause differences in productivity. Abundance of a subspecies results from a balance between the productivity and mortality of that subspecies. Because productivity may vary between lesser and Taverner's Canada geese, and harvest is an important component of mortality of Canada geese (Rexstad 1992), identifying migratory and wintering locations, where most of the harvest occurs, is important to allow for differential harvest regulations to ensure proper management of both subspecies.

Numerous molting lesser or Taverner's Canada geese have been banded since 1941 at Teshekpuk Lake on the North Slope of Alaska (Fig 1.1) (King and Hodges 1979). Because of difficulties in distinguishing between lesser and Taverner's Canada geese (King and Hodges 1979, Johnson et al. 1979), our understanding of any differences in migration routes, staging, and wintering areas is poor. For example, the poor quality of data available at the time lead Bellrose (1980) to confound migration routes, staging, and wintering areas of the two subspecies. He suggested that the majority of both lesser and Taverner's Canada geese stage in Izembek Lagoon on the Alaska Peninsula each fall, follow a coastal path along western and south-central Alaska to western Washington, and then cross the coastal range to central Washington and Oregon, with a few continuing south to the Central Valley of California. Bellrose (1980) further suggested that these geese winter in central Washington and Oregon and then follow a spring migration route to Interior Alaska via the Okanagan and Fraser River valleys of British Columbia to the Yukon Basin, then on to their nesting grounds, thereby completing a non-overlapping fall and spring migration pattern.

King and Hodges (1979) banded 1,692 Canada geese from 1971 to 1978 near

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Teshekpuk Lake, Alaska, an important molting area for non-breeding and failed breeding geese in Alaska (Derksen et. al. 1982). They proposed that the number of molting Canada geese near Teshekpuk Lake was too high to be produced only by those Taverner's Canada geese that had nested on the North Slope of Alaska and suggested that molting lesser Canada geese from Interior Alaska also molted in this area. They reported variation in body size of molting Canada Geese among lakes, which they hypothesized indicated that both lesser and Taverner's Canada geese molt near Teshekpuk Lake. Geese they banded near Teshekpuk Lake were recovered in Interior Alaska and central British Columbia during fall migration and in Washington, Oregon, and California in winter. King and Hodges (1979) also caught three Canada geese near Teshekpuk Lake that had been banded in central British Columbia during spring migration. In contrast to Bellrose's (1980) scenario, they concluded that lesser and Taverner's Canada geese molting near Teshekpuk Lake migrate through Interior Alaska and Central British Columbia in the fall, winter in Washington and Oregon then reverse this migration route in the spring.

Canada geese that migrate through Interior Alaska have not been systematically counted. Bellrose (1980) suggested that there were 60,000 lesser and 100,000 Taverner's Canada geese. A single aerial survey of the Delta Junction agricultural area on 2 May 1988 counted 15,600 Canada geese (R. King, U.S. Fish and Wildlife Service, Fairbanks, AK), indicating only a portion of the two subspecies uses the Delta Junction staging area.

Here we describe staging, migration, wintering, and morphological characteristics of Canada geese captured and neck-collared in Fairbanks and Delta Junction. We also

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flew weekly surveys and performed ground-based surveys to estimate the timing and number of geese using the two staging areas.

METHODS

Study Area

There are currently two known important staging areas for geese in Interior Alaska. In 1978 (24,500 ha) and 1983 (19,400 ha), the state of Alaska sold tracts of boreal forest near Delta Junction, Alaska (Fig.1.1) to stimulate development of grain agriculture (barley, *Hordium murina*) in the state. The land was cleared and planted over a ten-year period beginning in 1979. The area is near a warm water lake (Clearwater Lake) and nearby stream (Clearwater Creek) that provide the only open water for roosting in April when migratory waterfowl return to, or migrate through, Interior Alaska for breeding. Numerous islands in the nearby Tanana River also provide roost sites in fall.

The second major staging area is Creamer's Field Migratory Waterfowl Refuge and the University of Alaska Fairbanks experimental agricultural fields in Fairbanks. Creamer's Field was established in 1966 as a feeding area for migratory birds to allow public observation. Barley is planted for waterfowl use during the fall and is supplemented by additional grain spread in the fields in fall and spring. The University of Alaska maintains experimental agricultural fields approximately 10 km west of Creamer's Field, providing additional waste and unharvested barley. A small nearby lake (Smith Lake) and rock quarry approximately 5 km east of Creamer's Field are used as roost sites between feeding periods during the day only during fall staging. Canada geese using these areas are thought to be primarily lesser and Taverner's Canada geese

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(King and Hodges 1979).

Field Methods

We trapped geese using baited rocket nets (Wildlife Materials Inc.) near Fairbanks and Delta Junction AK in fall 1994 - 1997 and spring 1995 - 1997. Geese were held for a minimum of 2.5 h to allow their digestive tracts to clear before weighing (± 25 g) (Hupp et al. 1996). During this time, we determined their age class and sex and marked them with plastic neck collars containing unique alphanumeric codes (e.g., MacInnes et al. 1969, Ely 1993) and metal U. S. Fish and Wildlife Service leg bands, and measured total tarsus and exposed culmen with dial calipers (±1 mm) (Dzubin and Cooch 1992). We also measured flattened wing (±1 mm) and body-length (±1 mm) using a body-board. The body board was a 60 cm-long board with an attached meter stick and a short end-board perpendicular to the long piece. To measure body-length of each goose we tucked the head under the wing and placed it on its back, with the most anterior portion of its bent neck and distal end of the humerus in the folded wing pushed against the end board. We measured body-length as distance from the end board to the end of the pygostyle. This measurement reduced potential error associated with wear of tail feathers or extending the neck of a live goose. We then released geese together to help maintain family units.

We flew weekly aerial surveys from a fixed wing aircraft over the Delta Junction area to count geese during spring (12 April - 7 May) and fall (25 August - 10 October) from fall 1994 to spring 1997. All areas of open field and water that provided potential loafing, feeding, and roosting habitat were surveyed. We also performed ground-based

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surveys opportunistically (every 2 – 3 days) during fall staging in the Fairbanks area, and in Delta Junction before the initiation of aerial surveys each year. After the first year of the study, aerial surveys were initiated in fall when ground observations and observations from a local pilot regularly flying over the study area indicated Canada geese numbered more than approximately 500 in Delta Junction. We used band recoveries from the Bird Banding Laboratory, United States Geological Survey from the 1994-1995 through 1997-1998 hunting seasons and incidental sightings in British Columbia, Washington, and Oregon to determine migration routes and winter distributions.

Statistical Analysis

We used the four morphological measurements to calculate the first principal component scores (PC1) from the correlation matrix to index structural size. To calculate PC1 we pooled data across age class, sexes, seasons, and years (Alisauskas and Ankney 1987). We used the correlation matrix because the covariance matrix forces the greatest weight to be placed on the measurement with the greatest variation, in our case the wing measurement, which is a poor indicator of structural size in Canada geese (Moser and Rusch 1988). We used histograms to visually determine if there were clearly bimodal distributions of individual measurements and PC1 scores, which would indicate that more than one subspecies was present in the study area. We supplemented these visual assessments with an estimate of $\gamma 2$ (kurtosis) for each age, sex, and season class separately, because unknowingly sampling individuals from two separate but sufficiently overlapping distributions could produce a combined distribution that would appear platykurtic. We also compared PC1 scores and culmen lengths of geese among trapping

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sessions using the GLM procedure of SAS (SAS institute1990) with age, sex, and trapping location as independent variables, to assess variation in composition of geese for each season and study location separately. We excluded fall trapping events if fewer than 16 geese (approximately 3 families) were trapped and excluded spring trapping events if fewer than 4 geese (2 pairs) to increase our probability of using a representative sample of the geese in the area at the time of trapping. We chose a different threshold between spring and fall trapping because during spring family units have disintegrated, thus, a smaller group is more likely to represent the geese present. We chose a threshold of 16 geese during fall because the next smallest group captured was 24, so 16 provided an identifiable cut point. Similarly, we chose threshold of 4 in spring because the next smallest group was 11, so 4 provided an identifiable threshold. Using this criterion, we excluded 13 groups (138 individuals) during fall and 1 group (3 geese) during spring.

We tested for morphological variation between the two study locations (Fairbanks and Delta Junction) during fall, and between geese trapped in Fairbanks during fall and Delta Junction during spring using analysis of variance (ANOVA) (GLM procedure, SAS Institute 1990). In these analyses, we used PC1 or culmen length as dependent variables, age, sex, and trapping location as class variables and included pairwise interactions in the original model. When $P < 0.15$ for interactions between categorical variables we ran analyses with the interacting class variables (e.g., location and age) separated. We used culmen because it is the morphological characteristic that differs most between lesser and Taverner's Canada geese (Johnson et al. 1979), and PC1 because multiple morphological measurements are a better indicator of overall structural

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size than single measurements in Canada geese (Moser and Rusch 1988).

We used ANOVA (GLM procedure, SAS Institute 1990), with age class, sex, winter location, and pairwise interactions to test for a difference in body size and culmen length between geese observed wintering east and west of the Cascade Mountain Range. We used a 2-way contingency table and χ^2 statistic to test the hypothesis that the proportion of Canada geese captured in Interior Alaska wintering west of the Cascade Mountains differed between banding season and fall banding locations separately. Peak arrival during spring in the Delta Junction area and fall in the Fairbanks study areas was estimated as the date most neck-collared geese were initially observed that season, while peak departure was estimated as the date with the largest decline in the number of individual collars between consecutive observation periods.

RESULTS

We trapped 767 Canada geese in Fairbanks and 77 Canada geese in Delta Junction during the fall, and 223 Canada geese in Delta Junction during the spring (Table 1.1). No geese were trapped in spring in Fairbanks. Of geese trapped in fall, 49.9 % were hatch-year (HY) of which 54.9 % were males, while 47.7 % of the after-hatch-year (AHY) geese were males. Of the 1067 geese banded, hunters reported 164 bands, while 105 unique collars were sighted at least once outside our study areas (Fig. 1.2).

Fall Staging

Canada geese began arriving in Fairbanks and Delta Junction during the first week of August and were present until late September or early October. In Fairbanks, peak arrival in fall varied by 10 days among the 3 years (30 Aug., 20 Aug., and 26 Aug. in

1996, 1997, and 1998, respectively). We did not estimate peak arrival for fall 1995 because that sample of marked geese was too small. Ground-based surveys conducted in 1995, 1997, and 1998 indicated a maximum of approximately 2,800 geese were present in Fairbanks at any one time, and numbers peaked approximately the last week of August (Fig. 1.3a). Weekly aerial surveys in the Delta Junction peaked at 4,600 Canada geese in 1996, which occurred from the first to third week of September, depending on year (Fig. 1.3b). Aerial surveys were not conducted before 25 August because ground observations and anecdotal evidence from a local pilot indicated few Canada geese were in the area until the end of August or early September, including 1996, when ground and aerial observations by a local pilot indicated a large influx of Canada geese on 28 August.

Spring Migration and Staging

Each year the number of geese gradually increased in the Delta Junction staging area through mid April until 3,000 - 5,000 were present, then a large influx of 8,000 - 12,000 geese occurred over a 2-day period, followed by a gradual increase to a peak of 14,000 to 18,000 geese (Eichholz pers obs. Fig. 1.4). Geese then departed *en mass* in a 2-day period at the end of April. Peak arrival in the spring varied by 8 days among years (16 April 1996, 20 April 1997, and 12 April 1997).

Subspecies of Staging Geese

Within season, sex and age classes, we observed no obvious bimodal distribution for any of the individual morphological measurements or PC1 scores of fall or spring staging geese. None of the distributions of the four morphological measurements or PC1 scores in any of the six age, sex, and season classes were significantly platykurtic. In fact,

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distributions of measurements of geese trapped in Fairbanks tended to be leptokurtic (Table 1.2).

We did not detect significant variation in mean culmen length ($F_{12, 624} = 1.23$, $P = 0.26$) or PC1 scores ($F_{12, 621} = 1.22$, $P = 0.27$) among trapping sessions of geese trapped in Fairbanks during fall. Mean PC1 scores ($F_{3, 71} = 3.90$, $P = 0.01$) and culmen length ($F_{3, 71} = 4.94$, $P < 0.01$) significantly varied, however, among trapping sessions for geese trapped in fall in Delta Junction, and mean culmen length ($F_{9, 209} = 3.32$, $P < 0.01$) and PC1 sore ($F_{9, 209} = 1.88$, $P = 0.05$) varied among trapping sessions of spring staging geese in Delta Junction. Mean PC1 scores also varied significantly between sexes and age classes ($F > 17.2$, $P < 0.01$) for all seasons and locations). Mean culmen length, however, varied between sexes ($F > 8.3$, $P < 0.01$ for all seasons and locations), but was similar between age classes ($F < 0.10$, $P > 0.75$ for all seasons and locations).

When testing for variation in PC1 scores between geese trapped in Fairbanks and Delta Junction during fall staging, we found evidence of an interaction between location and sex ($P = 0.08$), so we reanalyzed the data for each sex separately. Both male ($F_{1, 435} = 25.4$, $P < 0.01$) and female ($F_{1, 403} = 6.27$, $P = 0.01$) geese trapped in Fairbanks were significantly larger than geese trapped in Delta Junction during fall and AHY geese were larger than HY geese of both sexes ($F > 23$, $P < 0.01$). When testing for variation in mean culmen length between fall staging locations, location and sex interacted ($P = 0.05$), so we reanalyzed the data by each sex separately. Mean culmen length of geese did not differ between age classes ($P > 0.25$ for both sexes) but was significantly longer for geese trapped in Fairbanks than for geese trapped in Delta Junction during fall

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staging for both males ($F_{1,435} = 35.14$, $P < 0.01$) and females ($F_{1,403} = 7.33$ $P < 0.01$). Mean PC1 scores were also greater for AHY geese trapped during fall staging in Fairbanks than for AHY geese trapped during spring staging in Delta Junction ($F_{1,619} = 37.75$, $P < 0.01$) and greater for males than females ($F_{1,619} = 461.80$, $P < 0.01$). Culmen length was longer for AHY geese trapped in Fairbanks during fall staging compared to AHY geese trapped in Delta Junction during spring staging ($F_{1,619} = 37.61$, $P < 0.01$) and AHY males ($F_{1,619} = 122.33$, $P < 0.01$) than for females and. We were unable to distinguish between first-year geese, which potentially were still growing, and after-first-year geese, which had completed growth (Hanson 1962, Raveling 1968). Thus, we compared measurements of the individual morphological characteristics of fall HY geese and spring AHY geese to assess the potential bias associated with the inclusion of second year geese in our spring sample (Table 1.4). We found mean wing length was smaller in fall HY geese than in spring AHY geese, however, body size did not differ and mean culmen and tarsus were actually larger in fall HY geese than in spring AHY geese.

Winter Distribution

Most of the geese banded in Interior Alaska that were later detected in winter were observed or recovered in central Washington and north-central Oregon, east of the Cascade Mountain range (n = 181), with sporadic sightings and recoveries in western Washington and Oregon (n = 23) and as far south as Beatty NV (Fig. 1.2). We found no evidence of movement by individual geese between wintering areas on the east and west sides of the Cascade Mountain Range. That is, no geese were observed on one side of the mountain range then observed or recovered on the other, indicating these were two

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different wintering populations. Only 7% ($n = 153$) of geese trapped in Fairbanks in fall but 31% ($n = 32$) of those trapped in Delta Junction in spring were observed west of the Cascade Mountains ($\chi^2 = 14$, $P < 0.01$, Table 1.3). The percentage (11 %) of geese trapped in Delta Junction in fall that wintered west of the Cascades was similar to that for geese captured in Fairbanks in fall ($\chi^2 = 0.1$, $P > 0.5$, Table 1.3). When testing for a difference in mean PC1 score between geese wintering east and west of the Cascade Mountains we found a significant interaction between age class and wintering location ($P = 0.02$), so we analyzed the data for each age class separately. There was no difference in mean PC1 score between HY geese east and west of the Cascade Mountains ($F_{1,76} = 1.57$, $P=0.21$), however, PC1 scores of AHY geese East of the Mountains were significantly larger ($F_{1,119} = 7.29$, $P < 0.01$) than for AHY geese west of the mountains and males were significantly larger than females ($F > 59.30$, $P < 0.01$ for both age classes). There was, however, no difference in mean culmen length for HY or AHY geese wintering east and west of the mountains ($F_{1,197} = 0.39$, $P = 0.50$)

DISCUSSION

Fall Migration

R. King (United States Fish and Wildlife Service) placed satellite transmitters on two Canada geese staging in Fairbanks Alaska in the fall of 1993. One Canada goose carrying a satellite transmitter required a maximum of 3, and another a maximum of 4 days to migrate from Fairbanks to Prince George in central British Columbia, where one transmitter failed (R. King pers comm.). The remaining goose stayed in the area until 1 November, after which it was recorded near Wallula, in south-central Washington near

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the Oregon border, where it remained throughout the winter. In our study, an individual goose was observed in Interior Alaska and then 10 days later in central Washington, indicating that individuals spent as little as 10 days migrating from central Alaska to the wintering areas in Washington. Most geese, however, depart from Fairbanks by the first week of September and Delta Junction by the third week of September. They then arrive in Washington and Oregon in late October or early November, indicating they spend about 4-6 weeks migrating south in fall. We did not have sufficient data to assess differences in the duration of migration between geese wintering east and west of the Cascade Mountains.

Spring Migration

Although in our study only four neck-collared geese were sighted during the spring migration before reaching Alaska, we believe Bellrose (1980) and King and Hodges (1979) were correct in suggesting geese wintering east of the Cascade Mountains and staging in Interior Alaska in the spring follow a migration path through central British Columbia, similar to the fall migration path previously hypothesized. We did not have sufficient evidence to determine whether geese wintering west of the Cascade Mountains follow the same migration path. Time that geese require to complete spring migration probably varies among individuals. For example, one goose was observed in central Washington on 27 March and on our study area 8 April, indicating it required a maximum of 12 days to migrate from Washington to Interior Alaska. Most geese, however, leave central Washington in late March or early April (M. Monda pers. comm.) and arrive on our study area mid- to late-April (Fig. 1.3), taking 2 to 4 weeks to migrate

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between the 2 areas.

Some of the geese staging on our study area during spring are lesser Canada geese that nest on the Tanana River within 150 km of our spring staging area (Eichholz pers. obs.). The remaining geese are apparently lesser Canada geese nesting farther north on the Yukon River and Taverner's Canada geese which nest on coastal tundra of Alaska (Johnson et al. 1979). Nesting habitat on the coastal tundra of northern Alaska is generally snow-covered, and thus unavailable for nesting, until early June (Bergman et al. 1977). Because nesting habitat for Taverner's geese is unavailable when they leave our study area in early May, they likely stage again farther north before nesting. Lesser Canada geese nesting on the Tanana River, however, begin nesting immediately after leaving the staging area (Eichholz pers. obs). Thus, the length of time lesser Canada geese spend migrating in the spring differs greatly from that of lesser snow geese (*Chen caerulescens caerulescens*), which spend about 3 months migrating north during spring (Alisauskas and Ankney 1992). The migration period for lesser Canada geese is only slightly longer, however, than that of dusky Canada Geese, which spend about 12 days migrating a similar distance in spring (Bromley and Jarvis 1993). Unlike lesser snow geese, which acquire nutrient reserves for nesting primarily during spring migration (Alisauskas and Ankney 1992), dusky Canada geese acquire most of their nutrient reserves on the wintering grounds, then use a portion of the fat reserves during the migration north (Bromley and Jarvis 1993). Our results suggest that geese in our study employ a strategy intermediate between that of dusky Canada geese and lesser snow geese. Alternatively, Canada geese in our study area may be less dependent than lesser

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snow geese on nutrient reserves for reproduction, or may acquire nutrient reserves at a faster rate than lesser snow geese.

Sub-specific Composition of Canada geese in Interior Alaska

Previous research suggested that both lesser and Taverner's Canada geese stage in Interior Alaska during fall and spring (King and Hodges 1979). Johnson et al. (1979) found these 2 subspecies are distinguishable using morphological measurements. We observed no clear bimodal distribution or evidence that we sampled from two distributions for tarsus, exposed culmen, wing, body length or PC1 scores of geese staging in the Fairbanks or Delta Junction area. The overall distribution of measurements of AHY female geese trapped in Fairbanks during fall however, was virtually identical to distributions reported by Johnson et al. (1979) for lesser Canada geese (Table 1.4), while the AHY males appear to be only slightly smaller, suggesting that lesser Canada geese dominated these samples (Table 1.4). We found that geese trapped in Delta Junction in spring and fall were significantly smaller than geese trapped in Fairbanks during fall and that HY geese trapped in Fairbanks in the fall were similar in size to AHY geese trapped in Delta Junction in the spring. These results support the hypothesis that there is a difference in the subspecific composition of flocks between Canada geese using the Fairbanks staging area during fall and the Delta Junction staging area during spring and fall.

Not only were geese trapped in Fairbanks larger than geese trapped in Delta Junction during spring and fall staging, geese staging in Delta Junction arrive later and remain later in the year than geese staging during fall in Fairbanks (Fig. 1.3a,b., Eichholz

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pers. obs.). Furthermore, only seven of > 600 geese observed were observed in both Fairbanks and Delta Junction during fall staging and only 2 of those seven were observed in both staging areas during the same year. Indicating individuals rarely use both staging areas, and the staging areas contain either geese from separate populations or geese from the same breeding population that use separate staging areas. Similarly, we found no indication of movement between the east and west sides of the Cascade Mountains by geese wintering in Oregon and Washington, which is consistent with the suggestion of separate wintering groups in each area (Simpson and Jarvis 1979).

A disproportionate number of geese sampled in Delta Junction during the spring, were observed on the west side of the Cascade Mountain Range. Furthermore, morphological measurements of geese sampled in Delta Junction during spring and fall staging were considerably more platykurtic than those sampled in Fairbanks (Table1.2), and some groups were within the size distribution characteristic of Taverner's Canada geese, suggesting that a larger proportion of geese staging in Delta Junction during spring were Taverner's Canada geese.

Only 11 of 153 geese observed in Fairbanks during fall and in winter were observed in winter west of the Cascade Mountains. We note that sampling effort for neck collars was substantially greater west of the Cascades, associated with a monitoring program for cackling and dusky Canada geese (R. Trost United States Fish and Wildlife Service pers. comm.). In addition, of the 11 individuals observed both during fall in Fairbanks and west of the Cascades during winter, eight were in the size range characteristics of lesser Canada geese. AHY geese wintering west of the Cascade

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Mountains were also overall, structurally smaller based on PC1 scores, than those wintering east of the Cascades were. While Canada geese nesting in Interior Alaska are thought to winter east of the Cascades (Johnson et al. 1979), those nesting around Anchorage, Alaska, are known to winter west of the Cascades. It is possible that some of these individuals were present in our fall Fairbanks sample as molt migrants. In summary: (1) lack of evidence for two size distributions of geese in Fairbanks in fall, (2) the disproportionate presence of these geese east of the Cascades in winter, (3) the larger size and similarity between geese in Fairbanks in fall and those previously described as lesser Canada geese, and (4) lack of mixing between fall staging and wintering geese, suggests that Canada geese staging in Fairbanks in fall are predominantly lesser Canada geese.

Based on our findings, we recommend wintering location be considered when harvest and other management decisions are made. For example, populations of small Canada geese wintering in Washington west of the Cascade Mountains seem to be increasing, while populations of small Canada geese wintering east of the Cascade Mountains seem to be decreasing (M. Monda pers. comm.). However, under current survey procedures, the ability to monitor population levels of discrete subspecies of Canada geese is limited. If patterns in winter distribution result from a change in abundance between two subspecies, further investigation into the causes of these different population dynamics is needed.

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Table 1.1. Canada geese banded in Fairbanks and Delta Junction.

Summary of Canada geese banded in Fairbanks and Delta Junction Alaska. Geese were trapped during fall staging in Fairbanks from 14 August - 14 September, during fall staging in Delta Junction from 14 September - 25 September, and during spring staging in Delta Junction from 15 April - 4 May.

		HY	HY	AHY	AHY	
Year	Location	Males	Females	Males	Females	Total
Fall						
1994	Fairbanks	12	3	6	5	26
1994	Delta Junction	14	11	7	7	39
1995	Fairbanks	32	43	42	42	159
1994	Delta Junction	15	7	8	8	38
1996	Fairbanks	104	68	109	121	402
1997	Fairbanks	57	49	35	39	180
Total		234	181	207	222	844
Spring						
1995	Delta Junction			23	20	43
1996	Delta Junction			47	26	73
1997	Delta Junction			60	47	107
Total				130	93	223

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Table 1.2. Kurtosis measurements.

Kurtosis measurements of the distribution of the four morphological measurements and PC1 for each age, sex, location, and season class. Negative values indicate leptokurtosis.

	Delta Junction Fall	Fairbanks Fall	Delta Junction Spring
HY-Males			
Body Length	-0.37 (29)	0.66 (205)	
Wing Length	2.54	0.20	
Exposed Culmen	-0.05	-0.12	
Total Tarsus	-1.08	0.86	
PC1	-1.08	0.14	
HY-Females			
Body	1.03 (18)	0.58 (160)	
Wing	-0.18	-0.07	
Exposed Culmen	-1.29	-0.39	
Total tarsus	-0.81	0.81	
PC1	-0.66	0.27	
AHY-Males			
Body	-0.73 (15)	0.84 (192)	1.41 (130)
Wing	-1.63	9.85	-0.35
Exposed Culmen	-0.47	-0.29	-0.49
Total Tarsus	-0.64	0.39	-0.05
PC1	-1.33	1.72	-0.30

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Table 1.2 (cont.)	Delta Junction Fall	Fairbanks Fall	Delta Junction Spring
AHY-Females			
Body	-0.01 (15)	0.27 (207)	0.44 (93)
Wing	2.24	1.18	1.68
Exposed Culmen	0.19	0.27	2.31
Total Tarsus	2.49	0.41	0.90
PC1	3.25	-0.71	2.91

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Table 1.3. Summary of recoveries and resighting.

Summary of the number of winter recovery and resighting locations for geese east and west of the Cascade Mountain range and banded in Delta Junction during spring, Fairbanks during fall, and Delta Junction during fall.

	Delta Junction Spring	Fairbanks Fall	Delta Junction Fall
Total banded	223	676	77
Observed East	22	142	17
Observed West	10	11	2

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Table 1.4. Means of morphological measurements.

Means and (SE) of morphological measurements of geese trapped in the fall in Fairbanks and spring and fall in Delta Junction Alaska.

	Hatch Year Males	Hatch Year Females	After Hatch Year Males	After Hatch Year Females
Body				
Fairbanks				
Fall	306.6 (0.9)	289.1 (0.9)	311.5 (0.9)	293.1 (1.2)
Delta Junction				
Fall	289.9 (2.6)	287.9 (4.3)	316.4 (4.4)	289.9 (3.8)
Delta Junction				
Spring			306.7 (1.4)	288.9 (1.4)
Wing				
Fairbanks				
Fall	416.0 (0.8)	397.6 (0.9)	431.1 (1.1)	409.6 (1.0)
Delta Junction				
Fall	409.4 (2.8)	396.7 (2.3)	428.9 (3.8)	403.8 (3.5)
Delta Junction				
Spring			428.8 (1.5)	403.2 (1.7)

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Table 1.4 (cont.)	Hatch Year Males	Hatch Year Females	After Hatch Year Males	After Hatch Year Females
Exposed culmen				
Fairbanks				
Fall	42.1 (0.2)	39.9 (0.2)	42.3 (0.2)	40.0 (0.2)
			[43.0]	[40.2]
			{37.8}	{36.1}
Delta Junction				
Fall	40.0 (0.5)	39.0 (0.6)	40.3 (0.8)	38.7 (0.8)
Delta Junction				
Spring			40.8 (0.2)	39.1 (0.3)
Total tarsus				
Fairbanks				
Fall	94.1 (0.2)	87.7 (0.3)	94.1 (0.3)	88.5 (0.3)
			[97.0]	[88.7]
			{92.8}	{87.1}
Delta Junction				
Fall	90.0 (0.8)	86.3 (0.9	92.8 (0.9)	87.5 (1.3)
Delta Junction				
Spring			92.7 (0.4)	86.9 (0.5)

[ ] = mean measurement for lesser Canada geese from Johnson et al. 1979
{ } = mean measurements for Taverner's Canada geese from Johnson et al. 1979

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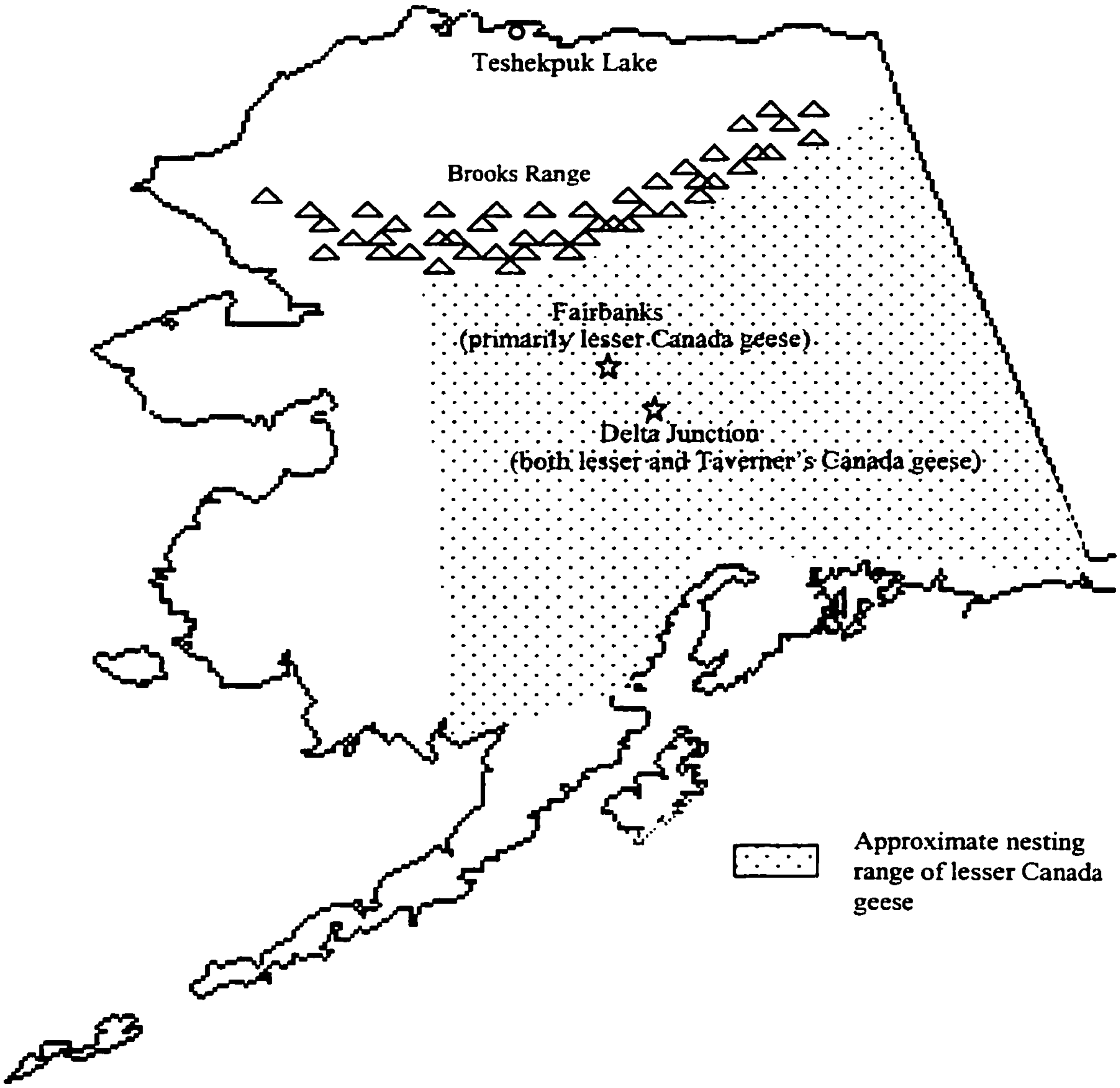

Figure 1.1 Map of Alaska.
Map of Alaska showing study areas, approximate breeding range of lesser Canada geese, and banding site of King and Hodges (1979). Lesser Canada geese are thought to breed south of the Brooks Mountain Range and east of the tree line in Interior Alaska and western interior Yukon Territory, Canada.

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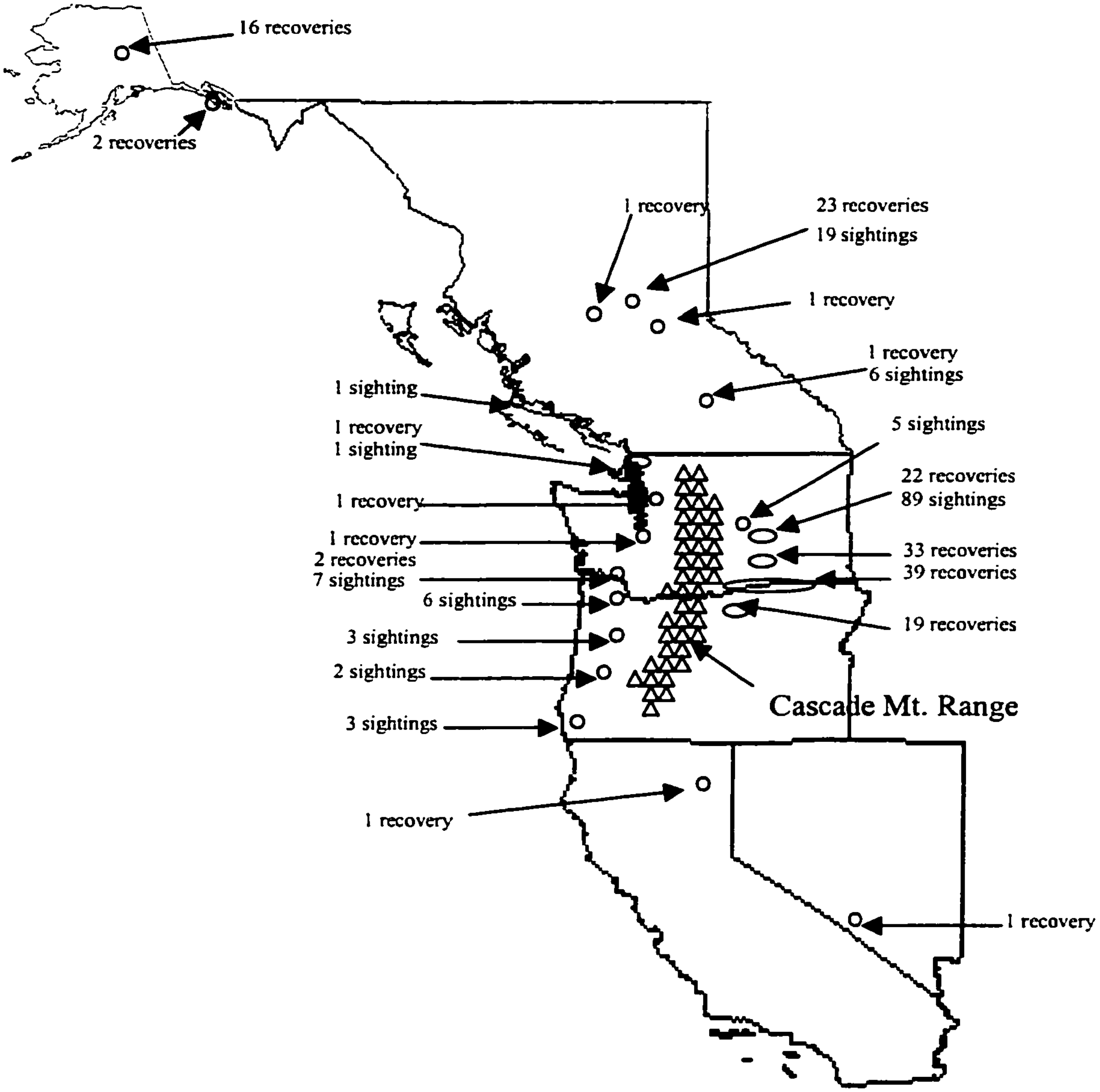

Figure1.2. Map of recoveries and sightings.
Map of recoveries and sightings of Canada geese banded during spring and fall staging in Interior Alaska. Some individuals were observed in more than one location so a represented by more than one observation.

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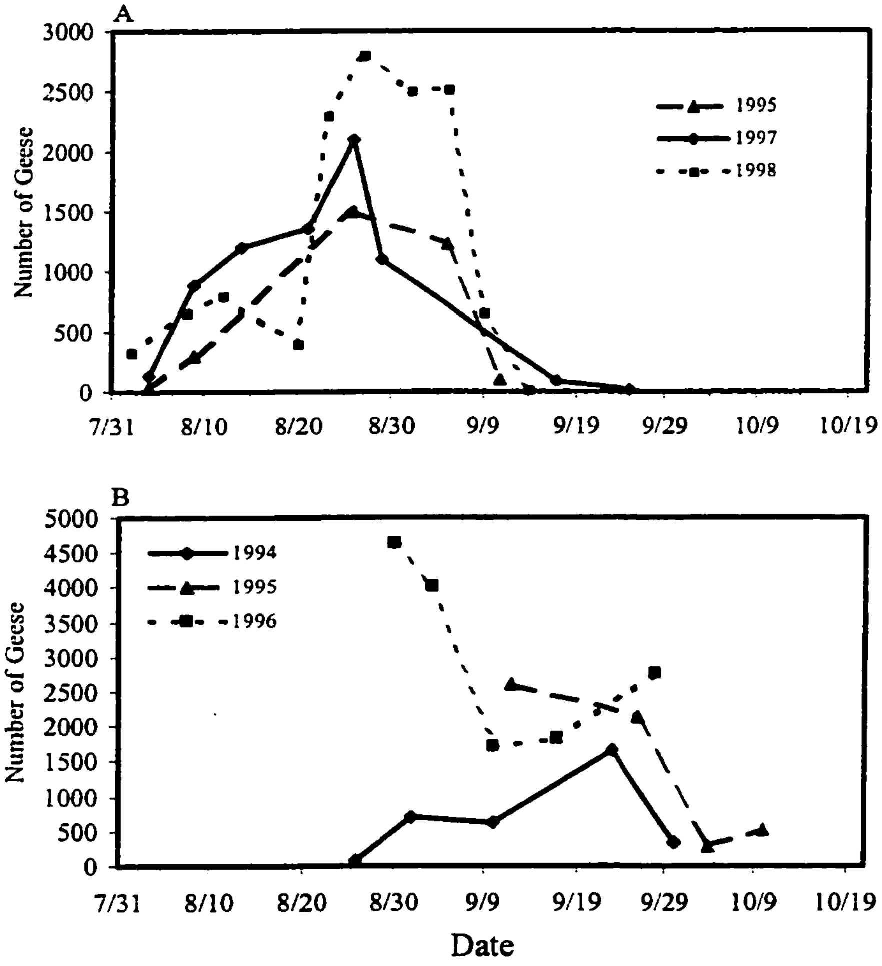

Figure 1.3. Abundance of geese during fall staging.
Results of opportunistic ground based surveys of fall staging Canada geese in Fairbanks, Alaska (A) and results of aerial surveys of fall staging Canada geese in Delta Junction, Alaska (B).

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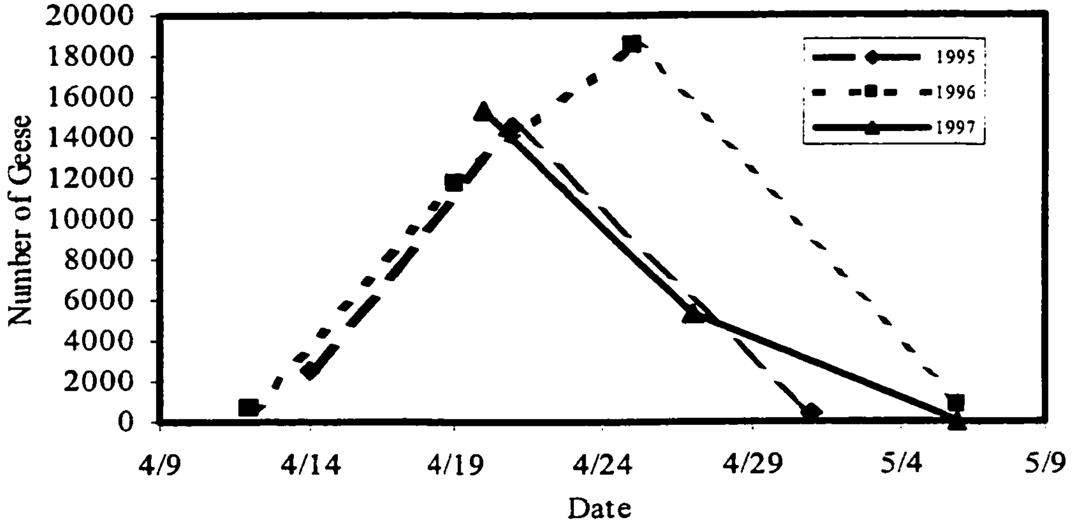

Figure 1.4. Abundance of geese during spring staging. Results of aerial surveys of spring staging geese in Delta Junction Alaska.

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CHAPTER 2

SURVIVAL AND RECOVERY RATE OF CANADA GEESE STAGING IN INTERIOR ALASKA.

Eichholz, M. W. and J. S. Sedinger. Survival and recovery rate of Canada geese staging in Interior Alaska. - Prepared for submission in the Journal of Wildlife Management.

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ABSTRACT

Because managers are unable to distinguish Canada geese (*Branta canadensis parvipes*) from other sub-species of small Canada geese on the wintering grounds using current survey methods, they are unable to adequately measure their abundance. Estimates of vital rates that influence abundance, such as annual survival are, therefore, critical for proper management. We calculated annual survival and recovery rates for different age and sex classes of Canada geese staging in Interior Alaska using Barker's model, and compared survival and recovery rates of Canada geese in our study with those of other Canada geese. The model with the lowest Akaike's Information Criterion, corrected for small sample size (AIC_c), allowed survival to vary by age class with point estimates of 0.49 for hatch-year (HY) geese and 0.67 for after-hatch-year (AHY) geese. This model allowed recovery rate to vary by age class and decrease each year additively across age and sex classes. A competitive model allowed recovery rate to vary by adult sex and estimated recovery rate to be 0.13 for HY, 0.08 for AHY female, and 0.05 for AHY male geese during the study period. Estimates of annual survival of Canada geese in this study are among the lowest and recovery estimates are among the highest for migratory populations of geese. Low survival estimates of Canada geese in our study suggest that a better understanding of population parameters such as reproductive success and recruitment is needed to properly manage this population. Furthermore, we recommend monitoring abundance and harvest of small Canada geese east and west of the Cascade Mountain Range separately to better determine harvest pressure on Canada geese wintering east of the Cascades.

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INTRODUCTION

Because, current survey methods do not distinguish between lesser Canada geese and other sub-species of Canada geese on the wintering grounds, managers are unable to adequately measure abundance of this subspecies. Thus, knowing estimates of vital rates that influence abundance, such as annual survival, are important for managing this subspecies. Banding of Canada geese was limited to molting flocks mixed with Taverner's Canada geese (*B. c. taverneri*) on Alaska's arctic coast (King and Hodges 1979) and no estimates of annual survival have been published for this subspecies.

Sex- and age-related variation in survival has been observed in several goose species (e.g., Francis and Cooke 1992, Francis et al. 1992, Samuel et al. 1990, Owen and Black 1989), although some studies have been unable to detect variation in survival between sexes or among age classes (e.g., Castelli and Trost 1996). Typically, young of the year survive at lower rates than adults, which has been attributed primarily to their lack of sufficient nutrient reserves during the early stages of migration (Francis et al. 1992, Owen and Black 1989), although greater vulnerability to harvest also likely adds to this difference in survival (Samuel et al.1990, Francis et al. 1992). The proportion of mortality due to harvest versus natural mortality may vary among population due to environmental differences or differences in harvest pressure. This is important because, although most population models of waterfowl indicate that population abundance is most sensitive to adult survival (e.g., Schmutz et al. 1997, Flint et al 1998), juvenile survival is more variable than adult survival in geese (Owen and Black 1989, Francis et al. 1992), thus, juvenile survival is most susceptible to management actions. There is a

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need; therefore, to understand the cause of that variability, allowing managers to determine habitat implementation strategies that will most benefit the population.

The lesser Canada goose is usually considered a small-bodied Canada goose, however, is genetically most closely affiliated with large-bodied Canada geese (Quinn et al. 1991). The nesting distribution of lesser Canada geese extends from the Upper Cook Inlet to the southern edge of the Brooks Range in Alaska, west to the edge of the tree line and east into the Yukon Territory, Canada (Johnson et al. 1979). A portion of the subspecies uses areas near Fairbanks, Alaska for spring and fall staging (King and Hodges 1979, Eichholz 2001). The fall migratory route for most of the lesser Canada geese using the Fairbanks staging areas is from Interior Alaska to central British Columbia and south to central Washington and north central Oregon where they winter (Eichholz 2001). These geese then reverse this migration pattern during spring (Eichholz 2001).

Here we report estimates of annual survival of Canada geese trapped during early fall staging in Fairbanks, Alaska, which, based on morphology and winter distribution, are primarily (> 90 %) lesser Canada geese (Eichholz 2001). We allow for variation in survival and recovery rates between age and sex classes and discuss how and when these differences might occur. We also compare survival and recovery estimates of Canada geese in our study with those for other Canada geese.

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METHODS

Study Area and Banding Procedure

The study was conducted during spring and fall staging periods from 1994-1998 on agricultural areas in Fairbanks and Delta Junction Alaska. We trapped geese using baited rocket nets (Wildlife Materials Inc.) in Fairbanks in the fall and Delta Junction in the spring. Because of limitations of Barker's survival model, we limited our analysis to geese that were trapped or observed in Fairbanks during fall staging (Barker 1997). Including fall staging geese also served to exclude most Taverner's Canada geese from the analysis because fall staging geese in Fairbanks are primarily Canada geese (Eichholz 2001). Geese were held for 2.5-8 h in wooden crates to allow for contents of their digestive tracts to pass before weighing. During this time, geese were marked with plastic neck collars containing unique alphanumeric codes (e.g., MacInnes et al. 1969, Ely 1993) and metal U. S. Fish and Wildlife Service leg bands. After the waiting period, we released geese together to help maintain family units. We used band recoveries received from the Bird Banding Laboratory, United States Geological Survey from the 1994-1995 through 1997-1998 hunting seasons in the analysis. Geese captured or sighted during the fall staging period were considered captures, while sightings during spring staging in Delta Junction Alaska (see Eichholz 2001) and incidental observer sightings in British Columbia, Washington, and Oregon were defined as resightings between capture periods.

Survival Analysis

We used Barker's model (Barker 1997), as modified by White and Burnham (1999) in

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program MARK to estimate the following parameters:

$S_{(i)}$ = the probability an animal alive at i was alive at i +1

$p_{(i)}$ = the probability an animal at risk of capture at i was captured at i

$r_{(i)}$ = the probability that an animal that died in the interval i to i +1 was found dead and the band reported

$R_{(i)}$ = the probability that an animal that survived from i to i + 1 was resighted (alive) some time between i and i + 1

$R'_{(i)}$ = the probability an animal that died in i to i + 1 without being found dead was resighted alive in i to i +1 before it died

$F_{(i)}$ = the probability an animal at risk of capture at i was at risk at capture at i + 1

$F'_{(i)}$ = the probability an animal not at risk of capture at time i was at risk of capture at i + 1

Equivalencies in the parameterization of White and Burnham's (1999) model in program MARK and the original model proposed by Barker (1997) are shown in Table 2.1. Barker's model allowed us to include mark-recapture data from the study site, as well as resightings during the intervals between capture periods and band recovery data from the hunting season. Including data from an area separate from the capture area allowed us to separate permanent emigration from mortality, enabling us to estimate true survival, rather than apparent survival, which is estimated from traditional Cormack-Jolly-Seber models (Barker 1997). Furthermore, including the recovery data enabled us to estimate band recovery for the population, which can be used to estimate harvest rate if band reporting rate is known (Nichols et al. 1991).

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We selected models using Akaike's Information Criterion corrected for small sample size ($QAIC_c$) (Burnham and Anderson 1998). Parameter estimates (S, r, p, R, F) of competing models were allowed to vary by year, age class (after-hatch-year and hatch-year), and adult sex, in additive or fully interactive models (Lebreton et al. 1992). Preliminary results suggested a trend in r over time, so we included a model that allowed r to change directionally over time. We also tested for a capture effect on survival and recovery by allowing survival and recovery to vary between the first survival and recovery period after banding and all other survival and recovery periods. Estimates of S_5, r_5, F_4, and F'_3 were dependent on recoveries in the last period. However, at the time of our analysis few recoveries from that period were available, causing estimates of S_5, r_5, and F_4, to be potentially biased. Therefore, we estimated S_5, r_5, F_4, and F'_3 separately to prevent models with time effects for each of these parameters from being selected based on an artifact in the data rather than temporal variation in the underlying processes.

To identify the best model, we divided the selection process into two phases. We first used QAICc to select the best model that allowed the "nuisance" parameters (all parameters except S and r) to vary by time, age and adult sex. Using the model with the lowest $QAIC_c$ from the first phase, we then identified the model that fit the data best while still allowing S and r to vary by time, age, and adult sex. To make our analysis comparable to other research, we also estimated recovery rate f (Brownie et al. 1985 p.6), which is the product of the proportion of the bands recovered by hunters and the probability of a recovered band being reported. Thus, we calculated f from the equation:

$$f_i = (1-S_i)\bullet r_i.$$

then used the Delta method to calculate the variance and 95% confidence intervals for each point estimate of *f* (Seber 1982). To estimate an average *f* for each sex and age class over the entire study period, we included results from the most parsimonious model that held *r* constant over time.

RESULTS

We neck-collared 567 individual Canada geese for the study. Of the 567, seventy-four were recovered during the hunting season and 324 neck collars were observed between capture periods (Table 2.2).

The model with the lowest $QAIC_c$ allowed *S* and *r* to vary by age (Table 3). In this model, *r* decreased through time linearly across age classes. That is, declines in *r* were parallel across age classes. Another model that competed well with the best model and deserves consideration allowed reporting rate to differ between adult sexes; reporting rate for adult females was higher than for adult males. We estimated that 67% of the after-hatch-year (AHY) and 49% of hatch-year (HY) individuals survived annually under the model with the lowest $QAIC_c$ (Table 4). Reporting rate and estimated recovery rates were higher for HY than for AHY geese. Recovery rates (*f*) declined annually for HY and AHY geese (Table 4).

DISCUSSION

First Year Survival

Because most studies use data from geese banded on brood rearing areas before fledging, researchers are unable to determine whether observed differences in annual survival between HY and AHY geese is due to mortality before fledging, just after fledging, or

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later in the juvenile period. Little mortality occurred in giant Canada goose (*B. c. maxima*), barnacle goose (*Branta leucopsis*), or black brant (*B. bernicla nigricans*) goslings late in brood rearing (Zicus 1981, Prop et al. 1984, Flint et al. 1995), suggesting the difference in annual survival between young and adults was due to differential mortality after fledging. While geese in our study were banded near brood rearing areas and may not have completed wing feather growth, all geese banded in our study had gained flight. Thus, similar to other studies, the difference in survival between age classes of geese in our study is due to mortality factors after fledging.

If the difference in survival between age classes is due to a difference in post-fledging mortality, as the previous discussion suggests, a question remains regarding whether this difference occurs due to differential natural mortality, differential susceptibility to harvest, or both, and if the proportion of these two mortality factors varies across populations. Survival differed between HY and after-second-year (ASY) geese of a non-hunted population of barnacle geese banded during brood rearing (Owen and Black 1989). They concluded most first-year mortality occurred during a long oceanic migratory flight. This result indicates that in some populations differential natural mortality between age classes is sufficient to lead to differential survival (Owen and Black 1989). Sedinger et al. (1997) reached similar conclusions in a hunted population of black brant. To assess when a difference in mortality between age classes of geese in a hunted population occurred, Francis et al. (1992) compared survival of HY and ASY lesser snow geese banded at 5 locations: La P'erouse Bay breeding colony, North and South Dakota, Missouri, Texas, and Louisiana. Survival was almost twice as

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high for ASY geese than HY geese (81.6 ± 1.6 % vs. 42.4 ± 1.9 %) banded on the breeding colony, significantly different, but only about 17 % (82.4 ± 2.2 % vs. 65.8 ± 4.1 %) greater than HY geese banded in the Dakotas, and similar between age classes for geese banded at the other 3 banding locations. They also assumed little mortality occurred between banding and fledging, and suggested that the difference in mortality between the two age classes was primarily due to young having insufficient reserves for a long non-stop flight early in migration; however, a difference in vulnerability to harvest apparently lead to differential survival between age classes of geese banded in the Dakotas. The primary cause of the differential mortality between age classes, however, appears to differ between lesser snow geese and the Canada geese in our study.

Recovery rate of HY Canada geese in our study was about twice as high as that estimated for HY lesser snow geese in Francis et al.'s (1992) study. A difference in recovery rate between the two populations could result from either a difference in the proportion of recovered bands that are reported (λ), or an actual difference in the proportion of the population that is harvested. Although we have no way to determine whether λ differed between the two studies, we have no reason to believe it did, thus favor the latter explanation, a difference in the proportion of the population that is harvested.

Francis et al. (1992) estimated recovery rate of HY lesser snow geese banded during brood rearing to be 6.7 % and survival to be 42 %. Assuming λ to be about 33 % (Nichols et al. 1991), Francis et al. (1992) estimated harvest rate at about 20 %, or about 1/3 of the annual HY mortality was due to harvest. We estimated recovery rates to be

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about 13 % during the study period (Table 2.4). Making the same assumption as Francis et al (1992) regarding λ, harvest rate of Canada geese in our study is about 39 %, or about 76 % of the mortality is due to harvest. Because the assumption that $\lambda = 0.33$ may be invalid, estimates of the proportion of harvest versus natural mortality may be incorrect. Regardless of the true value of λ, however, a substantially greater proportion of the HY mortality was due to harvest in our study than in Francis et al.'s (1992) study, assuming λ did not vary between studies. The population in both Francis et al. (1992) and Owen and Black's (1989) study had no access to agricultural crops early in migration. In contrast, agricultural areas with grain and pasture are just a short flight (< 100 km) for most of the Canada geese staging in our study area. We suggest agricultural areas in such close proximity to the nesting areas allowed HY geese to acquire relatively large amounts of nutrient reserves before attempting nutritionally demanding flights early in migration. Thus, young Canada geese in our study display relatively high survival during early migration. In our study population, however, low natural mortality relative to lesser snow geese was offset by a higher proportion of first year mortality due to harvest on migration and wintering areas.

Differences in Recovery and Survival between Sexes

Although the model that allowed recovery rates to differ between sexes was not the best model, it competed well with the best model and should be considered (Burnham and Anderson 1998). Band recovery rates were higher for adult females than for adult males. Although differences in survival and recovery rates between sexes are commonly found in ducks (e.g., Burnham et al. 1984, Hestbeck 1993), to our knowledge only four of

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thirteen studies of geese have found sex differences in harvest or survival rates. Francis and Cooke (1992) found estimates of survival differed between sexes in some populations of lesser Snow Geese. They attributed this difference to males emigrating to different breeding and migration areas and being exposed to different harvest pressure than females, which remain in their original breeding colony. Raveling et al. (1992) found that survival of female cackling Canada Geese (*B. c. minima*) was higher between the time geese left the wintering grounds in the spring and the time they returned in the fall. Raveling et al. (1992) suggested higher female survival during summer may be a result of lower mortality of females from depredation because females nest on islands in relative safety, whereas males loaf on pond shores during incubation. They also suggested that males might be more susceptible to depredation than females during brood rearing because males guard the brood. Giroux and Bedard (1986) found more adult female than adult male greater snow geese (*C. c. atlantica*) were harvested by hunters along firing lines near sanctuaries. Similarly, Giroux and Bedard (1986) suggested higher susceptibility to harvest of female greater snow geese was due to behavioral differences between males and females when defending the young. They hypothesized that adult females were more likely to follow young lured off sanctuaries by hunters than are adult males, and were thus more susceptible to harvest.

Results of the model allowing recovery rate to vary between adults sex classes are consistent with Giroux and Bedard's (1986) findings that adult females are more susceptible to harvest than adult males; however, we are unable to suggest a mechanism that would cause this difference. A difference in λ between adult females and males

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could lead to a difference in recovery, however, aside from a slight difference in size, male and female Canada geese are similar in appearance, thus it is unlikely that hunters would be able to distinguish between sexes and report their bands at a different rate. Alternatively, adult females may survive the early stages of migration at a higher rate; thus, relatively more adult females survive to be available to harvest. Again, however, we are unable to suggest a mechanism that would cause more adult females than males to survive during the early stages of migration.

Comparison of Annual Survival among Populations

Our estimates of annual survival of Canada geese are among the lowest and recovery estimates among the highest for migratory populations of geese marked with neck-collars and leg bands, or leg bands only (Table 2.5). Two assumptions must be met to interpret survival estimates as being representative of the population as a whole. The first assumption is that markers have no effect on survival. There is increasing evidence that neck collars may increase mortality of some geese (Samuel et. al. 1990, Castelli and Trost 1996, Schmutz and Morse 2000, Alisauskas and Lindberg in review). Alisauskas and Lindberg (in review) conducted a study specifically designed to test the effect of neck collars on survival, breeding propensity, and harvest rate of white-fronted (*Anser albifrons frontalis*) and Richardson's Canada geese (*B. c. hutchinsii*). They estimated that neck collars decreased survival by as much as 24% in some years. Although we had no ability to directly test the assumption that the neck collars had no impact on survival, our point estimates of non-harvest mortality were similar to those measured in populations of leg banded geese, suggesting little if any impact (Table 2.5).

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The point estimate for annual survival of HY geese was approximately 49% (Table 2.4), while the recovery rate was approximately 13% over the 4 years of the study. In a reward band study of mallard ducks, Nichols et al. (1991) estimated 32% of the bands that were recovered by hunters were reported. A reward band study has not been conducted on neck-collared geese; however, so the reporting rate of bands recovered from this study is unknown. Assuming the reporting rate of neck-collared geese was similar to that for mallards, approximately 39% of the HY population was harvested annually, leaving 12% dying from non-hunting causes. The point estimate of survival for adults was about 67%; thus, annual mortality was approximately 33%. We estimated recovery rate at about 8% and 5% for AHY females and males respectively (Table. 2.4). Using similar reasoning, we calculated 10% of the AHY females and 18% of the AHY males died annually from natural causes. Although no data on reporting rate of neck-collared geese have been collected, 10% natural mortality is consistent with studies of non-hunted populations of geese in Europe (Owen and Black 1989), and only slightly higher than the 5 to 6% natural mortality we calculated from Alisauskas and Lindberg (in review), using assumptions described above. Although our analysis suggests the low survival observed in our study is primarily due to high harvest rates, we cannot exclude the possibility that hunters are selecting neck collared geese; thus our estimates of harvest rates may not be representative of the subspecies as a whole.

Neck-collar loss could also bias our results. Estimates of neck collar loss from other studies have varied from 0 – 25 % (Hestbeck and Malecki 1989, Hestbeck 1994, Schmutz and Morse 2000, Alisauskas and Lindberg in review). We re-trapped only 13

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previously marked geese in which we could directly estimate neck collar loss. Of those 13 geese, none had lost their neck collar. To better understand the potential effect of neck collar loss could have had on our study, we calculated the probability of capturing 13 geese of which none had lost their neck collar, under different scenarios of neck collar loss. If annual neck collar loss was 5 %, then the probability of re-trapping 13 geese, none of which had lost their neck collar is 0.51. If annual loss was 20%, the likelihood of recapturing 13 with no loss would only 0.05. Furthermore, we observed more than 5,000 geese on ice and bare ground where their legs were visible. Approximately 10% of these geese were marked. During these observations, no geese had leg bands only, indicating little if any collar loss. We conclude neck collar loss was unlikely to have substantially influenced our estimate of survival.

MANAGEMENT IMPLICATIONS

Assuming no immigration or emigration, population size reflects the balance between reproduction or recruitment and survival. Previously, no estimates of recruitment or survival have been made for lesser Canada geese. Monda (1998) reported harvest of small-bodied Canada geese (i.e., lesser and Taverner's Canada geese *B. c. taverneri*) in Washington declined from 47,270 in 1979-1980 to 24,649 in 1997-1998. He attributed the decline to a possible change in wintering distribution from central Washington to western Oregon over that period. A decline in the population or reduced hunting pressure are alternative explanations. Raveling (1978) and Hestbeck (1994) proposed an alternative explanation to perceived changes in Canada goose distribution. They proposed perceived distribution changes might actually be differential mortality among

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subpopulations using different wintering grounds. Eichholz (2001) found that 93% of Canada geese banded in Fairbanks Alaska wintered in central Washington and north central Oregon, indicating that a shift in the wintering area did not occur. Furthermore, the population of Canada geese that wintered in western Oregon and nested in the Anchorage area, (T. Rothe unpub. data), has increased substantially during recent years. Thus, the perceived shift in wintering distribution (Monda 1998) may reflect a change in the size of different populations of Canada geese. Low survival in our study suggests that more information on population parameters such as reproductive success and recruitment is needed to properly manage this population. Furthermore, we recommend monitoring abundance and harvest of small Canada geese both east and west of the Cascade Mountain Range separately to better determine population size and harvest pressure.

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Table 2.1. Parameterization of program MARK.

Equivalencies for the program MARK and Barker (1997) parameterization of the Barker Model.

Program MARK	Barker (1997)
F'_i	$(1-F'_i)$
$(1-R_i)$	θ_i
$S_i R_i + (1-S_i)\{r_i + (1-r_i) R'_i\}$	f_i
$1-(1-S_i r_i)/f_i$	ν_i

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Table 2.2. Summary of capture, recoveries, and resightings.

The captured column represents newly collared geese as well as previously marked geese captured (resighted) during the capture period.

Year	Captured	Recovered	Resighted
1994	26	3	8
1995	198	26	102
1996	206	21	102
1997	304	23	124
1998	145	1	2

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Table 2.3. Best models selected using AICc.

Results of survival analysis using Barker's model in program MARK. *S* (the probability of surviving from i to $i + 1$)and *r* (the probability that the band from a goose that dies is recovered during the hunting season and reported) were allowed to vary by age (a), adults sex (as), change over time (t), and a trend in change over time (tre) in an interactive or additive manner with age and adult sex. Preliminary analysis indicated there was a trend in the way *r* changed over time, so we included a model that allowed *r* to increase or decrease over time. We also allowed *S* and *r* to differ for the period directly after banding to test for a capture effect (c).

Model						
s	*r*	QAICc	ΔQAICc	$QAIC_c$ Weight	K	Dev.
(a)	**(a+tre)**	**1299.6**	**0.0**	**0.345**	**23**	**2753.6**
(a)	(a+tre,as+tre)	1299.7	1.1	0.196	24	2751.6
(a)	(a)	1300.4	1.8	0.142	22	2762.1
(a, c)	(a+tre,as+tre)	1300.8	2.2	0.113	25	2749.4
(a)	(a,as)	1301.3	2.8	0.087	23	2759.7
(a)	(a+tre,as+tre,c+tre)	1301.8	3.2	0.070	25	2751.5
(a, as)	(a+tre,as+tre)	1304.8	6.2	0.016	23	2767.3
(.)	(a+tre,as+tre)	1305.8	7.2	0.009	24	2764.9
(a)	(.)	1307.5	8.9	0.004	25	2764.1
(a+t)	(a+tre,as+tre)	1309.3	10.7	0.002	29	2749.7

Best model including all parameters:
s(a) *p*(a) *r*(a+tre,as+tre) *R* (a+t) *R'* (.) *F*(a*t,as*t) *F'* (a+t,as+t)

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Table 2.4. Point estimates from best model.

Point estimates of survival (*S*), Seber's reporting rate (*r*), and Brownie's recovery rate (*f*) ± 1 standard error (SE), from a study of Canada geese staging in Interior Alaska. Estimates are from the model with the lowest AICc in table 2.3.

	S		*r*		*f*	
Year	HY	AHY	HY	AHY	HY	AHY
94-95	0.49	0.67	0.40	0.34	0.20	0.11
	±0.06	±0.03	±0.10	±0.10	±0.06	±0.04
95-96	0.49	0.67	0.31	0.26	0.16	0.09
	±0.06	±0.03	±0.07	±0.06	±0.03	±0.02
96-97	0.49	0.67	0.24	0.20	0.12	0.07
	±0.06	±0.03	±0.06	±0.04	±0.03	±0.02
97-98	0.49	0.67	0.17	0.14	0.09	0.05
	±0.06	±0.03	±0.06	±0.04	±0.03	±0.01
94-98	0.49	0.67	0.26	0.20	0.13	0.07
	±0.06	±0.03	±0.06	±0.04	±0.03	±0.01

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Table 2.5. Summary of point estimates from other studies.

Summary of estimates of apparent survival (ϕ), survival (S), and Brownie's (1985) recovery rate (f) for various species of geese. In some cases, we converted Seber's r, which was originally reported by the authors to f_i using the equation $f_i = (1-S_i)\bullet r_i$.

Species	Marker	Years	ϕ	SE	S	SE	f	SE
[1]Canada geese -HY	NC	1994 -1998			49.0	4.0	13.0	2.0
[1]Canada geese-AHY	NC	1994 -1998			67.0	2.0	5.0 - 8.0	1.0
[2]Richardson's Canada geese	LB	1991 -1998			89.6	4.0		
[2]Richardson's Canada Geese	NC	1991 -1998			80.1	5.0	2.6	
[3]Vancouver Canada Geese	LB	1956 -1969			83.6	4.3		
[4]Canada Geese	LB	1984 -1986			77.3	3.8	3.7	0.2
[5]Canada Geese	NC	1984 -1988	70.4	1.2				
[6]Cackling Canada Geese	NC	1982 -1984			51.6-64.1	1.6-4.0		
[7]Canada Geese	LB	1974 -1980			78.6	3.1	4.2	0.3
[7]Canada Geese	NC	1974 -1980			76.9	3.4	4.6	0.4
[8]Canada geese	LB	1984 -1989			79.7	3.4	4.1	0.3
[8]Canada geese	NC	1984 -1989			69.2	3.6	4.8	0.3
[9]Western Canada geese	LB	1965 -1984			46.3		12.6	
[10]Emperor geese	NC	1988 -1991	63.1	2.3				
[11]Ross' geese	LB	1965 -1977			84.2	6.0	3.2	0.3
[12]Lesser snow geese	LB	1970 -1988			81.6	1.6	3.8	0.2

[1]This study, [2]Alisauskas and Lindberg in review, [3]Ratti et al. 1978, [4]Hestbeck and Malecki 1989, [5]Hestbeck 1994, [6]Raveling et al. 1992, [7]Samuel et al. 1990, [8]Castelli and Trost 1996, [9]Rexstad 1992, [10]Schmutz et al. 1994, [11]Melinchuk and Ryder 1980, [12]Francis et al. 1992.

LB - Indicates geese were marked with leg bands only.

NC - Indicates geese were marked with neck collar in addition to leg bands.

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CHAPTER 3

THE EFFECT OF BODY CONDITION ON ANNUAL SURVIVAL OF CANADA GEESE STAGING IN INTERIOR ALASKA: AN EXPERIMENTAL APPROACH

Eichholz M. W. and J. S. Sedinger. The effect of body condition on annual survival of Canada geese: an experimental approach. - Prepared for submission in Condor

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ABSTRACT

Six previous studies of waterfowl have described a positive association between survival and body condition. The association between survival and condition could, however, be confounded by multiple correlations among survival, condition, and other variables such as individual quality or disease. In this study, we first test for an association between survival and body condition of free ranging Canada Geese (*Branta canadensis*), which are primarily Lesser Canada Geese (*B. c. parvipes*), staging in Interior Alaska. We then report the results of an experiment in which we manipulated the nutrient availability and storage to test whether the relationship between survival and body condition is a direct relationship between body condition and survival, or a result of confounding between body condition, individual quality, and survival. In the free-ranging population, the best models of survival contained a term for body size for all sex and age classes and body condition for after-hatch-year (AHY) females. None of the best models for survival rate of experimental geese contained terms of either body size or condition, suggesting that neither variable influenced survival of experimental geese. Our evidence is most consistent with the hypothesis that the association between survival and body condition is a result of a correlation among body condition, individual quality, and survival, not a result of a direct relationship between body condition and survival. We also found a positive association between survival and body size and propose 3 hypotheses for this association.

Key words: Branta canadensis, *Body condition, Body Size, Canada Geese, Individual quality, Life history traits, Survival*

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INTRODUCTION

The question of whether a general association exists between body condition and winter or annual survival of waterfowl, and the cause of that potential association is still unresolved. Hepp et al. (1986) addressed the potential association between body condition and survival by testing for a correlation between body condition and recovery rate of Mallard Ducks (*Anas platyrhynchos*) in the Mississippi alluvial valley. They found a negative relationship between body condition and recovery rate for adult males and immature females in 1 of 3 years, weak evidence for a negative correlation for immature males, and no relationship for adult females. They suggested that individuals in good condition may use habitats where they are less susceptible to harvest, behavioral differences, or flocking as potential mechanisms for the observed relationship.

The first attempt to address the relationship between natural mortality and physical condition of waterfowl was conducted by Haramis et al. (1986) in a study of a non-hunted population of Canvasback Ducks (*Athya valisinaria*) banded in the upper Chesapeake Bay. They found heavier adult male and juvenile male and female Canvasbacks were more likely to be observed over the 12 weeks following banding in some years, but the results were inconsistent and did not indicate a strong relationship. Furthermore, it is difficult to draw conclusions about the effects of body mass because variation in body mass is a combination of variation in structural size and body condition (Piersma and Davidson 1991), and either of these variables could be related to life history traits.

Schmutz and Ely (1999) found a positive relationship between body condition of

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adult female Greater White-fronted Geese (*Anser albifrons frontalis*) and survival for the period encompassing spring migration, breeding, and fall migration and the period encompassing the hunting season. They found no relationship between body composition and survival, however, for the period between the end of the hunting season and beginning of fall migration or for adult males or juveniles during any period. They concluded that adult females were more likely to display a negative impact of poor condition because of their larger investment in reproduction. They further suggested that they observed no relationship between body composition and survival of immature geese because most immature geese in their study were captured near the end of migration, after most of the mortality from migration had likely occurred.

In none of the previous studies were the authors able to identify the factors causing some individuals to maintain lower reserves, nor were they able to directly link condition and survival because of the potentially confounding effects among survival, condition, and individual quality. While individual quality is difficult to define, we use the term to characterize covariation among traits affecting fitness, such as body size, reproductive investment, and survival (e.g., Thomas and Coulson 1988). For example, if low quality or diseased geese are more likely to have both poorer body condition and a lower probability of survival, independent of body condition, then we might observe an association between body condition and survival even though a direct relationship between these two variables did not exist.

Variation in condition of individuals leading to a positive association between survival and body condition is interpreted as evidence of a limitation in nutrient

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availability during the non-breeding season by most North American Waterfowl Management Plan (NAWMP) Habitat Joint Ventures in migrating and wintering regions (e.g., Loesch et al. 1994). Understanding the importance of food availability and interpreting studies designed to test the assumption that energy is the limiting factor during the non-breeding period are vitally important for ensuring that habitat managers use limited resources most efficiently. Nevertheless, the relationship between nutrient availability and survival remains virtually untested.

In this study, we first test for a correlation between body condition and survival of Canada Geese (*Branta canadensis*) staging in Interior Alaska (Eichholz 2001). We then used a manipulative experiment to separate the potential confounding between individual quality, body condition, and survival. We also test for a relationship between body size and survival, independent of condition, because body size has been found to be related to other life history traits (Ankney and MacInnes 1978).

METHODS

Study Area

The study was conducted during spring and fall staging periods from 1994-1998 on agricultural areas near Delta Junction and Fairbanks Alaska. The study site near Fairbanks consisted of Creamer's Field Migratory Waterfowl Refuge and agricultural fields on the campus of the University of Alaska Fairbanks. Barley is planted for waterfowl during the fall and supplemented by additional grain in both spring and fall. Barley is grown on the University of Alaska agricultural fields for livestock feed and large quantities of non-harvested or waste grain are available to waterfowl (Eichholz

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pers. obs.). Morphological measurements and winter distribution indicate Canada Geese using the Fairbanks area during fall are primarily Lesser Canada Geese (*B. c. parvipes*), but the fall staging population may also include some Taverner's Canada Geese (*B. c. taverneri*) (Eichholz 2001).

Trapping and Banding Procedure

We trapped geese at bait stations using baited rocket nets (Wildlife Materials Inc.) near Fairbanks Alaska in the falls of 1994 to 1997. Geese were held for 2.5-8 h in wooden crates to allow for contents of their digestive tracts to pass before weighing (Hupp et al. 1996). Geese were marked with plastic neck collars containing unique alphanumeric codes, (e.g., Ely 1993) and metal U. S. Fish and Wildlife Service leg bands. We measured length of exposed culmen, total tarsus, flattened wing chord, and body length following (Eichholz and Sedinger 1998). After the waiting period, we weighed geese to the nearest ± 25 g with a 5000 g spring scale and released geese together to help maintain family units.

Estimating Body Size and Nutritional Condition

We used principal components analysis (PROC PRINCOMP, SAS Institute 1990) of the four morphological measurements (exposed culmen, total tarsus, flattened wing chord, and body length) to calculate PC1 scores (calculated from the correlation matrix), then used PC1 scores as an index of structural size for each age and sex category independently (Alisauskas and Ankney 1987). We used the correlation matrix in contrast to the covariance matrix because the covariance matrix forces the greatest weight to be placed on the measurement with the greatest variation, in our case the wing

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measurement, which is a poor indicator of structural size in Canada Geese (Moser and Rusch 1988). We then used the residual of the regression of body weight on PC1 as an index of body condition.

Experiment

Control geese were trapped, measured, weighed, and released in 1996, as described above. Experimental geese were rocket-netted in 1996 as previously described, then held 10-14 days in 50 x 8 x 2 m pens. During the holding period, geese in the high nutrition group were fed a pelleted alfalfa corn mix and ground corn *ad libitum*, while geese in the low nutrition group were fed pelleted alfalfa corn mix to supply food for one of the two diurnal feeding periods. Three feeders were placed in a uniform distribution in the pens of both groups to preclude a dominant family group from controlling access to food. High- and low-nutrition paired-groups were trapped and released within one day of each other to remove possible confounding of treatment, date, and holding effects. Control groups were trapped between trapping sessions of experimental geese trapped early and later in the season but were not held in captivity. Food was withdrawn from pens 3 hours before banding and release to ensure gut contents had cleared before weighing at the time of release.

We calculated PC1 scores and residuals for each age and sex class separately as described above; however, we pooled measurements across treatment groups to allow for comparison among treatment groups for each age and sex class separately. To determine if the treatment affected the body condition of geese we used Proc GLM (SAS Institute 1990) to test for variation in mean body condition among the 3 groups of geese (high and

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low nutrition, and control), with group as the class variable for each age and sex class separately.

Survival Analysis

We used Barker's model (Barker 1997) as modified by White and Burnham (1999) in program MARK to estimate the following parameters:

$S_{(i)}$ = the probability an animal alive at i was alive at $i+1$

$p_{(i)}$ = the probability an animal at risk of capture at i was captured at i

$r_{(i)}$ = the probability that an animal that died in the interval i to $i+1$ was found dead and the band reported

$R_{(i)}$ = the probability that an animal that survived from i to $i + 1$ was resighted (alive) some time between i and $i + 1$

$R'_{(i)}$ = the probability an animal that died in i to $i + 1$ without being found dead was resighted alive in i to $i+1$ before it died

$F_{(i)}$ = the probability an animal at risk of capture at i was at risk at capture at $i + 1$

$F'_{(i)}$ = the probability an animal not at risk of capture at time i was at risk of capture at $i + 1$

Equivalencies in the parameterization of White and Burnham's (1999) model in program MARK and the original model proposed by Barker (1997) are shown in Table 3.1. Barker's model allows researchers to include mark-recapture data from the study site, as well as resightings from the interim periods between capture periods, and band recoveries data from the hunting season. Including data from an area separate from the study site allowed us to separate permanent emigration from survival estimates, enabling

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us to estimate actual survival, rather than apparent survival traditionally estimated from Cormack-Jolly-Seber models (Barker 1997).

We selected models using Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 1998). AIC_c identifies the most parsimonious model; the model that describes the data best with the fewest parameters. Parameters of competing models (S, r, p, R, F) were allowed to vary by age, year, and adult sex, in additive and interactive models (Lebreton et al. 1992). An additive model restricts parameters to vary in parallel, while interactive models allow parameters to vary independently. For example, a model in which survival varies additively with age and time would force survival estimates for adults and juveniles to differ by a constant amount across years. Preliminary results suggested a trend in r across years, so we included a model that forced r to increase or decrease across years. Estimates of S_5, r_5, F_4, and F'_3 were dependent on recoveries in the last period. At the time of our analysis, however, few recoveries from the last recovery period were available thus, estimates of S_5, r_5, and F_4, were potentially biased. Therefore, we fixed $S_5 = 1$, $r_5 = 0.001$, and $F_4 = 1$, to prevent models with time effects for each of these parameters from being selected based primarily on estimates for the last interval. We also fixed R' at 0.01 and F' at 0.001 because of a lack of data to support those parameters estimates.

For the parameters of interest to this study (S, r) as well as the "nuisance" parameters that had enough data to support the inclusion of a covariate (p, F, R) we included a covariate of PC1 score as an index of body size and the residual of mass regressed on PC1 as an index of body condition. We tested for interactions between

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covariates and categorical variables only for *S* and *r* because our interest was limited to those variables. To identify the most parsimonious model, we divided the selection process into three phases. We first used AIC_c to select from among candidate models that allowed the "nuisance" parameters (all parameters except *S* and *r*) to vary by time, age class, and adult sex, and included a covariate of body size (PC1) and mass residuals. Using the model with the lowest AIC_c from the first phase, we then identified the most parsimonious model allowing *S* and *r* to vary by time, age, and adult sex. Finally, in the third phase, we used the model with the lowest AIC_c from the second phase to select the model with the lowest AIC_c that included a covariate of body size or mass residuals for *S* and *r*.

Survival analysis for the experimental group was similar to the more general analysis described above except that during the first phase we allowed the nuisance parameters to vary by experimental group and fixed *F* at 1 as well as fixing *R'* and *F'* at 0.01 and 0.001, respectively. We predicted that if survival were directly related to body composition at the time of release, the association between body condition and survival would be stronger for the experimentally manipulated geese, because we artificially increased the range in body condition. We also predicted that if survival was directly related to body condition, geese held on the low plane diet would survive at a lower rate than control geese, or geese held on the high plane diet. As evidence for the first prediction, we compared fit of a model that included a covariate for the effect of individual condition on the *S* and *r* parameters of the experimental geese with that of a similar model without the covariates. As evidence for the second prediction, we

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compared fit of a model that allowed *S* and *r* to vary by experimental group to that of a model that held *S* and *r* constant across experimental groups.

Geese captured or sighted during the fall staging period were considered captures, while sightings during spring staging in Alaska and incidental observer sightings in British Columbia, Washington, and Oregon during the spring and fall migration period and on the wintering grounds were defined as resightings between capture periods. Band recoveries came from bands reported to the Bird-banding Laboratory of the United States Geological Survey. We attempted to read all neck collars at least every other day in the Fairbanks area during the fall staging period and in Delta Junction Alaska during spring staging.

RESULTS

We trapped and measured 480 free-ranging geese, of which 63 were recovered during the hunting season, and 253 were resighted between capture periods (Table 3.2). The model with the lowest AIC_c from the first phase of the selection process allowed *p* to vary by age and year, including a covariate for mass residuals, *R* to vary by age and year, and *F* to vary by age, year, and adult sex. When we allowed *S* and *r* to vary, we found the model that allowed *S* to vary by age and *r* to decrease over time to have the lowest AIC_c. The model that allowed *r* to decrease over time, however, was included after we observed this pattern in the data, and inference from this result should be limited (Burnham and Anderson 1998). When we included covariates that represented body condition and size in models for survival and recovery parameters, we found the model that included HY body size and AHY female body condition had the lowest AIC_c (Table

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3.3). This model also included a single positive coefficient for the effect of body condition on recovery rate for adult males, females, and juveniles (Table 3.3).

Experiment

We assigned 130 geese to the high plane, 141 geese to the low plane, and 130 to the control group. Of the 401 geese used in the experiment, 52 were recovered during the hunting season, and 203 were resighted between capture periods (Table 3.4). As intended, body condition of geese varied among groups ($F_{2,396} = 178$, $P < 0.01$). Hatch-year (HY) geese held on the low plane diet had the lowest mean residual mass (males = -281 g, SE = 34, n = 37, females = -256 g, SE = 45, n = 25), while HY geese that were not held and manipulated (males = 137 g, SE = 48, n = 26, females = 101 g, SE = 67, n = 20), and HY geese held on the high plane diet had similar mean residual mass (males = 184 g, SE = 53, n = 37, females = 169 g, SE = 63, n = 26). Similar to HY geese, after-hatch-year (AHY) males and females held on the low plane diet had the lowest mean residual mass (females -272 g, SE = 31, n = 40; males -261 g, SE = 35, n=39); while AHY male and female geese held on the high plane diet had a similar mean residual mass, (females 107 g, SE = 40, n = 37; males 99 g, SE = 39, n = 34) to AHY male and female geese that were not held or manipulated (females 157g, SE = 24, n = 44; males 180g, SE = 35, n = 40).

In the analysis of survival for the experimental geese, the model with the lowest AIC_c allowed p to vary by age, and p of AHY geese on the high plane diet to be lower than p of the control AHY geese and AHY geese on the low plane diet; R to vary by age; with R', F, and F' all fixed. We then found that the model that allowed S to vary by age and *r* to be held constant had the lowest AICc (Table 3.5). We found no strong evidence that survival (Table 3.6a) or recovery rate (Table 3.6b) varied among groups, although the model that allowed survival for HY geese to vary between the control and experimental groups deserves consideration (Burnham and Anderson 1998). Although the model that allowed survival to vary among groups did not compete well, we report the point estimates of survival from the model in Table 3.7 to allow readers to more clearly examine potential differences. We found no evidence to indicate any association between survival and body condition of AHY females, AHY males, or HY geese was maintained in the experimental birds (Table 3.8). Furthermore, there was no evidence of an association between survival and body size of the experimental geese, and the strength of the association between body composition and *r* was reduced in the experimental geese (Table 3.8), relative to the non-manipulated geese (Table 3.3).

DISCUSSION

Body Condition and Survival

Similar to Schmutz and Ely (1999), we found females that were in better condition had a higher probability of annual survival while we observed no association between annual survival and body condition for AHY male or HY geese (Table 3.3). We also observed no relationship between annual survival and body condition of juveniles even though we banded geese near nesting and brood-rearing areas of some individuals. Thus, our results suggest that a relationship between survival and condition does not exist for juvenile geese in our study.

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A positive association existed between recovery rate and body condition of adult males, females, and juveniles (Table3.3). Our results, while different from previous studies, would be expected if natural mortality in this population occurs during fall migration before the hunting season (Owen and Black 1989; Schmutz and Ely 1999), and geese in the best condition are most likely to survive migration. Thus, these results indicate that the association between survival and condition is a result of events that occur in the early stages of fall migration.

Our experiment was intended to decouple the potential association between quality of individuals and their condition, allowing a direct assessment of the role of condition on survival. Our results clearly indicate that the experiment had the desired effect of decreasing the body condition of geese held on the low plane diet. HY geese held on a high plane diet, however, had only a slightly higher mean residual mass than control HY geese, and AHY geese held on the high plane diet actually had a slightly lower mean mass residual than control geese. The modest difference between the condition of the high plane and control geese could be the result of a negative experimental effect on condition; however, it could also indicate that resources available in the environment at the time of the experiment are comparable to those provided during captivity.

Similar to other studies (Conroy et al.1989, Bergan and Smith 1993, Schmutz and Ely 1999), we observed a positive relationship between survival and body condition of adult females in this population. We observed little evidence that survival varied among experimental groups (Table 3.6a), however, even though mean body condition of the low

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plane group differed from that of the other groups. We also found no compelling evidence for an association between body condition and survival in the experimentally manipulated geese (Table 3.8). We propose two alternative explanations for the lack of an association between survival and body condition between or within our experimental geese.

The impact of holding geese may have overwhelmed any difference in survival between the two experimental groups. The model that allowed survival to vary between the experimental and control groups competed well with the model with no variation in survival across groups (Table 3.6). The point estimate of survival for HY geese in the control group was higher than the point estimate for HY geese in the experimental groups, and the point estimate of survival for AHY male geese in the control group was higher than for experimental AHY male geese (Table 3.7). These results suggest that holding geese had a negative impact on survival, which might have masked any difference between the two experimental groups. We have no reason to believe, however, that the handling effect would have had a greater impact on geese in the high plane group, resulting in similar estimates of survival between the two experimental groups.

Alternatively, the contrast between our experiment and field results suggests that a relationship between body condition and individual quality explains most of the association between body condition and survival. That is, some attribute of individuals contributed to their having both higher survival probability and better body condition, but survival was not directly associated with body condition at the time of release.

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Variation in individual quality may be a result of disease (Shutler et al. 1999, Horak et al. 1999, Tella et al. 2000) or some heritable trait resulting in variation in the fitness of individuals (Perrins and Jones 1974, Batt and Prince 1979, Bryant and Westerterp 1982). For example, during breeding, adult females of most arctic- and sub-arctic-breeding geese draw both protein and energy reserves down to extremely low levels (Ankney and MacInness 1978; Raveling 1979). The immune system can be compromised when body condition is reduced to extremely low levels (Martarese 2000). A decrease in the immune system caused by poor body condition due to the extensive investment in reproduction would increase the potential for infection by disease or parasites and could affect fitness (Shutler et al. 1999). If the positive association between survival and body condition is the result of disease independent of body condition, the relationship between body condition and survival is more likely to be manifested in adult females because of greater fluctuation in their physical condition during nesting (Ankney and MacInness 1978; Raveling 1979, Schmutz and Ely 1999).

Body Size and Survival

We suggest three explanations for the positive relationship between survival and body size of HY geese in this study. First, the relationship could be a result of banding more than one subspecies. Canada Geese staging in Fairbanks Alaska are primarily Lesser Canada Geese (Eichholz 2001). Some Taverner's Canada Geese, a slightly smaller subspecies, may however, have been inadvertently included. Other studies suggest smaller species or subspecies of waterfowl have a higher mortality rate; and, our results could have resulted from inclusion of smaller subspecies in our analysis. If this were the

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case, however, we would expect a similarly strong, if not stronger relationship between body size and survival for adults than young, which was not the case (Table 3.3). The model that included a covariate for body size for HY geese had 0.6 fewer AIC_c points than the model that included a covariate of body size for all age and sex classes. Furthermore, harvest and associated mortality rates are expected to be lower for Taverner's Canada Geese, the smaller subspecies, than for Lesser Canada Geese because of the restrictions of harvest in the winter range of Taverner's Canada Geese (M. Monda 1998) and individual behaviors that make Lesser Canada Geese more vulnerable to harvest (Simpson and Jarvis 1979).

A second explanation for our results is larger individuals may survive at a higher rate due to their ability to carry absolutely more nutrient reserves and use them more efficiently due to their lower mass-specific metabolic rate.

Finally, the association with body size of HY geese and survival might be correlated with dominance of family units. Adults of family units of geese with more goslings are more vigilant for predators (e.g., Sedinger et al.1995a), are more dominant (e.g., Raveling 1970, Loonen et al. 1999), allowing greater access to food, and their goslings grow at a faster rate (Loonen at al. 1999). Goslings from these families are, consequently, more likely to survive fall migration (e.g., Loonen et al. 1999). Dominant geese also acquire favorable roost sites in winter (Raveling 1970), thus may be exposed to lower predation pressure. The association we observed between body size of HY geese and survival may result from the correlation between family dominance, gosling growth rate prior to fledging, and survival after fledging, and not a direct relationship

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between body size and survival. We believe this is the most likely explanation for the association between body size and survival. Our results do not allow us to separate potential confounding between the last two hypotheses, however; thus, a manipulative study to test these hypotheses would be useful.

Results of this study suggest observed associations between individual body condition and survival do not necessarily indicate a direct relationship between body condition and survival. Alternative explanations such as correlations among disease or individual quality, body condition, and survival may explain the relationship between condition and survival in this population, and caution should be used in interpreting results of studies testing for correlations between body condition and mortality. Future work similar to this should be conducted on other wintering populations in which habitat management decisions are being based on the assumption that energy is the limiting factor in the non-breeding period.

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Table 3.1. Equivalencies for the program MARK and Barker (1997) parameterization of the Barker Model.

Program MARK	Barker (1997)
F'_i	$(1-F'_i)$
$(1-R_i)$	θ_i
$S_i R_i+(1-S_i)\{r_i+(1-r_i) R'_i\}$	f_i
$1-(1-S_i r_i)/f_i$	ν_i

Table 3.2. Summary of captures, resightings, and recoveries.

Summary of capture, recovery, and resighting data used in the analysis testing for an association between body condition and survival of non-manipulated Canada geese trapped in Fairbanks, AK fall 1994-1998. Number captured includes newly collared geese as well as neck collars sighted during the capture period. Number of newly collared geese is in parentheses.

Year	Captured	Recovered	Resighted
1994	26 (26)	3	8
1995	151 (150)	19	67
1996	193 (130)	18	78
1997	266 (174)	22	98
1998	137	1	2

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Table 3.3. Best models from free ranging geese.

Results of a survival analysis of Canada geese staging in Interior Alaska using Barker's model in program MARK. Best model including all parameters:

s(res+af,pc1-j,a) p(a+t,res) r(res) R(a+t) R'(fixed) F(a,t,as,) F'(fixed)

Model structure			Delta	AICc		
S	*r*	AICc	AICc	Weight	K	Deviance
(res-af,pcl-j,a)	**(res)**	**2201.2**	**0.0**	**0.27**	**25**	**2149.9**
(res-af,pc1,a)	(res)	2202.1	0.9	0.17	25	2152.6
(res-af,a)	(res)	2203.0	1.8	0.11	24	2153.8
(res-af,pc1-j,a)	(pc1,res)	2203.1	1.9	0.10	26	2149.6
(pc1-j,a)	(res)	2203.4	2.2	0.09	24	2154.2
(res-af-j,pc1-j,a)	(res)	2204.2	3.0	0.06	26	2150.8
(res,pc1-j,a)	(res)	2204.2	3.0	0.06	26	2151.3
(res-af,pc1-ad,a)	(res)	2204.9	3.7	0.04	25	2153.1
(res-am,pc1-j,a)	(res)	2205.2	4.0	0.04	25	2153.9
(a)	(res)	2205.2	4.0	0.04	23	2158.1
(res,pc1,a)	(res)	2205.4	4.2	0.03	26	2152.0
(res-af-j,pc1-j,a)	(.)	2209.2	8.0	<0.01	24	2160.0

a = age, **t** = time, **as** = adult sex, **h** = high plane group, **c** = control group, **l** = low plane group, **j** = hatch-year, **adf** = after-hatch-year females, **adm** = after-hatch-year males **res** = covariate of mass residuals, **PC1** = covariate of body size, **PC1-j** = body size covariate for hatch-year geese only, **PC1-ad** = body size covariate for after-hatch-year geese only, **res-j** = mass residual covariate for hatch-year geese only, **res-af** = mass residual covariate for after-hatch-year female geese only, **res-af-j** = mass residuals for adult females and juveniles

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Table 3.4. Summary of resighting and recovery data of experimental geese.

Summary of recovery and resighting data from the experimental geese released in 1996.

	Fall 1996	Interim 1996-97		Fall 1997	Interim 1997-98		Fall 1998	Interim 1997-98	
Group		Rec.	Res.		Rec.	Res.		Rec.	Res
High Plane Diet	130	19	23	31	4	23	33	0	0
Low Plane Diet	141	13	30	41	2	25	32	1	1
Control	130	9	40	53	4	39	44	0	0

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Table 3.5. Best models from experimental geese allowing survival to vary by age, adult sex, and time. Results of a survival analysis of Canada geese experimentally manipulated body condition staging in Interior Alaska using Barker's model in program MARK. Best model including all parameters:

S(a) p(a-ad*c-n=p) r(.) R(a) R'(fixed) F(fixed) F'(fixed)

S	*r*	AICc	Delta AICc	K	Deviance
(a)[a]	(.)	1863.9	0.00	11	1841.6
(a)	(t)	1864.9	0.99	12	1840.5
(a)	(a)	1866.2	2.26	13	1839.7
(a,as)	(.)	1866.2	2.28	13	1839.7
(a)	(a,as)	1868.1	4.21	14	1839.6
(.)	(.)	1871.8	7.89	11	1849.5
(.)	(a)	1877.5	13.63	12	1853.1

[a] **a** = age, **as** = adult sex, **t** = annual variation

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Table 3.6. Best models allowing survival and recovery to vary by group.

Results of a survival analysis of Canada geese with experimentally manipulated nutrient reserve levels. Models allow for variation in *S* and *r* among experimental groups.

A. Models allow *S* to vary among experimental groups.

Model structure			Delta	Model		
S	*r*	AICc	AICc	Weight	K	Deviance
(a)[a]	(.)	1863.9	0.00	0.26	11	1841.6
(a, j-h=l-c)	(.)	1864.0	0.10	0.24	12	1839.6
(a, ad-h=l-c)	(.)	1865.3	1.41	0.13	12	1840.9
(a*h=l-c)	(.)	1865.4	1.52	0.12	13	1839.0
(a, j-hcl)	(.)	1865.7	1.83	0.10	13	1839.3
(a*h=c-l)	(.)	1866.7	2.79	0.06	13	1840.2
(a*c=l-h)	(.)	1867.6	3.69	0.04	13	1841.1
(a*hcl)	(.)	1869.2	5.25	0.02	15	1838.5
(a*hlc,as*hlc)	(.)	1873.6	9.71	<0.01	18	1836.7

B. Models allow *r* to vary among experimental groups.

Model structure			Delta	Model		
S	*r*	AICc	AICc	Weight	K	Deviance
(a)	(.)	1863.9	0.00	0.22	11	1841.6
(a)	(h=c-l)	1864.5	0.62	0.16	12	1840.1
(a)	(c-h-l)	1864.6	0.70	0.15	13	1838.2
(a)	(h=l-c)	1865.5	1.60	0.10	12	1841.1

[a] **a** = age, **as** = after-hatch-year sex, **h** = high plane group, **c** = control group, **l** = low plane group, j = hatch-year, j-h=l-c = variation of juveniles between the experimental groups and the control group, ad-h=l-c = variation of adults between the experimental groups and the control group.

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Table 3.7. Point estimates for survival of experimental geese.

Point estimates and 95% CI of survival from the model that allows survival to vary by group, age, and adult sex (Table 3.6a, Δ AICc = 5.25).

Group	Hatch-Year	After-Hatch-Year Females	After-Hatch-Year Males
High Plane	0.44 (0.31-0.58)	0.68 (0.48-0.82)	0.50 (0.31-0.68)
Low Plane	0.38 (0.25-0.53)	0.64 (0.46-0.69)	0.60 (0.43-0.75)
Control	0.55 (0.37-0.71)	0.67 (0.50-0.80)	0.67 (0.49-0.81)

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Table 3.8. Best models of experimental geese that include covariates for body condition and body size.

Results of a survival analysis of Canada geese with experimentally manipulated nutrient reserve levels (see text for details of manipulation). Models test for correlations between an index of body condition and *S* and *r*, and an index of body size and *S* and *r*.

Model structure						
S	*r*	AICc	Delta AICc	Model Weight	K	Deviance
(a)[a]	(res-exp)	1862.9	0.00	0.29	12	1838.6
(a)	(.)	1863.9	1.00	0.18	11	1841.6
(a,pc1-exp-j)	(res-exp)	1864.0	1.04	0.17	13	1837.5
(a, res-exp-adf)	(res-exp)	1864.2	1.27	0.15	13	1837.8
(a,pc1-exp)	(res-exp)	1864.8	1.89	0.11	13	1838.4
(a, res-exp)	(res-exp)	1865.0	2.07	0.10	13	1838.5

[a] **a** = age, **j** = juveniles, **adf** = adult females, **res-exp** = covariate of mass residuals in the experimental (high and low plane diet) geese only, **PC1-exp** = covariate of body size in the experimental (high and low plane diet) geese only, **res-exp-adf** = covariate of mass residuals in the experimental (high and low plane diet) adult female geese only, **PC1-exp-j** = covariate of body size in the experimental (high and low plane diet) juvenile geese only.

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CHAPTER 4

NUTRIENT RESERVE DYNAMICS OF SPRING AND FALL STAGING CANADA GEESE IN INTERIOR ALASKA

Eichholz, M. W. and J. S. Sedinger. Nutrient reserve dynamics of spring and fall staging Canada geese in Interior Alaska. - Prepared for submission in The Auk.

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ABSTRACT

During winter, when energetic demand is low relative to the migratory or reproductive period, geese maintain few nutrient reserves. However, before energetically demanding periods, such as reproduction or long migratory flights, geese store large amounts of nutrient reserves. A better understanding of when and where geese acquire nutrient reserves will enable wildlife managers to better understand population dynamics of arctic and sub-arctic nesting geese. We collected Canada geese staging in Interior Alaska in the fall of 1995 to 1997 and the springs of 1996 and 1997 to study nutrient reserve dynamics during spring and fall staging. Spring staging geese gained weight at a rate of 18 g per day, and female geese gained fat at a rate of 9 g per day. Breast muscle weight and mineral level tended to increase with collection date in spring staging geese. Breast muscles in AHY geese averaged 19 g heavier and AHY geese averaged 17 g more minerals than HY geese during fall staging. During fall staging, GI tracts of AHY geese averaged 158 g heavier than for HY geese. Weight of GI tract varied among years, and increased with collection date in fall for HY geese. Fat reserves of females did not differ between spring and fall, but males averaged 118 g more fat during fall than spring. Finally, gizzards tended to be 5.3 g heavier and GI tracts were 9.4 g heavier in fall than in spring. We hypothesize that vigilance of males allows females to spend more time feeding and acquire nutrients at a faster rate than males during spring. We hypothesize the availability of large quantities of barley, a cereal grain high in carbohydrates, but low in protein, enabled females to increase fat but not protein reserves during spring, in contrast to most populations feeding on natural vegetation. We hypothesize geese reduce

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energetic demand during spring migration by acquiring minerals needed for reproduction and molt on the final staging area or nesting grounds. Our findings that HY geese have lower mineral levels and lighter breast muscles and GI tracts than AHY geese during fall staging indicates HY geese are not fully developed during this period.

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INTRODUCTION

Nutrient reserves of geese vary substantially during the annual cycle (e. g. Hanson 1962, Raveling 1979). During winter, energy demand is low relative to either the migratory or reproductive period, thus geese maintain only small nutrient reserves (Hanson 1962, Raveling 1968, Raveling 1979, McLandress and Raveling 1981a). Before energetically demanding periods such as reproduction, however, geese accumulate large amounts of nutrients (Hanson 1962, Raveling 1979, McLandress and Raveling 1981a). Because geese are capable of storing sufficient nutrients before reproduction to meet both maintenance and reproductive requirements (Calder 1984, Alisauskas and Ankney 1992a), and geese occupy seasonal environments (Sedinger and Raveling 1990) in which they cannot maintain nutrient balance during migration or breeding (Hanson 1962, Alisauskas and Ankney 1992a), it is important to link the nutrient dynamics of the varying periods of a goose's annual cycle.

Typically, geese acquire primarily lipid during fall for use during fall migration and winter (Wypkema and Ankney 1979), while they acquire both protein and to a lesser extent lipid during molt for fall migration (Hanson 1962, Raveling 1979, Ankney 1984), and both protein and lipid during spring for use during the later part of spring migration and reproduction (Raveling 1979, McLandress and Raveling 1981a, Alisauskas and Ankney 1992b). Individuals of some populations acquire reproductive nutrients on staging areas during long spring migrations to nesting areas (Ankney 1982, Thomas 1983, Alisauskas and Ankney 1992b, Krapu et al. 1995), while those in other populations acquire nutrients for reproduction before spring migration and then supplement reserves

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used during migration on the nesting grounds before egg-laying (Gauthier et al. 1992, Bromley and Jarvis 1993). Females and males of many populations are at maximum weight just before a last short spring migratory flight, or immediately before egg laying, suggesting reproduction is the most energetically demanding period (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979, McLandress and Raveling 1981a).

Nutrient reserves are also associated with the probability that an individual will complete fall migration successfully (Owen 1982, Schmutz and Ely 1999, Eichholz 2001); however, few studies have examined nutrient reserve dynamics of geese between summer molt and early winter (Wypkema and Ankney 1979, Sedinger and Bollinger 1987). Cackling Canada geese (*Branta canadensis minima*) achieve peak weight in early fall migration before a 2,800 km non-stop trans-Pacific migratory flight (Sedinger and Bollinger 1987). Thus, some evidence suggests long fall migratory flights can be energetically demanding as reproduction (Owen 1982, Wypkema and Ankney 1979, Sedinger and Bollinger 1987).

Regardless of when geese in North American acquire nutrient reserves for reproduction or spring migration, most geese depend on agricultural crops as a primary source of food (e.g., Alisauskas and Ankney 1992b, Krapu et al. 1995). Agricultural crops often occur in greater quantity and are higher in digestible carbohydrates than natural vegetation used by geese (Joyner et al. 1987). Thus, geese feeding on agricultural crops are thought to acquire more nutrient reserves at a faster rate than geese feeding on natural vegetation (Joyner et al. 1987, McWilliams 1993, Abraham et al 1996). For arctic and sub-arctic nesting geese, however, agricultural crops are typically

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not available near breeding areas in the spring or early stages of fall migration (Owen 1982, Wypkema and Ankney 1979, Sedinger and Bollinger 1987).

Unlike most other populations of arctic or sub-arctic nesting geese, Canada geese (*B. c. parvipes*) breed and initially stage in Interior Alaska near agricultural fields (Fig. 4.1, Johnson et al. 1979, Eichholz 2001). In this study, we describe nutrient dynamics of Canada geese during spring and fall staging on agricultural habitat in Interior Alaska. We compare estimates of nutrient reserves and rate of change in nutrient reserves with collection date between age and sex classes and geese staging in spring and fall. We also compare nutrient reserve levels and rate of change in nutrient reserves with collection date between this population staging in Interior Alaska on agricultural fields and populations of subarctic- and arctic-nesting geese feeding on natural habitat during spring and fall staging to determine if the rate of change is greater for geese feeding in agricultural fields.

METHODS

Study Area

There are two known important staging areas for geese in Interior Alaska. In 1978 (24,500 ha) and 1983 (19,400 ha), the state of Alaska sold and cleared boreal forest near Delta Junction Alaska over a ten-year period (Fig. 4.1) to stimulate development of grain agriculture (barley, *Hordeum murinum*) in the state. The area is near a warm water lake (Clearwater Lake) and a small stream (Clearwater Creek), which provide open water for roosting in April when migratory waterfowl return to Interior Alaska for breeding. In addition to Clearwater Lake, numerous islands in the nearby Tanana River provide roost

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sites in fall. The second major staging area is Creamer's Field Migratory Waterfowl Refuge and the University of Alaska agricultural fields near Fairbanks, approximately 180 km northwest of Delta Junction. Creamer's Field was established in 1966 as a staging area for migratory birds to allow public observation. Barley is planted for waterfowl use during the fall and supplemented by additional grain spread in the fields in the fall and spring. The University of Alaska maintains experimental agricultural fields approximately 10 km west of Creamers Field, providing additional waste and unharvested barley as well as a small lake (Smith Lake). Smith Lake is used as a roost site during the day between diurnal feeding periods and islands in the nearby Tanana River are used for roosting at night during fall staging. Canada geese in this study used the Delta Junction area as the primary staging area in spring and the Fairbanks area as the primary staging area in fall (Eichholz pers. obs.).

Although both Canada geese and Taverner's Canada geese (*B. c. taverneri*), a slightly smaller subspecies (Johnson et al. 1979), are thought to use the Delta Junction spring staging area, we believe geese collected for this study were primarily Canada geese. Canada geese on the wintering grounds are partially segregated from Taverner's Canada geese because of a tendency to feed in smaller fields relative to Taverner's Canada geese (Simpson and Jarvis 1979). Canada geese collected in the spring were collected from a group that arrived earlier and fed in smaller fields relative to later arriving geese (Eichholz pers. obs.). Furthermore, 78 % of females examined had begun rapid follicle development, indicating they were within 12 days of nesting (Raveling 1978). Because Taverner's Canada geese migrating through Interior Alaska breed on

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Alaska's North Slope (Johnson et al. 1979), where nesting begins in early June (Bergman et al. 1977), females in rapid follicle development must have been Canada geese. All Canada geese collected during fall staging were collected in Fairbanks. Canada geese staging in Fairbanks arrive and depart earlier in the fall and average slightly larger than Canada geese in Delta Junction, thus are thought to be primarily Canada geese (Eichholz 2001).

Collection

We collected geese in the springs of 1996 and 1997 near Delta Junction by shooting them in fields while they fed. Geese were collected during the falls of 1994-1997 on the Fairbanks study area by trapping them using baited rocket nets (Wildlife Materials Inc.) in fields or at roost sites. Geese trapped in rocket nets were asphyxiated with a lethal dose of Halothane. Geese were weighed with an electronic balance (± 0.1 g) and culmen and total tarsus were measured with dial calipers (± 0.1 mm) (Dzubin and Cooch 1992), while flat wing chord and body were measured with a measuring board (± 1 mm) (Eichholz and Sedinger 1999). Geese were frozen within 12 hours of collection and remained frozen until they were later thawed for proximate analysis. Methodology was approved by the University of Alaska Animal Care and Use Committee.

Body Composition Analysis

Geese were thawed and plucked and the right breast muscles (pectoralis, supracoracoideus, corabrachialis) were removed and weighed ± 0.1 g on an electronic balance. The esophogus, gizzard, and gastro-intestinal tract (GI tract - duodinum, large intestine, small intestine, and cecae) were removed, weighed, stripped of contents, and

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reweighed with an electronic balance to determine weight of the organs and ingesta. Below, fresh body weight refers to fresh weight minus ingesta. During dissection, we examined the ovaries of nine of the 17 AHY female geese collected in spring to determine their reproductive stage (Ankney and MacInnes 1978). For each specimen, we froze the entire dissected carcass, cut it into small pieces with a band saw and ground it in a commercial meet grinder three times, mixing contents between each grinding to ensure a homogeneous mixture. After grinding we took three 25 g - 35 g samples from each ground carcass to estimate total lipid, protein, and mineral content with proximate analysis following Horwitz (1975). Because some carcasses remained frozen for extended periods between steps of the process, each carcass was weighed immediately before and immediately after being placed in or removed from the freezer to account for water loss while in the freezer and during processing. Water loss from these periods was then totaled and used to adjust wet weight of samples for water loss during processing. Samples were oven dried at 60° C until weight stabilized to determine water content.

We determined percent lipid by placing dried samples in a soxhlet apparatus containing petroleum ether for a minimum of 12 hours (Dobush et al. 1985). We considered all weight loss from the petroleum ether extraction to be neutral fat (Dobush et al. 1985) and calculated percent fat as weight lost during extraction divided by initial wet weight of samples. We incinerated dry lean samples in a muffle furnace at 500° C for eight hours to estimate ash content. We assumed fat free, ash free, dry weight represented protein and that noncombustible ash represented minerals (Raveling 1979). The mean concentration of fat, protein, and ash for the three samples was used as the

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estimated carcass concentration for each component. We calculated total fat, total protein, and total mineral weight by dividing the weight of each component by the wet weight of the sample, then multiplying the fresh body weight by the mean percentage of that component in subsamples.

Statistical Analysis

We used general linear models (PROC GLM, SAS Institute 1990) to test for a relationship between the body components (body weight, total fat, total protein, total minerals, breast muscle weight, gizzard weight, and GI tract weight) and collection date and for variation in the body components between sexes, 2 age classes, and among years for fall and spring separately. We included all two-way interactions in these analyses. In cases where the P value of the interaction was > 0.15, we removed the interaction and reran the analysis. We also tested for differences in body components between spring and fall staging using GLM with season and sex as independent class variables, allowing all two-way interactions.

Structurally larger individuals potentially maintain greater amounts of fat, protein, and minerals that are not available for use as reserves (Alisauskas and Ankney 1992a). Thus, we used principal components analysis (PROC PRINCOMP, SAS Institute 1990) of four morphological measurements (exposed culmen, total tarsus, flattened wing chord, and body length) to calculate first principal component (PC1) scores (using the correlation matrix), then used PC1 scores as an index of structural size for all age and sex categories combined (Alisauskas and Ankney 1987). We then controlled for variation in body components due to variation in structural size by

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including PC1 in all analyses.

RESULTS

We collected 33 staging geese in spring and 45 staging geese in fall for proximate analysis (Table 4.1). However, two females and one male in the spring sample had a measurable bursa and thus were likely sub-adults, so we excluded them from further analysis. Samples from 10 individuals were lost before estimates of protein and minerals were conducted during laboratory processing; thus, sample sizes of some analyses that include estimates of protein and minerals are smaller than indicated here.

All four measurements loaded positively on the first principal component, which described 71% of the total variation in the original data. Fresh weight, total fat, total protein, total ash, breast muscle, gizzard weight, and GI tract weight were related to PC1 ($P < 0.05$ for all variables), so we controlled for variation in body size for all analyses.

Within-Season Variation in Spring

There was no variation in body weight between sexes ($F_{1,25} = 0.92$, $P = 0.4$) or years ($F_{1,25} = 0.0$, $P = 0.6$), but there was a positive relationship between body weight and collection date (Fig. 4.2). Fat levels were similar between years ($F_{1,25} = 1.35$, $P = 0.18$), tended to increase with collection date (Fig. 4.3), and were 184 ± 71 g greater for females than males ($F_{1,25} = 6.68$, $P = 0.02$). Protein level did not vary with collection date ($F_{1,22} = 0.38$, $P = 0.5$) or between sexes ($F_{1,22} = 0.53$, $P = 0.5$), however, protein levels tended to vary between years with geese in 1996 having a mean of 47 ± 25 g less protein than geese in 1997 ($F_{1,22} = 3.52$, $P = 0.07$). Breast muscle weights were similar between sexes ($F_{1,25} = 0.29$, $P > 0.6$), but increased with collection date (Fig. 4.4).

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Similar to total protein, breast muscles were 23.5 ± 11.5 g lighter in 1996 than in 1997 ($F_{1,25} = 4.23$, $P = 0.05$). Gizzard weight did not vary between sexes ($F_{1,24} = 0.03$, $P = 0.9$), but there was a significant interaction between collection date and year ($P = 0.05$), so we tested for a relationship between gizzard weight and collection date for each year separately. There was no relationship between gizzard weight and collection date in 1996 (Fig. 4.5A); however, gizzard weight tended to decrease with collection date in 1997 (Fig. 4.5B). GI tract weight was similar between sexes ($F_{1,24} = 2.06$, $P = 0.16$), but collection date and year tended to interact ($P = 0.06$), so we analyzed the data for each year separately. There was no relationship between GI tract and collection date in 1996 (Fig. 4.6A), but GI tract weight tended to increase with collection date in 1997 (Fig. 4.6B). There was no variation in mineral level between years ($F_{1,22} = 0.51$, $P = 0.5$) or sexes ($F_{1,22} = 0.29$, $P = 0.6$), however, there was a tendency for an increase in mineral level with collection date (Fig. 4.7).

Within-Season Variation in the Fall

When testing for variation in fresh weight between sex and age classes, among years, and for a relationship between fresh weight and collection date, we found the relationship between fresh weight and collection date was driven by one outlying datum (Fig. 4.8A). All nutrient levels of this goose were substantially lower than those of other geese, indicating it was an anomaly, so we removed this sample from further analysis. We reanalyzed the data without the outlying datum and found males tended to weigh 90 ± 61 g more than females ($F_{1,37} = 2.17$, $P = 0.15$) and AHY geese weighed 117 ± 51 g more than HY geese during fall staging ($F_{1,37} = 5.14$, $P = 0.03$). Fresh weight did not vary among years ($F_{2,37} = 0.79$, $P = 0.46$), and there was no relationship between fresh weight and collection date (Fig. 4.8B). When testing for variation in fat levels among collection dates and years, and between sex and age classes, we found an interaction between date and year ($P = 0.01$), and a tendency for an interaction between age and sex ($P = 0.08$), so we analyzed the data separately for each of the interacting variables. There was no relationship between fat level and collection date for 1995 or 1996, however, fat level tended to increase with collection date in 1997 (Fig. 4.9). When testing for variation in fat levels between sexes for each age class separately, we found no difference between sexes of HY geese ($F_{1,23} = 0.11$, $P = 0.7$), or AHY geese ($F_{1,10} = 1.15$, $P = 0.30$). There was no difference in protein levels between age classes, sexes, or years ($F_{1,30} < 1.75$, $P > 0.2$ for all variables), or a relationship between protein level and collection date ($F_{1,30} = 0.67$, $P = 0.5$). There was no relationship between breast muscle weight and collection date ($F_{1,37} = 0.29$, $P = 0.6$), or difference in breast muscle weight between sexes ($F_{1,37} = 0.44$, $P = 0.51$) or age classes ($F_{1,37} = 1.94$, $P = 0.17$); however, breast muscle weight tended to be 22 ± 22 g greater in 1996 than in 1997 and 20 ± 24 g greater in 1997 than 1995 ($F_{2,36} = 2.63$, $P = 0.08$). We found no variation in gizzard weight among years ($F_{2,37} = 0.37$, $P = 0.7$) or between age classes ($F_{1,37} = 0.61$, $P = 0.4$), but there tended to be an interaction between date and sex ($P = 0.10$) so we analyzed the data for each sex separately. We found no relationship between gizzard weight and collection date for males ($F_{1,17} = 1.14$, $P = 0.3$) or females ($F_{1,15} = 0.49$, $P = 0.5$) when we analyzed data for each sex separately. There was no difference in GI tract weight between sexes (Table 4.2), but GI tracts of AHY geese were 155 ± 73 g heavier than HY geese (Table 4.2) and

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GI tracts were on average 7.0 ± 4.1 g heavier in 1996 than 1997 and 7.0 ± 4.5 g heavier in 1997 than in 1995 (Table 4.2). Age and date interacted significantly (Table 4.2) so we tested for a relationship between GI tract weight and collection date for each age class separately. There was no relationship between adjusted GI tract and collection date for AHY geese (Fig. 4.10A); however, GI tract weight increased with collection date for HY geese (Fig. 4.10B). There was no relationship between mineral level and collection date ($F_{1,29} = 0.19$, $P = 0.7$), or variation between sexes ($F_{1,29} = 0.01$, $P < 0.9$), or among years ($F_{2,29} = 0.43$, $P = 0.7$); however, AHY geese averaged 17 ± 5 g more minerals than HY geese ($F_{1,29} = 11.84$, $P < 0.01$).

Between-Season Variation

We found no significant difference in weight residuals between seasons ($F_{1,42} = 0.34$, $P = 0.6$). There was the suggestion of an interaction between season and sex ($P = 0.06$) for fat level, so we analyzed data for each sex separately. Fat levels did not vary significantly between seasons for females ($F_{1,26} = 0.32$, $P = 0.6$), but males averaged 118 ± 50 g more fat during fall staging than spring staging ($F_{1,20} = 5.56$, $P = 0.03$). We found no difference in protein ($F_{1,38} = 0.01$, $P = 0.9$) or mineral ($F_{1,38} = 0.25$, $P = 0.62$) levels between seasons. Spring geese averaged 21 ± 7 g heavier right breast muscles than in fall ($F_{1,42} = 8.9$, $P < 0.01$). Adjusted gizzard weights tended to be 5.3 ± 3.4 g greater for geese collected during fall staging than geese collected during spring ($F_{1,42} = 2.39$, $P = 0.13$) and adjusted GI tract weight averaged 9.4 ± 3.1 g greater in fall-collected geese than in spring-collected geese ($F_{1,42} = 8.04$, $P < 0.01$).

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DISCUSSION

Spring

Nutrient reserves immediately prior to nesting are an important determinant of reproductive success in arctic and sub-arctic nesting geese (Ankney and MacInnes 1978, Raveling 1979). Ebbinge (1989) directly related reserves on spring staging areas to the probability of returning with young to wintering areas the following fall. There is, however, substantial variation in dependence on reserves for breeding among species of geese (Thomas 1983, Ankney 1984, Mainguy and Thomas 1985). For example, cackling Canada geese begin egg laying with about 29 % of their total body being composed of fat (Raveling 1979), while dusky Canada geese (*B. c. occidentalis*) begin laying with about 16 % body fat (Bromley and Jarvis 1993). There is also substantial variation in which portion of the annual cycle reproductive nutrients are acquired. Dusky Canada geese acquire most of their nutrients for migration and breeding on the wintering grounds before spring migration and spend only about 12 days from the time they depart the wintering grounds in the Willamette Valley of Oregon until arrival on the breeding grounds in the Copper River Delta of Alaska (Bromley and Jarvis 1993). After arrival on the breeding grounds, dusky Canada geese spend approximately 2 to 3 weeks feeding and slightly increase protein reserves before laying (Bromley and Jarvis 1993). In contrast, some populations of lesser snow geese (*Chen caerulescens caerulescens*) spend almost four months from the time they depart wintering grounds in Texas to arrival on breeding grounds in Ontario (Thomas 1983). These geese depart the wintering grounds

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with few reserves then acquire reserves for reproduction during the migration north (Ankney 1982, Thomas 1983, Alisauskas and Ankney 1992b).

Because of the unique juxtaposition of agricultural habitat to nesting areas in our study, classifying spring staging geese as either staging or pre-nesting was difficult. Typically, geese that aggregate in agricultural habitat before nesting would be considered staging (e.g., McLandress and Raveling 1981a); however, 7 of 9 adult females that were examined had entered rapid follicle development, and would be classified as pre-nesting in most studies (e.g., Ankney and MacInnes 1978, Raveling 1979, Bromley and Jarvis 1993). Thus, this study encompasses both the final staging and pre-nesting periods, and we compare our results to those of studies from both periods.

Geese in this study depart wintering grounds in late March or early April (M. Monda Washington Dept. of Fish and Game pers. comm.) and arrive at our study area in mid to late April, where they remain on the study area in agricultural habitats for about 10 to 15 days (Eichholz 2001, Table 1.4). During this period, geese increased their weight by approximately 18 g per day (Fig 4.2), and fat level at a rate of approximately 9 g per day (Fig. 4.3).

Of four previous studies of nutrient acquisition during the pre-nesting period (Budeau et al. 1991, Bromley and Jarvis 1993, Gates et al. 1998), only the population of greater white-fronted geese (*Anser albifrons frontalis*) studied by Budeau et al. (1991), showed a gain in fat. This population feeds primarily on grass shoots (*Arctophila fulva*), but arrowgrass bulbs (*Triglochin palustris*) and crowberries (*Empetrum nigrum*), which are high in both lipids and soluble carbohydrates (Sedinger and Raveling 1984), also

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compose a large proportion of their diet (Budeau et al 1991). Greater snow geese (*C. c. altantica*) and dusky Canada geese maintained fat reserves during pre-nesting, while interior Canada geese (*B. c. interior*) lost fat reserves during pre-nesting (Bromley and Jarvis 1993, and Gates et al. 1998). The diet of pre-laying dusky Canada geese is unknown, but interior Canada geese feed primarily on spring growth of grasses and sedges (Gates et al. 1998). Spring growth of sedges and grasses were high in digestible proteins but low in digestible carbohydrates relative to arrowgrass bulbs, berries, or agricultural grains, such as barley (Sedinger 1984, Joyner et al. 1987). Similar to geese feeding on the nesting grounds, geese feeding on natural grasses and sedges on their final staging areas gain protein but not fat (Wypkema and Ankney 1979), while geese on final staging areas with access to agricultural waste grain gain both fat and protein (Gates et al. 1998, Gauthier et al. 1992, McLandress and Raveling 1981a). We believe the introduction of agriculture to Interior Alaska has enabled Canada geese to replace some fat reserves used during migration, allowing females to begin nesting with greater fat reserves than was possible before the introduction of agriculture in Interior Alaska.

Unlike other populations of geese feeding in agricultural habitat (Gates et al. 1998, Gauthier et al. 1992, McLandress and Raveling 1981), protein level did not increase with collection date in our study. Geese fed in two pastures regularly, but because these pastures contained perennial grasses with little, if any, new growth before nesting (Eichholz pers. obs.) and individual geese fed less than 20 minutes each day in these pastures (Eichholz unpub. data), geese did not acquire protein beyond that needed for maintenance. In contrast, a large component of the diet of giant Canada geese, lesser

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snow geese, greater snow geese, and interior Canada geese was spring growth of grasses and sedges (Gates et al. 1998, Wypkema and Ankney 1979, Gauthier et al. 1992, McLandress and Raveling 1981a).

Despite our failure to detect a relationship between overall protein level and collection date, we observed a significant positive relationship between breast muscle weight and collection date (Fig. 4.4), a weak positive relationship between GI tract weight and collection date in 1997 (Fig. 4.6), and a weak negative relationship between gizzard weight and collection date in 1997 (Fig. 4.5). Reallocation of protein reserves to different muscle groups is common in geese (Hanson 1962, Ankney and MacInnes 1978). Thus, the change in muscle and organ weight with collection date may represent reallocation of protein from muscle groups or organs that are of little importance during reproduction, to those that are of more importance (Hanson 1962).

Numerous studies have shown a decline of mineral reserves in female geese during egg production, indicating minerals are an important component of reproductive nutrient reserves (e.g., Ankney and MacInnes 1978, Raveling 1979). Few data, however, are available on when these mineral reserves are acquired (McLandress and Raveling 1981a). McLandress and Raveling (1981a) hypothesized females acquire minerals for egg production on the final staging areas or on the nesting grounds during rapid follicle development. We found geese collected later in spring staging tended to have greater mineral levels (Fig. 4.7), supporting this hypothesis. Delaying acquisition of mineral reserves until the end of the spring migration would reduce body weight and save energy during migration. It is not clear to us, however, why male geese would also acquire

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mineral reserves. Both male and female geese use large amounts of mineral reserves for feather growth during molt (Hanson 1962). Thus, males may acquire mineral reserves during spring staging for use approximately six weeks later during molt, when most of their time is spent being vigilant for predators (Sedinger et al. 1995).

Females averaged approximately 184 g more fat than males during spring. The observed difference in fat level between males and females was most likely due to differences in behavior and energetic requirements during spring staging and nesting. During spring, male geese spend significantly less time feeding and more time vigilant than female geese (Gauthier et al 1988, Krapu et al. 1995), and female geese use considerably more fat during nesting than males (Ankney and MacInness 1978, Raveling 1979). Vigilance by males during spring staging likely allows females to feed more intensely, thereby acquiring nutrient reserves needed for egg laying and incubation at a faster rate (Gauthier et al 1988, Krapu 1995).

Protein level and breast muscles tended to be smaller in 1996 than 1997. Annual variation in nutrient reserves is common in arctic and subarctic nesting geese (e. g. Bromley and Jarvis 1993, Davies and Cook 1983). Davies and Cook (1983) found an association between droughts in the prairies and decreased reproductive success of snow geese. They hypothesized that drought conditions decrease food availability during spring migration; thus, lesser snow geese arrive on the nesting grounds with fewer reserves leading to a decrease in clutch size. Climate-induced variation in food abundance also provides a reasonable hypothesis for the annual variation in protein level we observed.

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Pre-breeding Canada geese in our study had few fat reserves relative to other populations (Table 4.3). Female geese were still acquiring fat reserves in our study and we are thus unsure of their final fat levels immediately before egg laying. At the estimated rate of fat deposition, however, most females would have begun laying with lower reserves than other populations, even after an additional 10 days of fat gain, assuming females gain fat at a linear rate. Thus, geese in our study may begin nesting with fewer fat reserves than most populations.

Fall

A substantial proportion of natural mortality of geese occurs during fall migration (Owen 1982, Ward et al. 1997, Schmutz and Ely 1999, Eichholz 2001). This mortality is presumably due to individuals having insufficient energy to complete migration (Owen 1992, Ward et al. 1997). Thus, acquisition of nutrients during the early stages of fall migration is an important determinant of survival during migration (Owen 1992, Ward et al. 1997, Schmutz and Ely 1999, Eichholz 2001). Wypkema and Ankney (1979) found lesser snow geese staging at southern James Bay increased their index of fat reserves by 70 to 110% depending on age and sex. They calculated that the fat acquired during staging allowed geese to increase flight range by 600 to 1,600 km. Sedinger and Bollinger (1987) found that adult, second year, and HY cackling Canada geese spent 53%, 73%, and 84% respectively, of their time feeding during fall staging at Ugashik Bay, Alaska. Although they were unable to detect an increase in weight, based on hunter-killed geese, they found both adult male and female geese weighed more than peak spring weight of geese reported by Raveling (1979), indicating fall migration is as

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energetically demanding as reproduction in this population. Cackling Canada geese lost 400 - 600 g during the nonstop flight from Ugashik Bay to the Klamath Basin on the Oregon-California border indicating a strong dependence on stored fat during fall migration (Nelson and Hansen 1959, Sedinger and Bollinger 1987).

We observed no measurable change in fresh weight, fat, or protein level during fall staging in this study. We believe it unlikely that geese are not gaining nutrient reserves during this period, and propose an alternative hypothesis. We hypothesize that the body condition of post-breeding females is an important determinant of the time of departure of family units from the fall staging area. Such a mechanism is consistent with the greater need of females than of males to recover nutrient reserves following breeding (Raveling 1979), survival of adults should also take precedence over that of juveniles (Charlesworth 1980). Based on observations of neck collared individuals, we observed a negative correlation between weight at capture of adult females and the duration of time families remained in Interior Alaska (Eichholz unpub data), suggesting that females attempted to reach a target weight before migrating. Continuous departure of the heaviest geese throughout fall staging could have prevented us from detecting a nutrient again.

Breast muscle weight was greater in AHY fall staging geese than HY fall staging geese. HY geese begin brood rearing and molt with little muscle development, and muscle development is initially in the legs to support locomotion (Sedinger 1986, Slattery and Alisauskas 1995). Thus, it is not surprising that breast muscles in HY geese

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are less developed than in AHY geese in early fall. Our results indicate that HY breast muscles are not fully developed, and protein is required for HY geese at this time.

We were surprised to find GI tracts of HY geese tended to be smaller than those of AHY geese. Digestive organs are typically the earliest developing organs of geese (Sedinger 1986, Slattery and Alisauskas 1995). Intestine size affects an individual's ability to absorb nutrients, thereby affecting the ability to acquire nutrients (Kehoe and Ankney 1985, Kehoe and Thomas 1987). Apparently, HY geese sacrifice their ability to absorb nutrients to build other tissues in preparation for migration.

Males had significantly greater fat levels in fall than spring, and digestive organ weight was greater for both male and female geese collected during fall than geese collected during spring. These results suggest that, similar to cackling Canada geese (Sedinger and Bollinger 1987), fall migration is an energetically demanding period for Canada geese staging in Interior Alaska. Eichholz (2001) suggested that geese depart fall staging areas of Interior Alaska and fly nonstop to agricultural areas in central British Columbia, a distance of approximately 1,700 km. Using calculations from Wypkema and Ankney (1979) for lesser snow geese, which are similar in size to Canada geese, we calculate that geese would need approximately 240 g of fat reserves to reach central British Columbia. Although all age and sex groups averaged well over 240 grams total fat (Table 4.4), one individual collected on 11 Sept. had only 203 g of fat, while four other geese had less than 240 g of fat. Thus, some geese in Interior Alaska had too little fat to immediately complete migration nonstop when they were collected in fall, indicating that additional energy was required to initiate migration.

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Agriculture and Population Dynamics

Population size is determined by a balance among fecundity, immigration, mortality and emigration (Wakeley 1982). For geese, fecundity is most likely limited by nutrient availability prior to and during nesting (Lack 1968, Ryder, 1971, Inglis 1977, Ankney and MacInnes 1978). More specifically, endogenous nutrient reserves, in conjunction with limited exogenous nutrients at the onset of laying, likely limit egg production and incubation constancy in arctic and sub-arctic nesting geese (Ryder 1971, Ankney and MacInnes 1978, Eichholz and Sedinger 1999). Nutrient availability is also thought to be an important determinant of waterfowl mortality during both the breeding and non-breeding periods (Ryder 1971, Ankney and MacInnes 1978, Owen, 1982, Conroy et al. 1989, Schmutz and Ely 1999). The introduction of agriculture to Interior Alaska may have positively influenced fecundity and survival of the population of Canada geese that stage there. This agriculture likely has allowed female Canada geese to replenish fat reserves used during migration more rapidly than was possible feeding on natural vegetation. Although female geese in this population appear to be less dependent on fat reserves than other populations of Canada geese, fat reserves may still influence clutch size and nest success (Harvey 1971, Inglis 1977, Ankney and MacInnes 1978, Raveling 1979). Fat reserves are also important for fall migration (Wypkema and Ankney 1979, Sedinger and Bollinger 1987). Therefore, the introduction of agriculture to Interior Alaska has likely altered the balance between fecundity and survival by increasing both fecundity and survival, thereby influencing the dynamics of the lesser Canada goose population in Interior Alaska.

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Table 4.1. Summary of collected geese.

Summary of geese collected for proximate analysis during spring staging in Delta Junction, Alaska and during fall staging in Fairbanks, Alaska.

Year	Hatch year males	Hatch year females	After hatch year males	After hatch year females
Fall				
1995	7	6	1	0
1996	4	8	4	6
1997	3	1	5	0
Spring				
1996			13	9
1997			0	8

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Table 4.2. ANCOVA test for variation in GI tract weight.

ANCOVA testing for variation in GI tract weight for fall staging Canada geese in Fairbanks, AK.

Source	df	MS	F	P
PC1	1	311	3.94	0.05
Date	1	321	4.08	0.05
Sex	1	4	0.06	0.81
Age	1	358	4.54	0.04
Year	2	1264	8.02	< 0.01
Date*Age	2	366	4.64	0.04
Error	36	79		

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Table 4.3. Comparison of nutrient levels among species of pre-nesting female geese. Nutrient levels of individual pre-nesting female geese of various species.

Results ± SE.

Species	n	Weight	Fat	Protein	Mineral
Lesser Canada[1]	6	2351	288 ±12.3	433 ±18.4	89 ±3.8
Cackling Canada[2]	4	1890	532 ±28.1	352 ±18.6*	
Giant Canada[3]	45	4585	726 ±15.8	640 ±14.0*	
Dusky Canada[4]	43	3134	492 ±15.7	525 ±16.8*	
Greater white-fronted[5]	8	2661	438 ±16.5	446 ±16.8*	
Lesser snow[6]	11	2893	642 ±22.2	390 ±13.5	97 ±3.4
Greater Snow[7]	16	2755	359 ±13.0	546 ±19.8*	
Atlantic Brant[8]	13	1384	124 ±9.0		

* Estimate of protein reserves includes minerals

this study[1], Raveling 1979[2], Mainguy and Thomas 1985[3], Bromely and Jarvis 1993[4], Budeau et al. 1991[5], Thomas 1983[6], Choiniere and Gauthier 1991[7], Ankney 1984[8].

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Table 4.4. Summary of nutrient levels.

Summary of nutrient levels of spring staging Canada geese collected in Delta Junction, Alaska and fall staging Canada geese collected in Fairbanks, Alaska. Results are means ± 1 SE.

Age-sex class	Weight	Fat	Protein	Mineral
Spring				
AHY-male	2865 ±78	389 ±40	482 ±19	112 ±5
AHY-female	2436 ±116	425 ±53	424 ±25	94 ±7
Fall				
HY-male	2371 ±134	403 ±31	426 ±16	90 ±4
HY-female	2275 ±186	423 ±43	391 ±22	80 ±5
AHY-male	2700 ±134	476 ±35	470 ±25	109 ±6
AHY-female	2426 ±82	393 ±58	419 ±40	97 ±10

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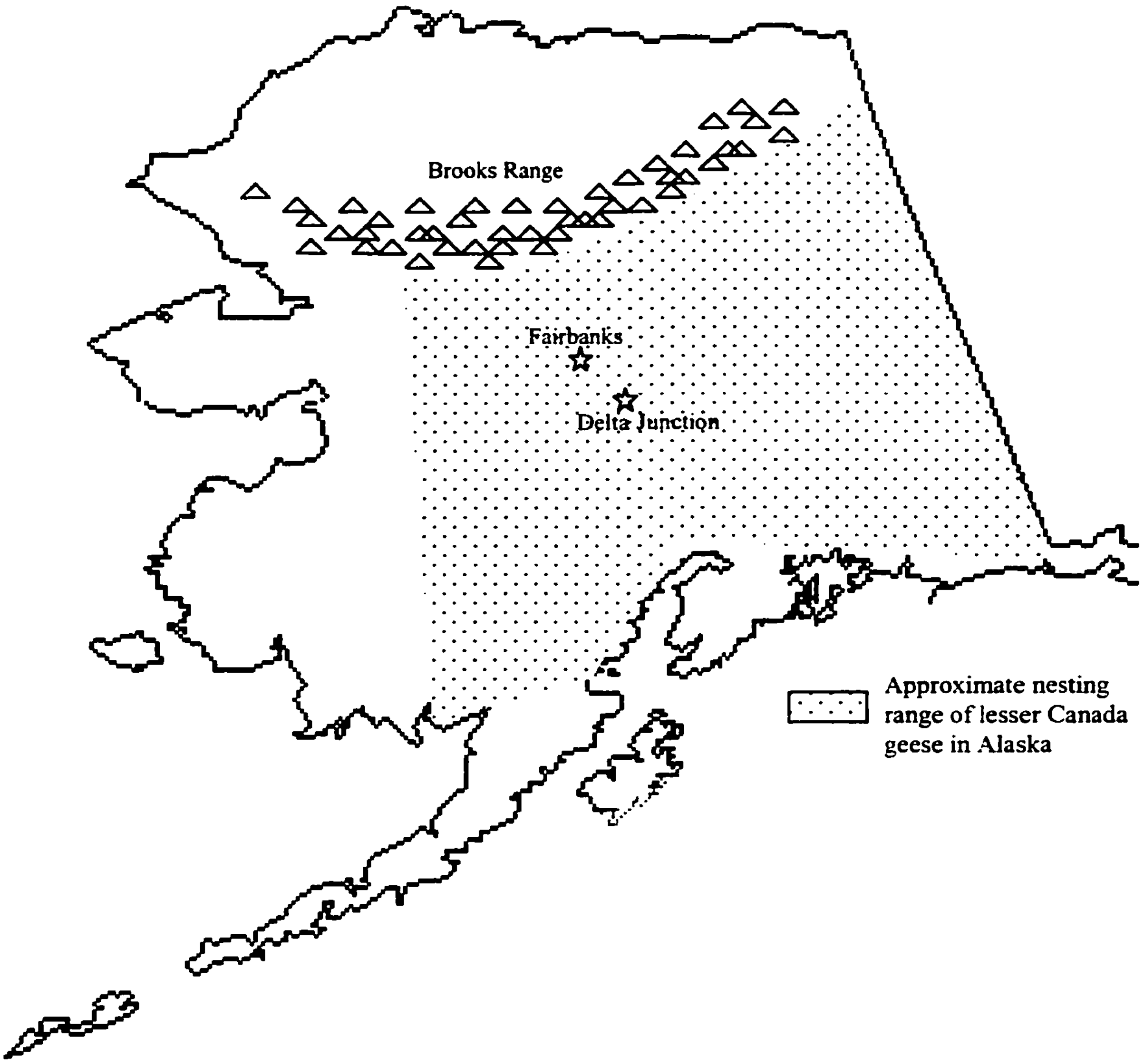

Figure 4.1. Map of Alaska.
Map of Alaska showing study areas and approximate breeding range of lesser Canada geese. Lesser Canada geese are thought to breed south of the Brooks Mountain Range and east of the tree line in Interior Alaska and western interior Yukon Territory, Canada.

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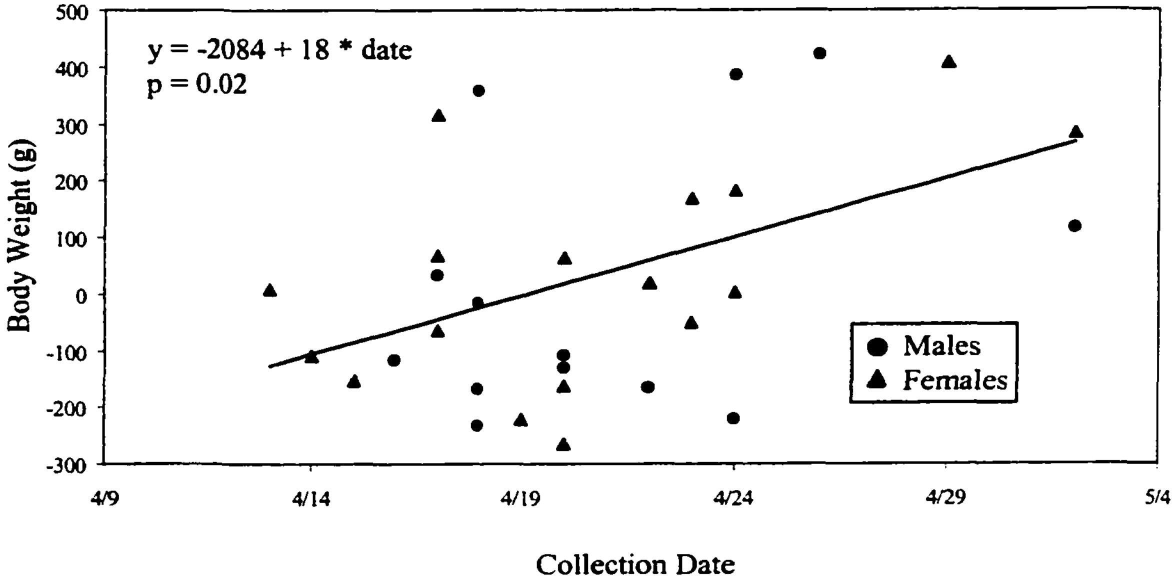

Figure 4.2. Body weight vs. collection date during spring.
Relationship between body weight corrected for body size and collection date of 30 spring staging Canada geese.

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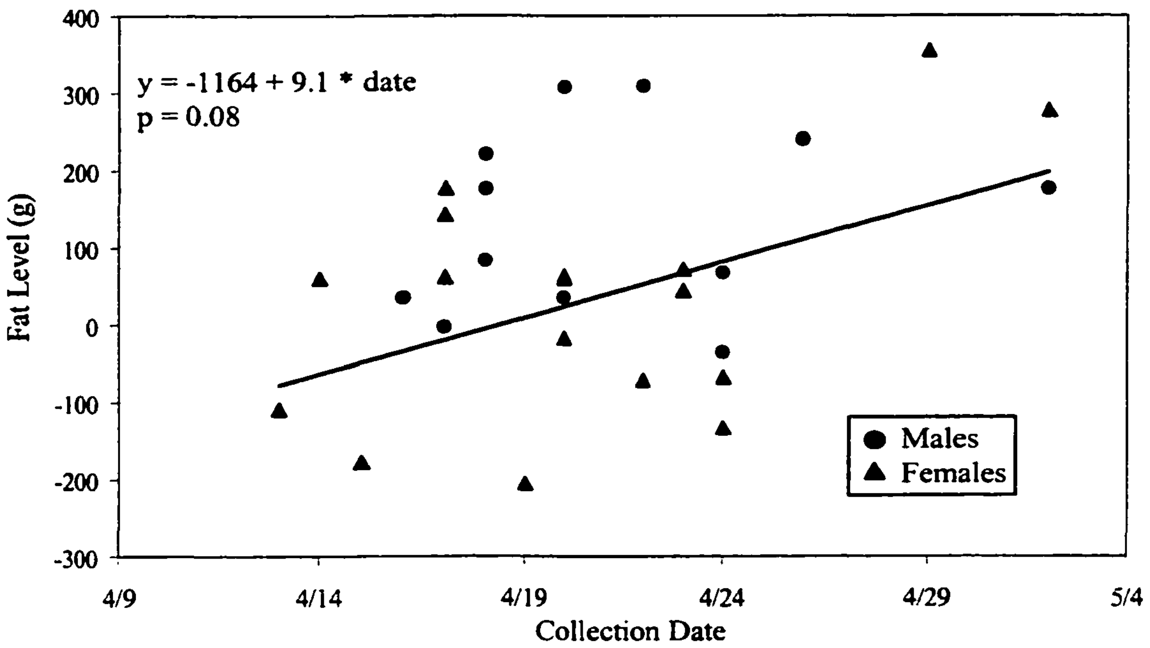

Figure 4.3. Fat level vs. collection date during spring. Relationship between fat level corrected for body size and collection date of 30 Canada geese collected during spring staging. Data points are corrected for variation between sexes by adding 184 g to each male data point.

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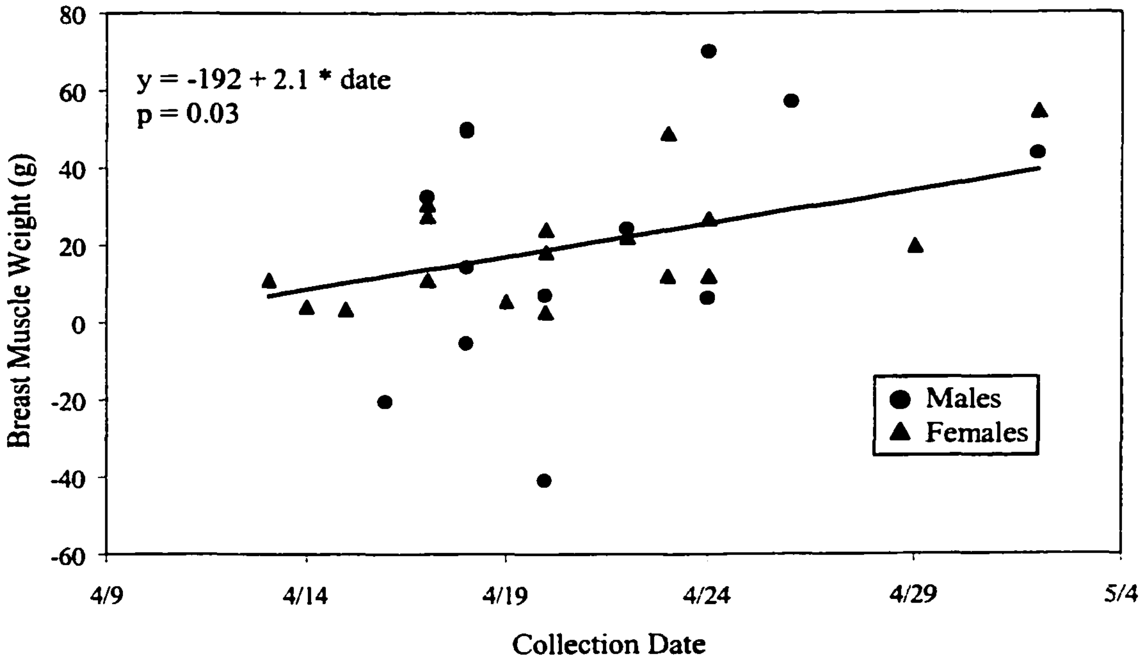

Figure 4.4. Breast muscles vs. collection date during spring. Relationship between right breast muscles weight, corrected for body size, and collection date of 30 Canada geese collected during spring staging in Delta Junction, Alaska. Data points are corrected for variation between 1996 and 1997 by subtracting 23.5 g from 1997 data points.

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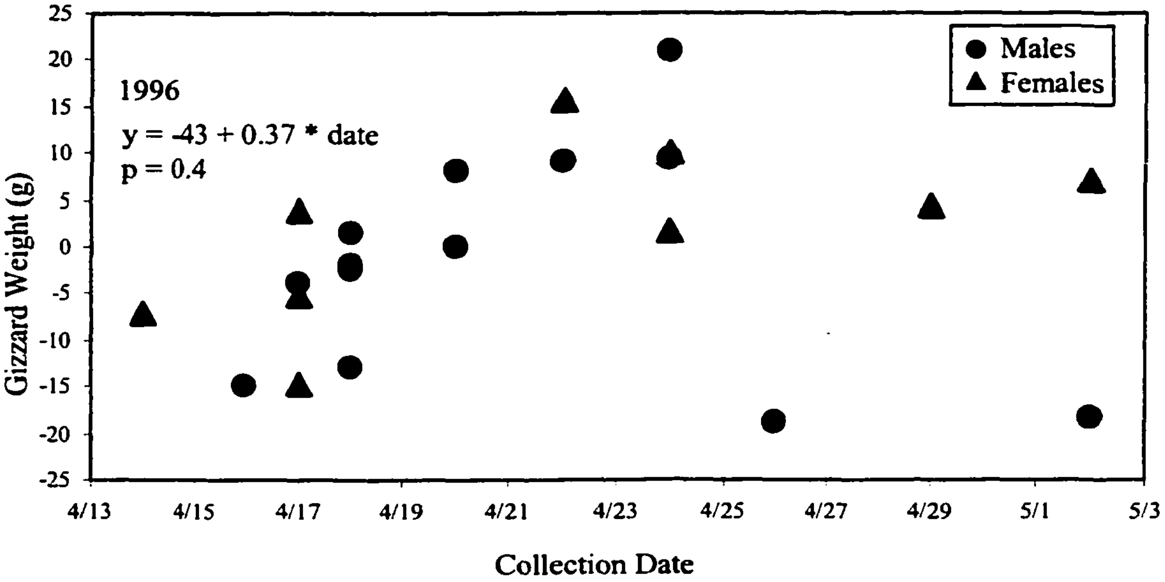

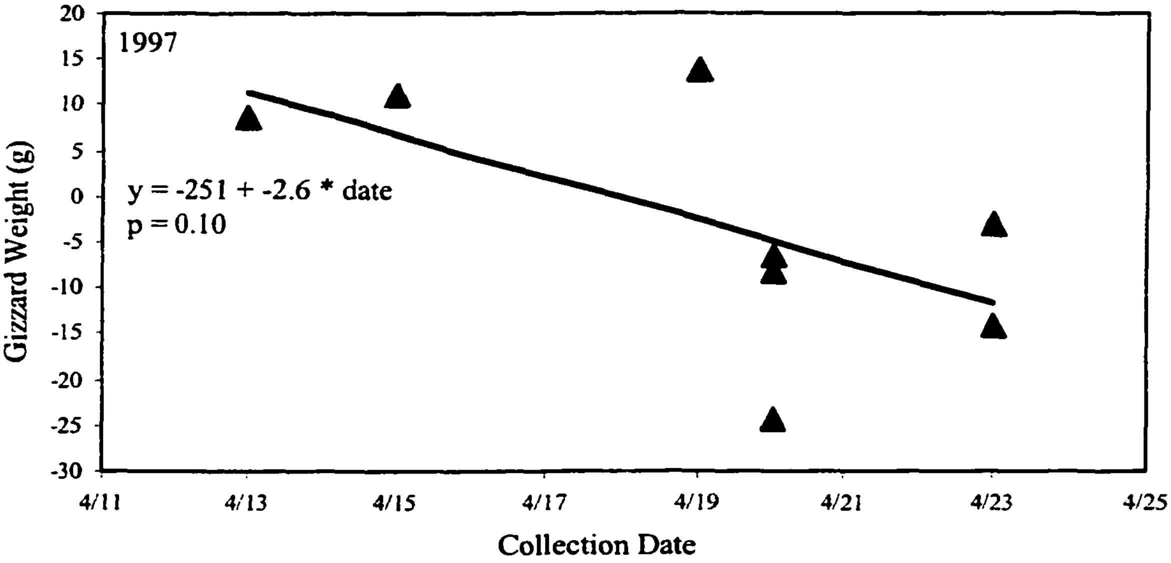

Figure 4.5. Gizzard weight vs. collection date during spring. Relationship between gizzard weight corrected for body size and collection date for 22 geese collected in 1996 and 8 geese collected in 1997.

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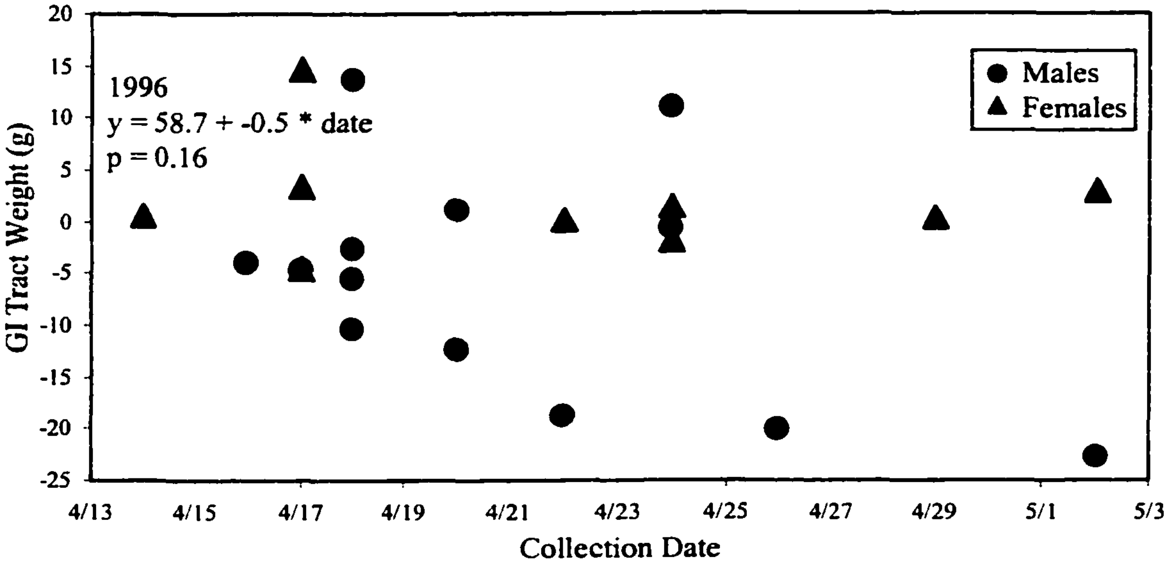

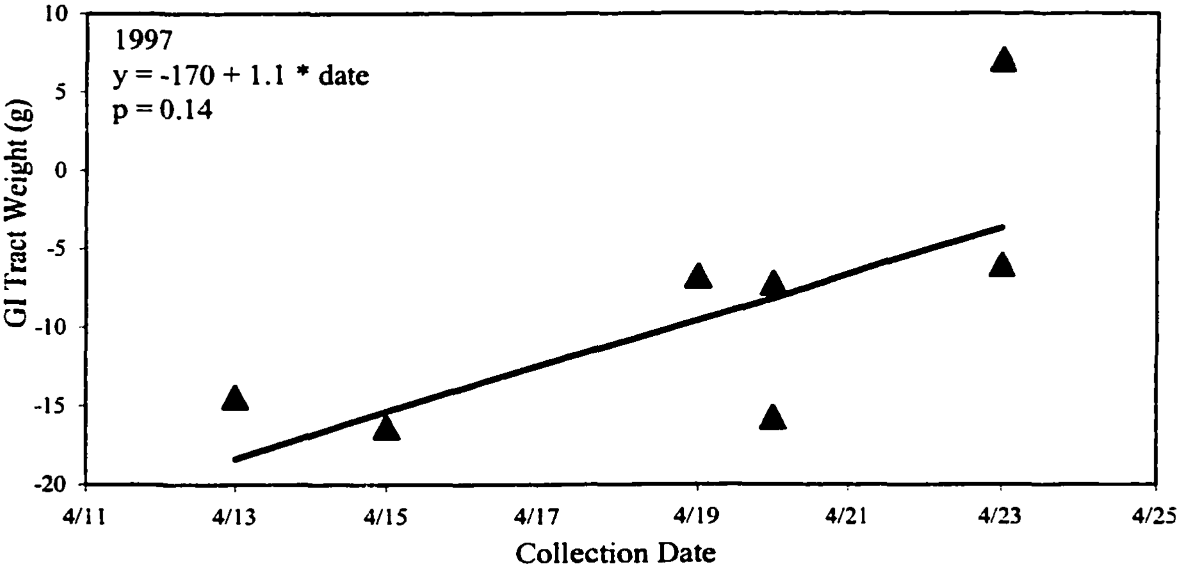

Figure 4.6. GI tract vs. collection date during spring.
Relationship between GI tract corrected for body size and collection date for 22 Canada geese collected in 1996 and 8 Canada geese collected in 1997.

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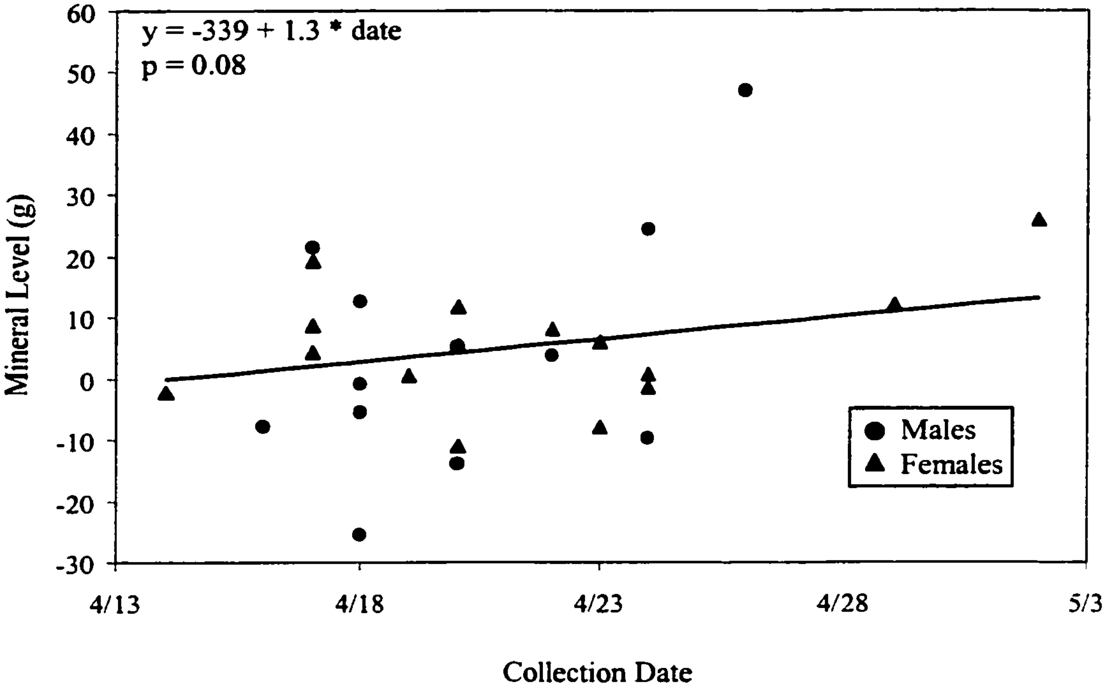

Figure 4.7. Mineral level vs. collection date during spring. Relationship between mineral level and capture date for 27 Canada geese collected in Delta Junction Alaska during spring staging.

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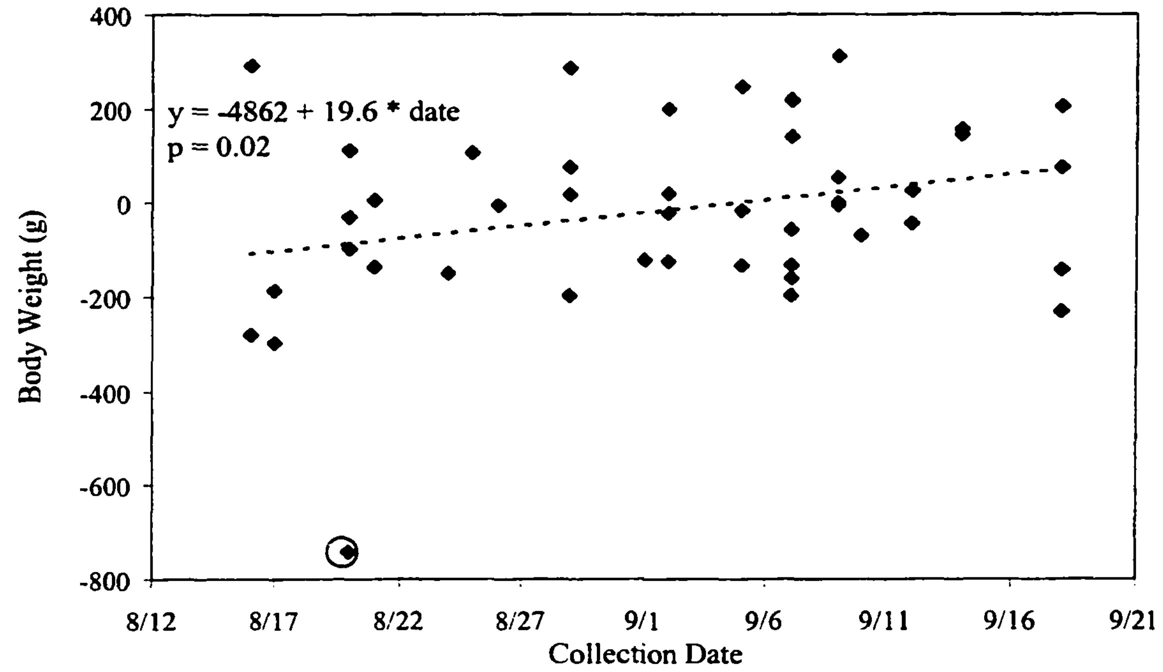

Figure 4.8. Body weight vs. collection date during fall.
Relationship between body weight corrected for body size and collection date of 45 Canada geese collected during fall staging in Fairbanks Alaska. We removed the circled datum point and reanalyzed because of the inordinate influence of the datum on the analysis. After removing the datum, the relationship between body weight and collection date was not significant ($y = -352 + 0.09 * \text{date}, P = 0.9$).

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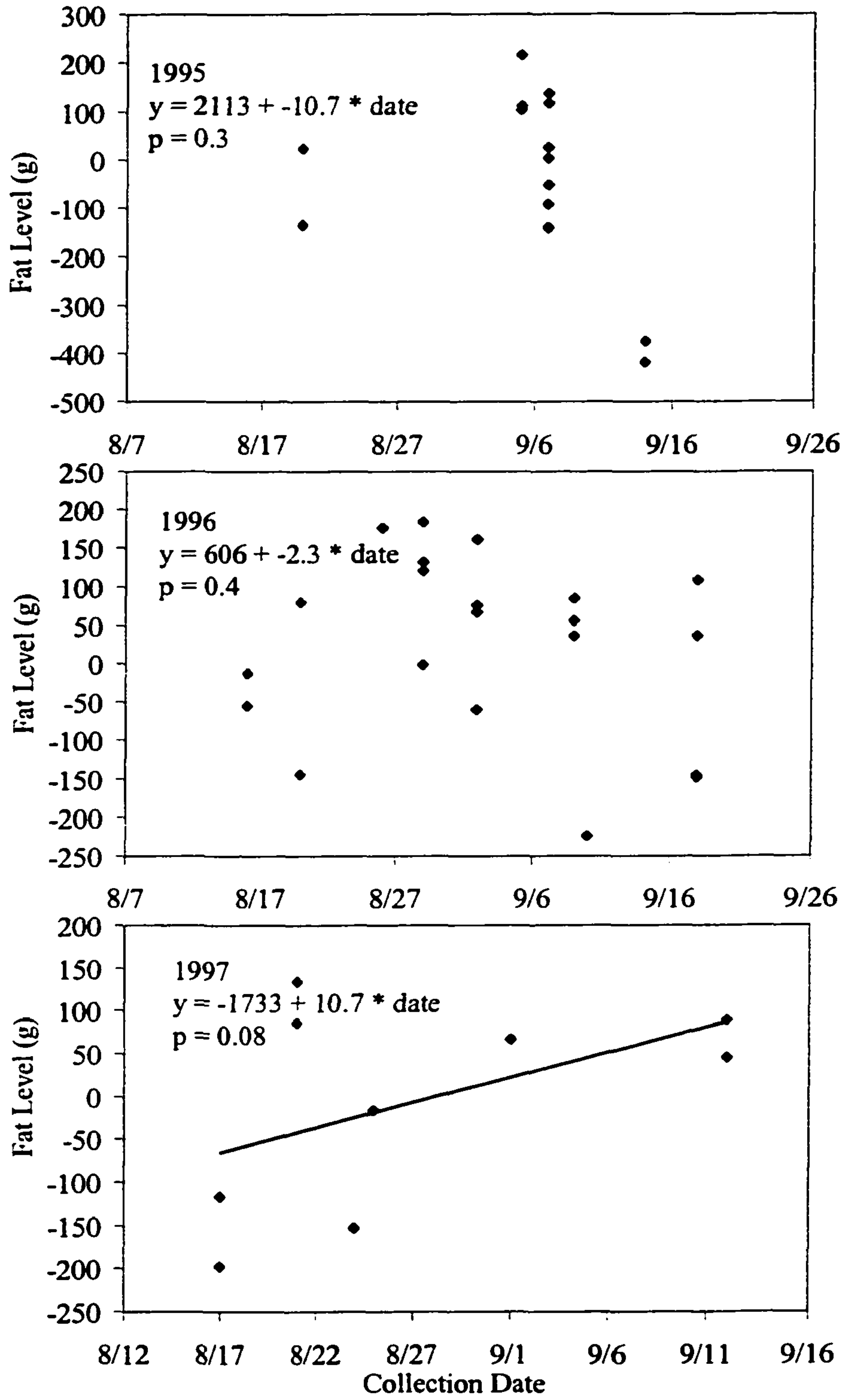

Figure 4.9. Fat level vs. collection date during fall.
The relationship between fat level corrected for body size and collection date of 14, 22, and 9 fall staging Canada geese collected in 1995, 1996, and 1997 respectively.

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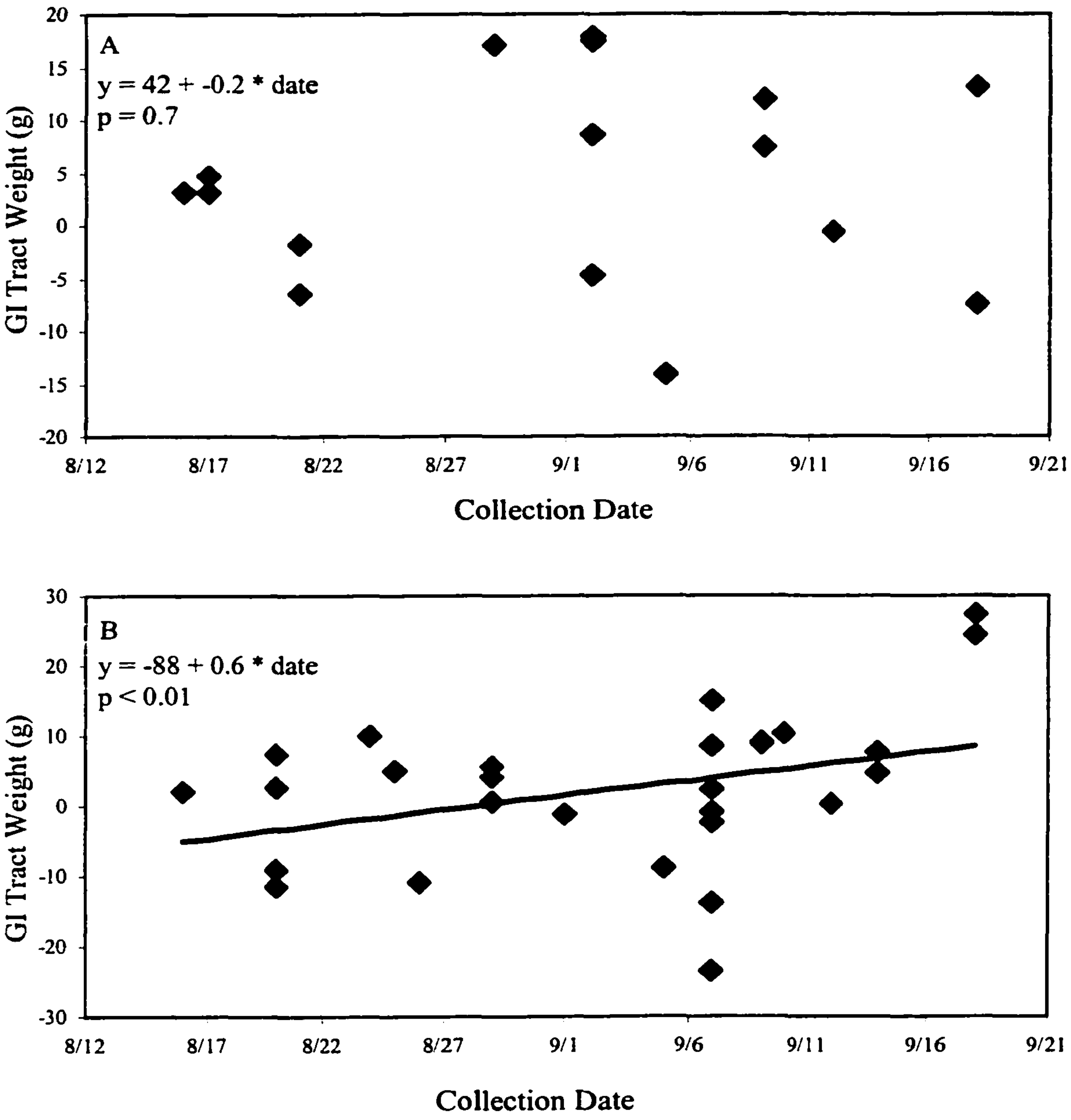

Figure 4.10. GI tract vs. collection date during fall.
Relationship between GI tract weight corrected for body size and collection date for 16 AHY (A) and 29 HY (B) Canada geese collected during fall staging in Fairbanks, AK.

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SUMMARY

My results indicate that two subspecies of Canada geese used interior Alaska for staging and partially segregate themselves during spring and fall staging. After-hatch-year (AHY) Canada geese trapped in Fairbanks during fall staging were larger than AHY Canada geese trapped in Delta Junction during both spring and fall staging suggesting that Canada geese trapped in Fairbanks were primarily lesser Canada geese. In Delta Junction, the size difference between geese trapped in spring and geese trapped in fall suggests that a greater proportion of Taverner's Canada geese staged there in spring than in fall.

Similar to most previous studies, I observed higher survival in AHY than hatch-year (HY) geese (Owen and Black 1989, Samuel et al. 1990, Francis and Cooke 1992). The age class variation in survival in our study was primarily due to the higher susceptibility to harvest by HY geese. Female AHY geese were also harvested at a higher rate than male geese. I speculated that this result may be due to higher survival of AHY females during early fall migration.

Estimates of annual survival of Canada geese in this study were among the lowest estimated for migratory populations of Canada geese (Ratti et al. 1978, Hestbeck and Malecki 1989, Samual et al 1990, Castelli and Trost 1996, Alisauskas and Lindberg in review), while band recovery rates were among the highest. Lesser Canada geese were more susceptible to harvest than either Dusky or Taverner's Canada geese wintering in Oregon (Simpson and Jarvis 1979). My low survival estimates in conjunction with the current inability to accurately estimate abundance suggest that a better understanding of

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lesser Canada goose population parameters such as reproductive success and recruitment is needed to properly manage the population of lesser Canada geese staging in Interior Alaska. Furthermore, I recommend monitoring abundance and harvest of small-bodied Canada geese both east and west of the Cascade Mountain Range to better determine population size and harvest rate.

Survival of AHY females was positively associated with their body condition at the time of banding. I performed an experiment in which I manipulated food availability to geese in fall to separate the potential confounding effects of body condition and individual quality, defined as a positive association among life history traits, on survival. The association between body condition and survival was not maintained in the experimentally manipulated groups, indicating the association between body condition and survival was not direct, but results from correlation among body condition, individual quality, and survival. High quality geese have both greater nutrient reserves and higher survival probability, than lower quality geese. Variation in individual quality may be a result of disease (Shutler et al. 1999, Horak et al. 1999) or early experience (Sedinger et al. 1995). For example, nutrient reserves vary more substantially for females than males during reproduction (Ankney and MacInnes 1978, Raveling 1979) and the emaciated condition of females at the end of incubation may increase their susceptibility to parasites or some other form of disease (Shutler et al. 1999, Tella et al. 2000). High parasite loads or some other form of disease could lead to a reduced ability to both acquire or carry nutrients and survive fall migration. Alternatively, some females may be higher quality females because of early experiences. Higher quality females

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should produce more young, thus have larger broods (Drent and Daan 1980). Family units with larger broods are more dominant (e.g. Raveling 1970, Loonen et al. 1999), thus have access to better feeding areas, allowing adult females to regain endogenous nutrients used during nesting at a greater rate (Loonen 1999). Males and females with larger broods also spend more time being vigilant for predators (Sedinger and Raveling 1990, Sedinger et al. 1995a), thus should be less susceptible to predation and in turn survive at a higher rate independent of body condition. Similarly, the relationship among dominance, gosling growth, and parental vigilance could explain my observed association between body size of HY geese and survival. Young from larger broods grow at a faster rate because of the greater access to food (Loonen et al. 1999), thus would be larger at the time of banding in my study. These young should also benefit from the greater vigilance of their parents by surviving at a higher rate, leading to the observed association between body size and survival.

Unlike other studies of geese on nesting grounds or final staging areas, geese in our study gained fat but not protein reserves during spring staging (McLandress and Raveling 1981, Budeau et al. 1991, Gauthier et al. 1992, Bromley and Jarvis 1993, Gates et al. 1998). This is likely due to the type of nutrients provided by the food available to geese at this time. Geese in Interior Alaska fed in two pastures regularly, but because these pastures contained perennial grasses with little, if any, new growth before nesting (Eichholz pers obs.) and geese fed less than 20 minutes a day in these pastures (Eichholz unpub. data), they did not acquire protein beyond that needed for maintenance. The high carbohydrate diet of waste barley, however, allowed geese to at least partially replace fat

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reserves used during the last stage of migration, allowing them to begin nesting with greater fat reserves for egg production and incubation.

Mineral reserves of spring staging geese increased with date. Mineral reserves are important for male geese during molt and female geese during egg production and molt (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979). Mineral reserves acquired during spring staging likely offset the need for minerals during later portions of the annual cycle.

I observed no increase in nutrient levels of adult geese in fall. I believe this is most likely due to the tendency for family units to depart the study area when adults females have achieved some threshold in nutrient reserves, thus adult geese with the largest nutrient reserve levels were never captured. In fall, total protein, pectoral muscle, and mineral levels increased with date for HY geese. Although I did not observe an increase in fat reserves for any age or sex class, fat reserves have been shown to be important for other population of geese at this stage of their annual cycle (Wypkema and Ankney 1979, Sedinger and Bollinger 1987). Fall staging AHY males at the start of their migration had greater fat reserves than spring staging AHY males at or near the end of their migration, while fall staging AHY females had similar amounts of fat reserves to spring staging AHY females, indicating fat reserves are important during early fall staging in this population of geese.

The increase in the abundance of white geese (lesser snow geese, greater snow geese, and Ross' geese) due to increases in food availability from agricultural sources (Abraham 1996) leads to the prediction that the introduction of agriculture to Interior

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Alaska could have similar effects on the populations of Canada geese using the study area. I believe this has likely not occurred because most populations of Canada geese, especially lesser Canada geese, are relatively more susceptible to harvest than white geese. Because of their tendency to feed in large flocks, often in the tens of thousands, the susceptibility of white geese to harvest is relatively low. In fact, harvest rates of lesser snow geese have declined over the last two decades (Francis et al. 1992). In contrast, Canada geese feed in small flocks and in general are more susceptible to harvest relative to white geese (Simpson and Jarvis 1979). Thus, unlike white geese, where hunting mortality did not increase to counter increased production and survival, Canada goose mortality due to harvest is high enough to offset an increase in fecundity or decrease in natural mortality the geese might experience with the introduction of agriculture.

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