

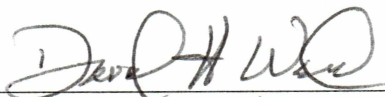


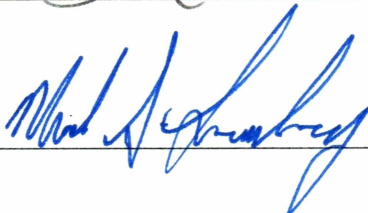
WINTERING STRATEGIES OF AN ARCTIC-NESTING GOOSE: COSTS OF
MIGRATION AND OVER-WINTERING FOR PACIFIC BLACK BRANT

By

Danielle D. Mather

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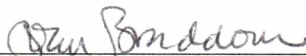


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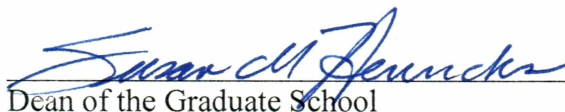


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WINTERING STRATEGIES OF AN ARCTIC-NESTING GOOSE: COSTS OF
MIGRATION AND OVER-WINTERING FOR PACIFIC BLACK BRANT

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Danielle D. Mather, B.S.

Fairbanks, Alaska

May 2005

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ABSTRACT

Birds wintering in different climates may have different strategies for storing and using energy. We documented changes in body morphology and composition of Pacific Black Brant (*Branta bernicla nigricans*) wintering in Alaska and Baja California and modeled the energetic costs of wintering at each location. We compared costs associated with two different wintering strategies: 1) to remain in an unstable and harsh environment but close to breeding grounds, or 2) to migrate long distances to a mild environment, but distant from breeding grounds. Despite dramatic differences in the timing and magnitude of energetic costs between sites, Brant stored similar amounts of lipid and maintained similar body mass throughout winter. Brant operate under similar physiological bounds but changes in organ mass and nutrient storage took place within these bounds. This flexibility allowed Brant to employ two contrasting winter strategies. We suggest that there may be reproductive and energetic advantages associated with shortening migration distance and remaining in Alaska over winter. The number of Brant wintering in Alaska should continue to increase if constraints on food intake do not impede energy storage and survival is similar between sites.

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ACKNOWLEDGEMENTS

This project would not have been possible without the support and assistance of many people. I would first like to thank my advisor, Perry Barboza, for the tremendous amount of time he spent working with me and for not breaking my kneecaps. I was continually impressed with his breadth of knowledge, his patience and the active role he played as mentor. David Ward was instrumental in making this project happen; I thank him for providing me with this opportunity and for everything he has taught me over the past six years. Committee members, Mark Lindberg and Ed Murphy, provided much helpful advice and contributed to the success of this project. Dan Esler and Joel Schmutz helped shape my career as a biologist and wrote numerous letters of recommendation for me along the way. Their passion for science and pursuit of excellence were an inspiration to me, and I hold them in the highest regard, despite how it must have seemed a lot of the time.

I am forever indebted to all the people that helped with data collection and logistics in both Alaska and Mexico, including: Diana Brann, David Duarte-Etchart, Rolando Duarte, Sergio Duarte-Etchart, Sergio Duarte, Jr., Josue Etchart, Alberto "Tiburón" Flores, Kevin and Lisa Fox, Pat Gonzales, Jerry Hupp, Desmond Johns, Dan Johnson, Jessie Labrador, Arturo Malo, Aaron Martin, Jeff Mason, Jeff Pelayo, Rick Poetter, Andy Ramey, Joaquin Sanchez, Christy Shaw, Marnie Shepherd, Kate Soetaert, and Kristine Sowl, Jeff Wasley and Johann Walker. Marnie Shepherd assisted me with pretty much everything from data collection to border crossings. Her help in the field and lab was invaluable and her zest for life, easy smile, and friendship helped get me through

it all - relatively sane. Alejandro Cabello-Pasini provided laboratory space at the Universidad Autónoma de Baja California, logistical assistance, equipment and temperature data for Bahía San Quintín. Financial support was provided by the U. S. Geological Survey-Alaska Science Center, U. S. Fish and Wildlife Service-Region 7 Migratory Bird Management and Izembek National Wildlife Refuge, Angus Gavin Migratory Bird Research Fund, and the Department of Wildlife and Biology, and the Institute of Arctic Biology at the University of Alaska Fairbanks.

I also would like to thank all my friends and fellow graduate students for their support, friendship, advice and amusing distractions. A special thanks to John Citta, Adrian Gall, Mike Knoche, Julie Morse, Lincoln Parrett, John Pearce, Dan Rizzolo, Dan Ruthrauff, Dave Safine, Kim Trust and Shiway Wang. I would also like to thank my family for always believing in me. Finally, Jeff Mason, I could not have done this without his encouragement, laughter and love.

INTRODUCTION

Birds living in temperate regions must contend with a constantly changing environment. These changes can have daily, tidal, lunar and seasonal periodicities. Seasonal changes in photoperiod and temperature produce dramatic environmental changes at high latitudes. Seasonal declines in food resources and deteriorating environmental conditions often trigger migration in many birds (Berthold 2001). Even though migration is energetically costly, the cost likely is less than that of wintering at high latitudes. All birds with an effective means of locomotion can migrate; however, some individuals remain near high latitude breeding grounds and contend with harsher winter conditions than conspecifics that migrate to lower latitudes.

The ability to accumulate and store nutrients is a life history trait that allows birds to survive periods of increased energy demand (Van der Meer and Piersma 1994) and thus enhance fitness through greater survival and reproductive success. Nutrients are stored in preparation for programmed events, such as reproduction (Raveling 1979), migration (Vangilder et al. 1985, Bromley et al. 1993) and over-wintering (Nolan et al. 1983). Birds also store nutrients in response to stress caused by environmental conditions (Lovvorn 1994) and changes in resource availability.

Birds generally increase nutrient stores and ultimately body mass in response to increases in stress levels and decreasing temperature (Blem et al. 1986). In harsh or unstable environments, birds are likely to carry larger nutrient stores as they are intermittently forced to rely on stored energy to survive periods of severe weather and low food availability (Bednekoff and Houston 1994). However, carrying excess mass

can be energetically costly, and birds wintering in areas with mild temperatures and reliable food sources may reduce stores to minimize costs of locomotion and risks of predation (Houston and McNamara 1993).

For Arctic-breeding birds, the energetic cost of migration may detract from reproductive investment because fat and protein may be lost in long distance migration before the breeding season in the spring (Berthold 1975). Although birds incur high costs associated with long distance migration, they likely benefit by wintering in a more stable environment characterized by relatively high food availability and mild weather. Survival is generally believed to increase with time spent in non-breeding areas (Greenberg 1980, Hestbeck et al. 1992), presumably because environmental conditions become milder as distance from breeding grounds increases, and daily energy expenditure decreases in the milder climate.

Avoiding long, energetically demanding migrations and remaining closer to breeding grounds may be advantageous if birds can successfully adapt to harsher winter climates. Individuals that migrate shorter distances between wintering and breeding areas may be able to save greater body reserves and respond more efficiently to changes in local weather conditions that influence the availability of food and cover in nesting habitats. Wintering closer to the nesting grounds is beneficial for individuals competing for breeding resources (e.g., high arctic breeders or nesting colonies experiencing density dependent factors) (Sedinger et al. 1998). Thus, geese that stay closer to the breeding grounds may be better able to improve life time reproductive success.

In the present study we examine changes in body morphology and composition for Brant during the non-breeding season at the extreme ends of their winter range, in Alaska and Baja California, to determine the effect of winter strategy on physiological state. These strategies are (1) remain in Alaska in an unstable and harsh environment but close to breeding grounds versus (2) migrate long distances to Baja California to a stable and mild environment, distant from breeding grounds. Pacific Black Brant (*Branta bernicla nigricans*, hereafter Brant) are an ideal study species as they rely on the same natively occurring food source (*Zostera marina*) throughout their range (Reed et al. 1998), show high winter site fidelity, and exhibit widely divergent wintering strategies. As a species, Brant show differential migration in which some birds shorten migration distance and winter closer to breeding grounds, whereas most migrate an additional 5,000 km and winter in more mild climates. In general, we predict that body morphology and composition of Brant should reflect the strategy employed as birds adapt to the different energetic demands and environmental conditions encountered at each location.

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CHAPTER 1. WINTER LOCATION AFFECTS MORPHOLOGY OF RESIDENT
AND MIGRANT PACIFIC BLACK BRANT¹

ABSTRACT. — We examined body size and mass of tissues of adult Brant (*Branta bernicla nigricans*) in Alaska and Baja California, Mexico during fall, winter and spring of 2002-2003. Female Brant wintering in Alaska were structurally larger than those wintering in Baja California based on lengths of culmen and tarsus, but those differences were small and likely due to differences in natal origins. Brant appear to have reached a morphological set point in mid-winter because masses of the body and all tissues were similar between wintering sites. Declines in adipose mass for birds in Alaska during early winter were equivalent to increases in adipose mass for birds in Mexico during late winter. Further, migrants used similar amounts of adipose during fall and spring migration between Alaska and Baja California. Seasonal adipose deposition may, therefore, equally favor winter residency and long-distance migration in Brant staging on the Alaska Peninsula in the fall. Gonad and liver masses increased in late winter in birds in Alaska but not for those in Mexico, suggesting that birds wintering in Alaska are able to commence reproduction in spring earlier than migrants from Mexico. The preferred wintering location of Brant may depend upon the magnitude and timing of energetic costs and feeding opportunities as winter habitats change in Alaska and Baja California.

¹Mather, D.D., P.S. Barboza, and D.H. Ward. 2005. Winter location affects morphology of resident and migrant Pacific Black Brant. *Auk*: in review.

INTRODUCTION

Winter at high latitudes is often characterized by adverse weather combined with short photoperiod and low resource availability. Birds breeding in north temperate and arctic regions employ a variety of wintering strategies that range along a continuum from obligatory residency to long-distance migration (Berthold 1975). Migration, in itself, also varies with respect to rates of movement and distances traveled from the breeding grounds. Birds that remain on or near breeding grounds at high latitudes (hereafter winter residents) must contend with harsh environmental conditions and unpredictable food resources; whereas long-distance migrants incur risks and demands of travel, but benefit from relatively mild winter weather and abundant food. Long-distance migrants show higher winter survival; whereas, winter residents have higher reproductive success (Greenberg 1980). Winter residency demands conservation of resources in harsh environments, whereas migration requires expending reserves for travel. Flexibility of migratory behavior suggests equality between the morphological constraints of winter residency and migration.

Tolerance of severe weather by winter residents is directly related to their ability to accumulate energy (primarily as adipose tissue) and conserve energy reserves. In harsh environments birds are likely to carry larger stores of adipose in winter than at other times of the year because they are more frequently forced to rely on stored energy to survive periods of severe weather and low food availability (Nolan et al. 1983). The added mass of adipose is costly because wing loading and risk of predation may increase with body weight (Houston et al. 1993). Winter residents may conserve energy during

periods of severe weather by reducing movement (Jorde et al. 1984), or by altering physiological set points such as body temperature (Sharbaugh 2001). Adipose mass is, therefore, likely to be closely associated with weather and food availability for winter residents at high latitudes (Baldassarre et al. 1986).

Variation in adipose mass is also associated with migration because lipid is the primary source of energy for long-distance flight (Berthold 1975). For birds, pre-migratory gains of body mass in fall can exceed 100% of summer mass as both lipid and protein are deposited (Klassen et al. 1996). During fall migration over half the body lipid can be depleted (Bromley et al. 1993), and proteins from muscle and nutritional organs are also mobilized during long flights (Lindström et al. 1992). Stores of adipose and lean tissue accumulated on winter and staging grounds are also important for reproduction (Afton and Ankney 1991, Alisauskas and Ankney 1992), and demands for these tissues may be greater during spring migration than during fall migration. Changes in mass of adipose tissues in migrants are reflected by significant changes in food intakes and mass of visceral organs, such as the gizzard, intestine and liver (Piersma et al. 1999, McWilliams et al. 2001).

Interspecifically, waterfowl exhibit widely divergent wintering strategies, and the relative costs and benefits of each strategy may be more apparent in arctic nesting geese and ducks than in other taxa. Pacific Black Brant (*Branta bernicla nigricans*; hereafter Brant) have developed both winter residency and long-distance migration behaviors. Differences in wintering strategies within a species present a unique opportunity to examine morphological and physiological correlates of migration and winter residency.

Brant breed in arctic and sub-arctic coastal areas of Alaska, western Canada, and northeastern Russia; the greatest concentration of nests (>70%) occur on the Yukon-Kuskokwim Delta in western Alaska (Sedinger et al. 1993, Reed et al. 1998). In fall, Brant stage at Izembek Lagoon and adjacent embayments on the Alaska Peninsula (Reed et al. 1989) before migrating $\geq 5,000$ km to primary wintering areas in Baja California, Mexico (Reed et al. 1998). However, mid-winter inventories have documented an increase in numbers of Brant wintering north of Mexico since 1980 (Trost and Drut 2002), with the highest number of birds (up to 15% of the Pacific flyway) at Izembek Lagoon and adjacent embayments on the Alaska Peninsula (Ward and Dau, in review). Ward and Dau (in review) showed that the wintering population of Brant on the Alaska Peninsula grew during a period of increasing winter temperatures (Zveryaev and Selemenov 2000) that reduced ice cover and increased food availability, thereby reducing risks of winter residence for Brant. The increase in number of wintering Brant in Alaska also coincided with an increase in density of birds nesting at the main colonies on the Yukon-Kuskokwim Delta (Sedinger et al. 1998). Poor foraging conditions resulting from increased grazing pressure on the breeding grounds have been shown to limit growth of juvenile Brant (Sedinger et al. 1998) and may inhibit pre-migratory gains of body fat for juveniles and adults in the fall. Brant that forgo fall migration from Izembek Lagoon may remain as residents simply because they lack sufficient fat reserves for the long flight (Dau 1992).

We compared body size, and tissue and nutritional organ masses of Brant at the extreme ends of their winter range, Alaska and Baja California, to compare the

morphological correlates of winter residency and long-distance migration. We predicted that Brant wintering in Alaska would be heavier and maintain a larger mass of adipose compared to long-distance migrants in Baja California because of the relatively severe and unpredictable environment in Alaska. Additionally, changes in mass of adipose, muscle and nutritional organs for birds in Baja California would likely be greater than those in Alaska during early and late winter because of the high energetic demands associated with long-distance migration. We also hoped to gain insights as to why the Brant population is increasing in Alaska by testing the hypothesis that Brant remain at Izembek lagoon over winter due to poor body condition.

STUDY AREAS AND METHODS

We studied Brant in Alaska on the Izembek National Wildlife Refuge (55° 15' N and 163° 00' W) at Izembek and Kinzarof lagoons, and in Baja California (30 °26' N and 115° 56' W) at Bahia San Quintin. Bahia San Quintin is the northernmost wintering area for Brant in Mexico, hosting >25% of the Pacific flyway population of Brant each winter (Conant and Voelzer 2004). Both wintering locations contain extensive areas of eelgrass (*Zostera marina*), the primary food for Brant during the non-breeding season (Ward et. al. 2004).

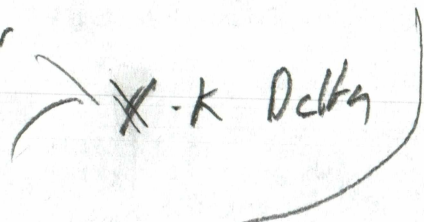
We collected adult Brant from fall 2002 through spring 2003. Collections were made during five two-week periods between late October and early May at Izembek Lagoon (IZ) and three two-week periods between early December and late March at Bahia San Quintin (BSQ). Timing of collections was based on the average timing of

migration and movement of Brant at each location (Ward and Stehn 1989, Lindberg et al. in review, Ward and Mather, unpublished data). The first and last collections at IZ coincided with fall and spring staging, and were timed to collect birds before peak migration to Mexico (early November) and after return from Mexico (early May), respectively. The second, third and fourth collections targeted Brant that were overwintering at IZ in early winter (late November-December), mid-winter (mid- January) and late winter (late March-April). Concurrent collections at BSQ during the three winter periods sampled post-migratory birds in early winter (early December), residents in mid-winter (mid- January), and pre-migratory birds in late winter (late March). We assumed that collected birds would have remained at the same location through winter because Brant have high site fidelity during winter (Reed et al. 1998). Changes in body mass and morphology of birds at each site were, therefore, assumed to reflect individual responses to food abundance and weather at each site rather than local emigration or immigration.

Brant were collected from natural feeding and/or roosting flocks by shooting. Decoys were not used during collections because decoys may attract a higher proportion of juveniles or birds in poor condition (Greenwood et al. 1986, Reinecke et al. 1988). Freshly killed Brant were weighed using an electronic balance (± 0.1 g). Age (adult or yearling) and gender were determined by plumage characteristics and cloacal examination. Gender was later confirmed through internal inspection of reproductive organs. The following morphometrics (± 1 mm) were measured following Dzubin and Cooch (1992): total and diagonal tarsus length, culmen length, wing chord, 9th primary feather length, mid-wing length, head length, and total body length. Brant were double

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wrapped in plastic, placed in sealed bags, and stored frozen in the field to minimize desiccation and degradation of tissues.

We thawed frozen carcasses in a refrigerator prior to dissection. Feather mass for adult females was measured as the mass lost after feathers were removed with an electric shears (Oster ShearMaster) and by manual plucking. We removed skins to the elbow joint along with adhering adipose tissue to determine the mass of skin and subcutaneous adipose tissue in adult females. Males were not sheared before skinning because of time constraints; therefore, feather and skin masses were not compared between genders.

We dissected and weighed the following tissues and organs on an electronic balance (± 0.1 g): visceral adipose (including abdominal fat pad and mesenteric fat), total pectoralis, total supracoracoideus, gizzard (including proventriculus), liver, intestines (including caeca), and reproductive organs (ovary or testis). The gizzards and intestines were weighed after the contents were removed. We did not dissect males from BSQ, preventing comparisons between sites and genders for body components.

Morphometric measurements were grouped using principal component analysis. Wing measures (wing chord, length of 9th primary feather, and mid-wing length) were excluded as indices of structural size because those measures appeared to be more susceptible to observer bias and were difficult to repeat. Lengths of total tarsus, diagonal tarsus, head, culmen and body all loaded positively and explained 81% of the total variance in the first two orthogonal axes. The first axis (67% of total variance) was best described by measures of the extremities (head, culmen, and tarsus) whereas body length loaded most heavily on the second axis (14% of total variance). We selected three

covariates for structural size, total tarsus and head length from the first axis and body length from the second axis (Table 1). Structural size was compared by ANOVA with site and gender as independent factors. We assessed effects of site and period on body and tissue mass with ANCOVA using the three structural covariates (head, tarsus and body length) to standardize for body size. All mass data are presented as adjusted least square means ($g \pm SE$) from the ANCOVA and are, therefore, corrected for structural size. Arithmetic means ($g \pm SE$) for all measured body components are listed in Tables 1.2 and 1.3. We used Bonferroni's adjustment for multiple pairwise comparisons among periods ($P < 0.05$). All statistical analyses were conducted using SYSTAT 10.2 (Systat Software Inc. 2002).

RESULTS

Males were structurally larger than females based on lengths of head, tarsus and body ($P < 0.001$, Table 1.1). Although mean lengths of head and tarsus did not differ by location for males, those morphometric measures were larger for females wintering in IZ than for females wintering in BSQ ($P < 0.011$, Table 1.1). Total body length did not vary between locations for either sex.

Female body mass was similar between fall staging and early winter at IZ, whereas females that had migrated to BSQ were lighter in early winter than females staging at IZ in the fall ($1442.2 \pm 21.0g$ vs. $1666.4 \pm 28.4g$, $P < 0.001$, Fig. 1.1a). For females wintering at IZ, body mass declined between early and mid-winter ($-160.7 \pm 53.9g$, $P = 0.011$) and increased between mid- and late winter ($+183.2 \pm 52.6g$, $P = 0.006$). In contrast, body mass of females wintering at BSQ remained stable between

early and mid-winter and increased between mid- and late winter ($+144.2 \pm 29.7\text{g}$, $P < 0.001$). There was no difference in body mass of females between sites in mid-winter, late winter or spring staging. For males, body mass dynamics followed a similar pattern to that of females between fall staging and early winter at each site (Figs. 1.1a and 1.1b). Male body mass was similar between fall staging and early winter at IZ, whereas males that migrated to BSQ were lighter than males during fall staging ($1516.8 \pm 60.6\text{g}$ vs. $1886.1 \pm 51.9\text{g}$, $P < 0.001$, Fig. 1.1b). Male body mass increased overall from early to late winter at BSQ ($+184.6 \pm 55.6\text{g}$, $P = 0.010$), whereas male body mass remained stable during the same period of time at IZ. Male body mass during spring staging was similar to late winter body mass at both sites. Overall body mass did not differ by gender.

Skin mass (including subcutaneous adipose) paralleled changes in visceral adipose mass for each site (Tables 1.2 and 1.3). Visceral adipose mass of female Brant was similar between fall staging and early winter at IZ, whereas females that migrated to BSQ had less visceral adipose in early winter than females during fall staging ($58.9 \pm 9.8\text{g}$ vs. $102.2 \pm 9.0\text{g}$, $P = 0.007$, Fig. 1.1c). Between early and mid-winter, visceral adipose mass declined for females at IZ ($-51.9 \pm 12.4\text{g}$, $P < 0.001$), and remained stable for those at BSQ. Visceral adipose mass of females was similar between sites in mid-winter. Visceral adipose mass remained stable between mid- and late winter for females at IZ, whereas visceral adipose mass increased for pre-migratory females at BSQ during the same time period ($+61.4 \pm 7.8\text{g}$, $P < 0.001$). Visceral adipose mass was greater for pre-migratory females at BSQ in late winter than for females during spring staging ($103.2 \pm 9.5\text{g}$ vs. $48.6 \pm 9.8\text{g}$, $P = 0.002$). For males, visceral adipose mass decreased over the

winter period ($-62.9 \pm 21.7\text{g}$, $P = 0.037$), following the same general pattern as females at IZ (Figs. 1.1d and 1.1c). Overall adipose masses did not differ by gender.

Gonad mass of males and females remained stable between fall staging and mid-winter at both sites (Figs. 1.2a and 1.2b). Between mid- and late winter, gonad mass increased for females ($+0.7 \pm 0.2\text{g}$, $P = 0.003$) and males ($+0.7 \pm 0.2\text{g}$, $P = 0.016$) at IZ and remained stable at BSQ. Gonad mass of females during spring staging was heavier than late winter gonad masses at either site ($P < 0.011$). Gonad mass of males during spring staging was similar to late winter gonad mass.

Liver mass of females was similar between fall staging and early winter at IZ; whereas, females that migrated to BSQ had lighter livers in early winter than females during fall staging ($31.4 \pm 1.9\text{g}$ vs. $52.0 \pm 1.8\text{g}$, $P < 0.001$, Fig. 2c). Liver mass of females wintering at IZ decreased between early and mid-winter ($-13.6 \pm 2.9\text{g}$, $P < 0.001$) and subsequently increased between mid- and late winter ($+25.0 \pm 2.8\text{g}$, $P < 0.001$). Conversely, liver mass of females at BSQ remained stable during winter. Female liver mass was similar during spring staging and late winter at IZ. For males, liver mass did not differ among periods (Fig. 2d). Overall liver mass was similar between genders.

Pectoralis mass of females was similar between fall staging and early winter at both sites (Fig. 1.3a). Thereafter, pectoralis mass increased between early and mid-winter for females at IZ ($+17.5 \pm 6.9\text{g}$, $P = 0.005$) and BSQ ($+11.9 \pm 4.0\text{g}$, $P = 0.015$). Pectoralis mass of females was similar between mid- and late winter at IZ; whereas pectoralis mass declined for females at BSQ during the same time period ($-13.5 \pm 4.2\text{g}$, $P = 0.007$). Overall, females that remained at IZ during winter maintained a larger mass of

pectoralis muscle than those wintering at BSQ ($220.1 \pm 2.3\text{g}$ vs. $201.5 \pm 2.3\text{g}$, $P < 0.001$). Supracoracoideus mass increased for females at IZ over winter ($+2.3 \pm 0.8\text{g}$, $P = 0.030$) and remained stable for females at BSQ (Fig. 1.3c). Overall mass of supracoracoideus muscles for females did not differ by site during winter. For males, muscle mass was similar among periods (Figs. 1.3b and 1.3d). Pectoralis mass was similar between genders, however, supracoracoideus mass was slightly heavier for males than for females ($23.6 \pm 0.4\text{g}$ vs. $22.5 \pm 0.3\text{g}$, $P = 0.043$).

Feather mass of females was similar between fall staging and mid-winter at both sites (Fig. 1.4). In late winter, feather mass was, however, greater for females at IZ than for those at BSQ ($157.5 \pm 6.5\text{g}$ vs. $107.1 \pm 4.3\text{g}$, $P < 0.001$). Feather mass was similar between late winter and spring staging at IZ.

Gizzard mass was similar between fall staging and mid-winter for females at both sites (Fig. 1.5a). By late winter, female gizzard mass was greater at BSQ than at IZ ($115.5 \pm 2.3\text{g}$ vs. $102.1 \pm 2.8\text{g}$, $P = 0.001$). Gizzard mass of females was similar between late winter and spring staging at IZ. For males, gizzard mass remained stable among all periods (Fig. 1.5b). Gizzard mass did not differ by gender.

Intestine mass of females during fall staging was greater than that of post-migratory females in early winter at BSQ ($42.8 \pm 1.2\text{g}$ vs. $38.0 \pm 1.3\text{g}$, $P = 0.021$, Fig. 1.5c). Intestine mass of females was similar in early and mid-winter at both sites. Intestine mass then increased between mid- and late winter for females at IZ ($+7.8 \pm 2.4\text{g}$, $P = 0.009$) and remained stable for those at BSQ over the same time period. Intestine mass of females during spring staging was greater than that of pre-migratory females at

BSQ in late winter ($49.3 \pm 2.0\text{g}$ vs. $40.9 \pm 2.0\text{g}$, $P = 0.024$). For males, intestine mass did not differ among periods (Fig 1.5d). Overall intestine mass was greater for males than for females ($48.3 \pm 1.1\text{g}$ vs. $44.3 \pm 1.0\text{g}$, $P = 0.020$).

DISCUSSION

Female Brant that remained at IZ during winter were structurally larger than those that migrated to BSQ. This structural size difference is consistent with the body-size hypothesis of Ketterson and Nolan (1976) that predicts that smaller-bodied birds may be expected to undertake longer migrations to milder winter habitats if survival is adversely affected by cold weather or high winds. Larger-bodied individuals may also be better equipped to survive thermal stress through increased heat retention (Marchand 1996). However, site differences in thermal conductance of female Brant are probably not significant because differences in the lengths of the tarsus and head were small ($< 2\text{ mm}$) and body lengths were similar between IZ and BSQ (Table 1.1).

Site differences in female body size probably reflect differences in natal origins of individuals within each wintering population. Re-sightings of banded birds at Izembek indicate that the wintering population in Alaska is composed primarily of arctic-breeders (Dau et al. 1997). Arctic-breeding geese tend to be structurally larger than more southerly breeders (Bellrose 1976, Owen 1980). The larger body size of females at IZ may therefore reflect the higher proportion of arctic-breeding birds that reside there in winter. The lack of evidence for a size difference between sites in male Brant may be due to the lower natal site fidelity of males compared to females (Lindberg et al. 1998).

Similarities in adipose mass for Brant during fall staging and early winter at IZ suggest that those birds did not remain there over-winter simply because they lacked the reserves needed for long-distance migration. Net change in adipose mass for birds wintering in Alaska between early and mid-winter was similar to that for birds wintering in Baja California between mid- and late winter (Fig. 1.1c). Seasonal adipose deposition may therefore equally favor winter residency and long-distance migration in Brant if mortality risks are similar between these wintering strategies. Brant also appear to use similar amounts of visceral adipose for both fall and spring migration between Alaska and Baja California. The southward migration for Brant between staging grounds in Alaska and primary wintering grounds in Baja California is generally a non-stop, transoceanic flight aided by favorable wind conditions (Dau 1992). The northward migration of Brant in spring is longer in duration than fall migration and involves a series of short hops along the Pacific coast, providing opportunities for birds to refuel (Moore et al. 2004, Ward and Mather, unpubl. data). Brant appear to operate within similar morphological bounds regardless of the winter strategy employed. Alisauskas (1998) suggested that Snow Geese may migrate shorter distances and winter further north due to the constraint of body fat on flight range, but this morphological constraint does not appear to influence wintering strategy of Brant staging at IZ in the fall.

The similarity in mass of body components between sites in mid-winter is surprising given the large geographic separation of these two wintering populations. These data do not support the positive correlations among winter body mass, size of energy stores, and latitude that have been documented for wintering passerines (Nolan et

al. 1983). We suggest that Brant in mid-winter have reached a lower threshold or set point for mass. By mid- January Brant have likely recovered from demands of migration and have not yet begun to prepare for the breeding season; mid-winter may therefore represent a lull in the annual cycle of energy expenditure. Winter declines in mass have also been documented for several other species of waterfowl (Reinecke et al. 1982, Whyte et al. 1984, Heitmeyer 1988) although the roles of endogenous and exogenous factors in these declines vary. Our study was not specifically designed to determine the underlying mechanisms controlling mass dynamics; however, cold temperatures, prolonged high tides, and freezing events in Alaska may have prevented birds from maintaining larger nutrient stores by increasing thermal costs and limiting feeding opportunities for birds wintering at IZ. Conversely, a mild environment in Baja California may not favor the deposition of excess adipose, especially if gains in body mass increase wing loading and reduce flight efficiency.

Changes in body and adipose mass of Brant during late winter suggest that nutrient stores are allocated and used differently between wintering sites. Although body mass of female Brant increased by similar amounts in late winter at both sites, adipose accounted for more than 80% of the observed mass change for birds at BSQ; whereas adipose mass remained stable for birds at IZ (Fig.1.1). The energetic demands experienced by these two geographically separate wintering populations of geese differ greatly. Izembek lagoon is characterized by high winds, short photoperiod (5 h of daylight at winter solstice), intermittent ice cover and cold (-2.5° to 2.0° C) air temperatures (Ward and Dau, in review); in contrast, climate at Bahia San Quintin is

generally Mediterranean with long days (10 h of daylight at winter solstice) and warm air (11° to 22° C) and sea surface (15° to 22° C) temperatures (Cabello-Pasini et al. 2003). Late winter body mass of Brant may fluctuate more at IZ than at BSQ depending upon the severity of winter conditions on the Alaska Peninsula.

The differences between sites in mass of adipose and non-adipose body components of Brant may reduce the accuracy of body mass as an indicator of nutrient stores in this species. Although body mass has been used as an indicator of energy stores in adipose (Haramis et al. 1986), direct measures of subcutaneous and visceral adipose through lethal or non-lethal techniques (Diet et al. 1999) may be more reliable than body mass alone. In the absence of these direct measures, site-specific relationships between body mass and adipose mass should be employed.

Annual reproductive cycles of many birds are entrained by seasonal changes in day length (Wingfield et al. 1992). Brant may be more strongly influenced by rapid changes in day length at IZ than at BSQ because rates of change in photoperiod increase with latitude. Although the actual number of daylight hours are similar (~ 11.5 h) between Alaska and Baja California in mid-March, gains of day length between mid-January and mid-March are much greater in Alaska (4 h) than in Baja California (1.5 h). Differences in gonad mass between sites in late winter indicate that Brant wintering in Alaska begin preparation for breeding earlier than birds wintering in Baja California. Delayed development of gonads may favor birds in Baja California by reducing mass and allocation of nutrients necessary for migration. Brant at IZ that travel relatively short distances between wintering and breeding areas may be able to respond more promptly to

changes in local weather conditions that affect the availability of nesting sites in the spring. Brant wintering at IZ and breeding on the Yukon-Kuskokwim Delta are best suited to develop tissues for reproduction as early as possible if conditions in spring are favorable for nesting.

Gains in mass of liver and intestine for females at IZ likely reflect reproductive readiness and relate to ovarian development rather than to any changes in food intake. Visceral organs often serve as protein stores for egg formation in the spring (Raveling 1979). Additionally, gains in adipose and gizzard mass of Brant at BSQ prior to spring migration were not associated with gains in liver mass, even though it is likely that those birds increased food intake before migration. Changes in mass of digestive organs (gizzard and intestines) are associated with hyperphagia (Piersma 1998, McWilliams et al. 2001,) and the refractory components of food such as fiber (Kehoe et al. 1985). An increase in gizzard mass for birds at BSQ may be due to geographical differences in the chemical composition of eelgrass (Cabello-Pasini et al. 2003) because gizzard muscles can enlarge when birds ingest more fibrous material (Starck 1999). If Brant at BSQ consume a less digestible diet of eelgrass with more fiber or ash than Brant at IZ, birds at BSQ will need to ingest and process more food to accumulate the same nutrient stores as birds at IZ. However, this hypothesis awaits exploration using direct comparisons of diet quality and digestibility of the diets for Brant wintering at IZ and BSQ.

Brant apparently do not gain muscle mass prior to spring migration as reported for other migratory species (Gaunt et al. 1990, Jehl 1997). Although there are several functional roles for increased muscle mass associated with greater activities such as

flight, the absence of a distinct gain in flight muscle mass for birds in BSQ prior to spring migration suggests that these effects may be minor for Brant. Alternatively, changes in the chemical composition of flight muscles may vary between sites if the proportion of lipid and protein change before migration. Muscle mass of Brant did not vary with body mass between phases of migration and winter as described for smaller-bodied migrants (Lindstrom et al. 2000). Females at IZ gained muscle mass in early winter when body mass was lost; whereas, females at BSQ lost muscle mass in late winter when body mass was gained (Figs 1.1a and 1.3a). Reasons for the observed changes in muscle mass at BSQ are unclear but are not likely related to changes in wing loading. Greater overall flight muscle mass for birds wintering in Alaska could confer a greater reserve of protein for reproduction (McLendress and Raveling 1981) and enhance abilities for shivering thermogenesis (Swanson 1991). Concurrent increases in feather mass may also aid in cold tolerance of birds at IZ (Grubb et al. 1991), but these and other thermoregulatory hypotheses require direct measurements of conductance and heat production in Brant at each location.

The geographical and seasonal variations in organ and tissue masses exhibited by Brant indicate that morphological flexibility is a life history trait that enables Brant to successfully employ either of two contrasting winter strategies: potentially breeding earlier at the risk of an austere winter at high latitudes versus risks associated with migrating long distances for a mild winter. Wintering closer to the nesting grounds may be beneficial for individuals competing for breeding resources (e.g., high arctic breeders or nesting colonies experiencing density dependent factors). Arctic breeding geese that

nest and hatch early generally have higher growth, survival and fecundity than those that nest and hatch later (Sedinger et al. 1991, Sedinger et al. 1995). Thus, arctic breeding birds that remain closer to breeding areas may attain higher reproductive success, even though they may incur additional risks of mortality due to unstable and harsh environmental conditions on wintering areas. Brant remaining at IZ over winter may benefit from current climatic changes. Weather patterns in the North Pacific have produced more stable and predictable winters with increased food availability in Alaska (Ward and Dau, in review), although long-term effects of climate change on Brant populations are unclear. Additionally, more frequent and severe El Niño events and increasing human activity in Baja California may produce more erratic winter weather and lower forage abundance at Bahia San Quintin (Ward et al. 2004). Long term changes in the location of wintering Brant may therefore depend upon the magnitude and timing of energetic costs as winter habitats change in both Alaska and Baja California.

ACKNOWLEDGEMENTS

We would like to thank the following people for their assistance with data collection, logistics and laboratory analyses: Diana Brann, Alejandro Cabello-Pasini, David Duarte-Etchart, Rolando Duarte, Sergio Duarte-Etchart, Josue Etchart, Alberto "Tiburón" Flores, Kevin and Lisa Fox, Pat Gonzales, Jerry Hupp, Desmond Johns, Dan Johnson, Jessie Labrador, Arturo Malo, Aaron Martin, Jeff Mason, Rick Poetter, Andy Ramey, Joaquin Sanchez, Christy Shaw, Kate Soetaert, and Kristine Sowl. A special thank you goes to Marnie Shepherd whose hard work and enthusiasm in the field and lab

were unparalleled and to Jeff Pelayo, Jeff Wasley, and Johann Walker for their steady aim. Mark Lindberg and Ed Murphy provided helpful advice and comments on the manuscript. Financial support was provided by the U. S. Geological Survey-Alaska Science Center, U. S. Fish and Wildlife Service-Region 7 Migratory Bird Management and Izembek National Wildlife Refuge, Angus Gavin Migratory Bird Research Fund, and the Department of Wildlife and Biology, and the Institute of Arctic Biology at the University of Alaska Fairbanks.

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TABLE 1.1. Mean morphometric measures (mm \pm SE) and associated principal component loadings for adult Brant from northern (IZ) and southern (BSQ) wintering grounds. Means with different superscripts within a row are significantly different ($P < 0.05$). Data from fall and spring staging were excluded from this analysis.

	IZ Females	BSQ Females	IZ Males	BSQ Males	PC1	PC2
Head	88 \pm 0.4 ^a	86 \pm 0.4 ^b	90 \pm 0.5 ^c	91 \pm 0.4 ^c	.851	.337
n	48	49	53	44		
Total tarsus	70 \pm 0.5 ^a	68 \pm 0.4 ^b	72 \pm 0.4 ^c	72 \pm 0.5 ^c	.919	.177
n	46	49	54	43		
Body Length	567 \pm 2 ^a	568 \pm 2 ^a	604 \pm 3 ^b	607 \pm 2 ^b	.258	.963
n	49	48	53	44		

TABLE 1.2. Collection date, sample size (n), and arithmetic mean mass (g \pm SE) of whole body and components in female Brant collected at northern (IZ) and southern (BSQ) sites during 2002-2003.

	Study area	Collection Period				
		Fall staging	Early winter	Mid-winter	Late winter	Spring staging
Median date	BSQ		8 December	13 January	28 March	
	IZ	27 October	20 November	15 January	5 April	6 May
Sample size (n)	BSQ		17	17	14	
	IZ	19	16	16	17	13
Body mass	BSQ		1430.7 \pm 26.9	1439.8 \pm 26.9	1575.9 \pm 28.6	
	IZ	1682.1 \pm 34.4	1619.7 \pm 43.8	1433.8 \pm 19.9	1554.7 \pm 37.4	1553.2 \pm 41.6
Feathers	BSQ		122.8 \pm 4.5	116.7 \pm 4.5	105.8 \pm 4.9	
	IZ	138.6 \pm 6.5	126.9 \pm 6.9	132.0 \pm 6.8	150.7 \pm 6.7	148.0 \pm 7.7
Skin	BSQ		239.0 \pm 8.9	239.1 \pm 8.9	314.9 \pm 9.8	
	IZ	364.7 \pm 17.4	356.9 \pm 15.5	224.7 \pm 15.5	230.7 \pm 15.1	236.2 \pm 17.2
Visceral adipose	BSQ		58.1 \pm 5.2	49.1 \pm 5.2	109.8 \pm 5.8	
	IZ	103.9 \pm 10.2	109.9 \pm 7.3	51.9 \pm 7.3	38.1 \pm 7.0	49.9 \pm 12.3
Pectoralis	BSQ		199.2 \pm 4.1	209.8 \pm 4.1	194.5 \pm 4.5	
	IZ	212.5 \pm 4.5	212.2 \pm 4.5	226.7 \pm 4.4	225.8 \pm 4.3	210.5 \pm 5.5
Supracoracoideus	BSQ		21.2 \pm 0.5	21.9 \pm 0.5	20.5 \pm 0.6	
	IZ	21.0 \pm 0.6	20.8 \pm 0.6	22.6 \pm 0.6	22.4 \pm 0.5	21.6 \pm 0.7
Liver	BSQ		31.3 \pm 1.2	29.7 \pm 1.1	31.3 \pm 1.3	
	IZ	52.7 \pm 1.8	45.7 \pm 1.9	32.5 \pm 1.9	53.5 \pm 1.9	51.0 \pm 2.1
Gizzard	BSQ		106.9 \pm 2.3	108.9 \pm 2.3	114.8 \pm 2.5	
	IZ	107.2 \pm 2.5	106.0 \pm 2.7	103.8 \pm 2.7	100.6 \pm 2.6	107.1 \pm 3.0
Intestine	BSQ		38.1 \pm 1.3	39.1 \pm 1.3	40.8 \pm 1.4	
	IZ	42.9 \pm 1.3	40.4 \pm 1.4	37.8 \pm 1.4	44.9 \pm 1.4	49.8 \pm 1.6
Ovary	BSQ		0.40 \pm 0.03	0.45 \pm 0.03	0.47 \pm 0.04	
	IZ	0.37 \pm 0.17	0.41 \pm 0.20	0.47 \pm 0.17	1.11 \pm 0.15	2.28 \pm 0.17

TABLE 1.3. Collection date, sample size (n), and arithmetic mean mass (g ± SE) of whole body and components of adult male Brant collected at northern (IZ) and southern (BSQ) sites during 2002-2003. Mass of body components were not measured for males collected in BSQ.

	Study area	Collection Period				
		Fall staging	Early winter	Mid-winter	Late winter	Spring staging
Median date	BSQ		8 December	13 January	28 March	
	IZ	27 October	20 November	15 January	5 April	6 May
Sample size (n)	BSQ		22	24	9	
	IZ	16	18	7	15	18
Body mass	BSQ		1554.4 ± 33.0	1563.3 ± 34.3	1766.1 ± 30.5	
	IZ	1886.1 ± 51.9	1803.6 ± 48.9	1678.9 ± 53.6	1625.8 ± 53.6	1678.8 ± 48.9
Skin + feathers	IZ	523.7 ± 27.8	475.6 ± 26.2	407.8 ± 45.4	335.1 ± 28.7	421.2 ± 27
Visceral adipose	IZ	97.1 ± 11.5	101.7 ± 14.5	47.7 ± 25.7	38.8 ± 16.1	66.2 ± 10.8
Pectoralis	IZ	243.3 ± 4.7	239.6 ± 6.4	256.4 ± 10.2	240.4 ± 6.1	238.6 ± 5.6
Supracoracoideus	IZ	24.6 ± 0.8	25.5 ± 0.7	26.1 ± 1.2	24.9 ± 0.8	23.8 ± 0.7
Liver	IZ	60.6 ± 2.7	48.4 ± 2.5	37.2 ± 4.1	56.8 ± 2.8	53.9 ± 2.5
Intestine	IZ	51.4 ± 2.2	48.2 ± 2.0	42.4 ± 3.3	50.0 ± 2.2	49.2 ± 2.0
Gizzard	IZ	120.3 ± 4.9	118.3 ± 4.6	114.1 ± 7.4	108.5 ± 5	104.1 ± 4.6
Testis	IZ	0.17 ± 0.12	0.17 ± 0.12	0.21 ± 0.19 ^a	0.83 ± 0.12	1.15 ± 0.11

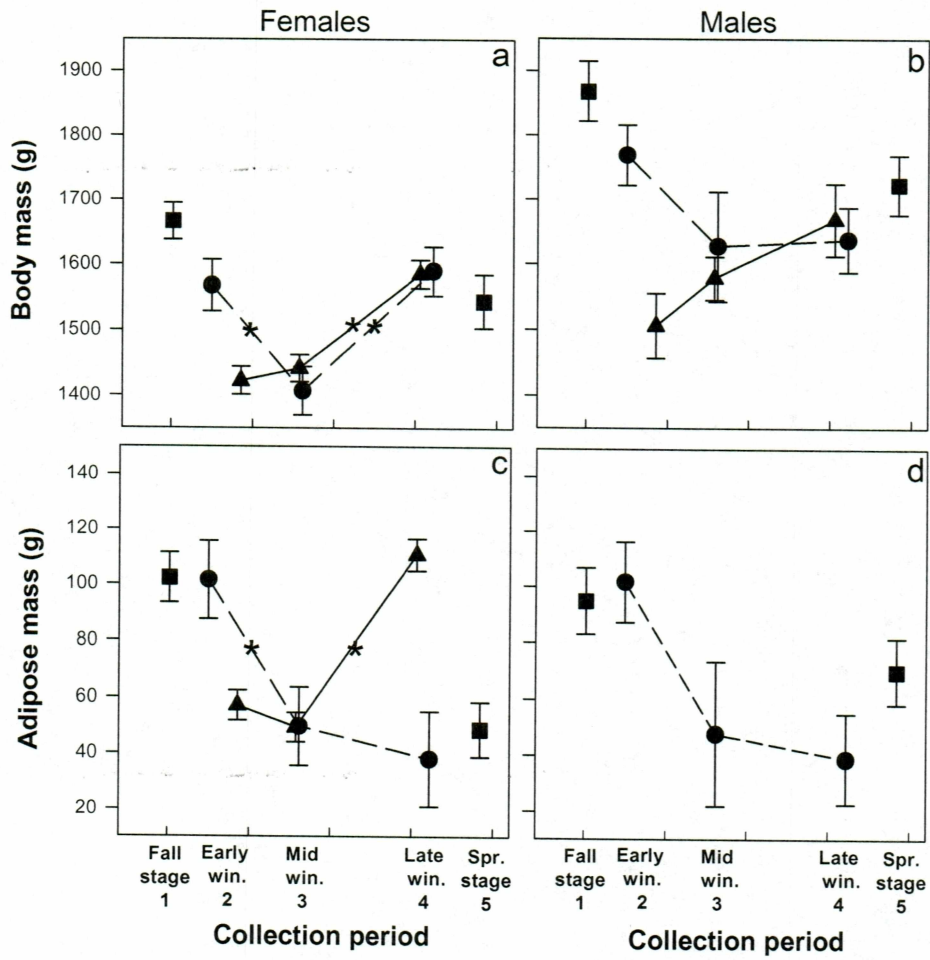


FIG. 1.1. Changes in mass ($g \pm SE$) of the whole body (a-b) and visceral adipose (c-d) for female and male Brant during staging (squares), winter at Izembek (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

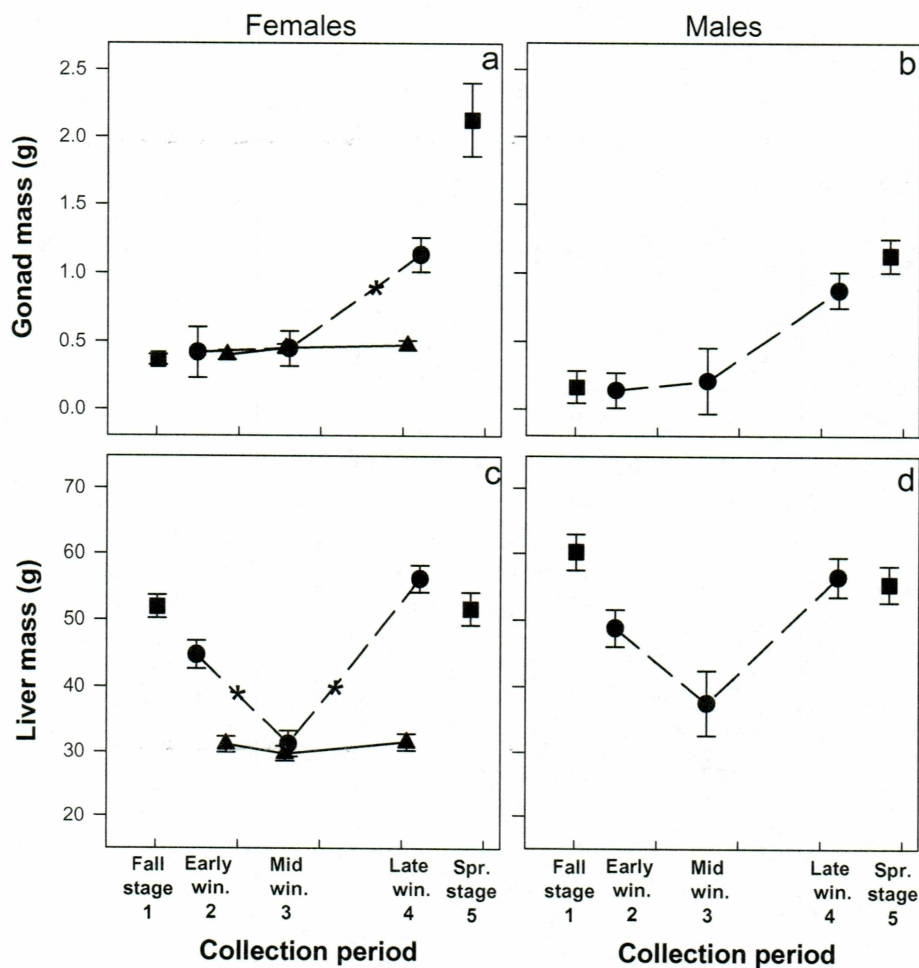


FIG. 1.2. Changes in mass ($g \pm SE$) of gonadal (a-b) and liver tissue (c-d) for female and male Brant during staging (squares), winter at Izembek (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

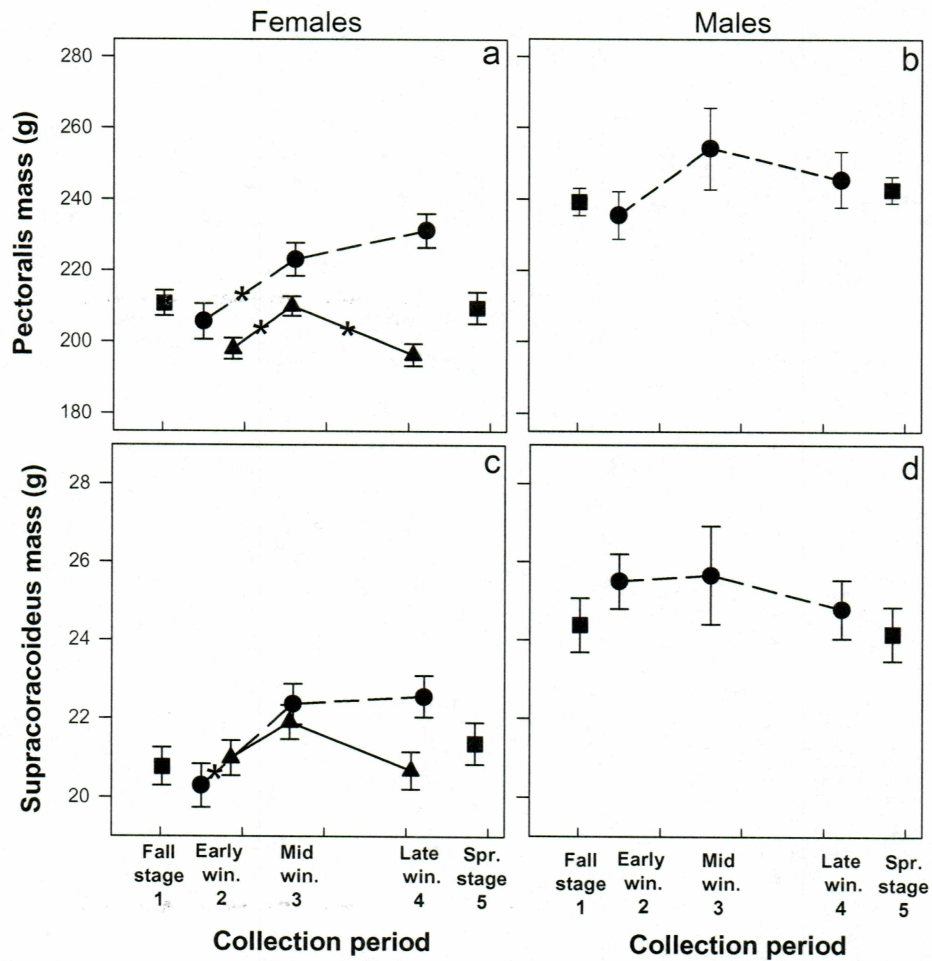


FIG. 1.3. Changes in mass ($g \pm SE$) of total pectoralis muscle (a-b) and total supracoracoideus (c-d) for female and male Brant during staging (squares), winter at Izembek (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

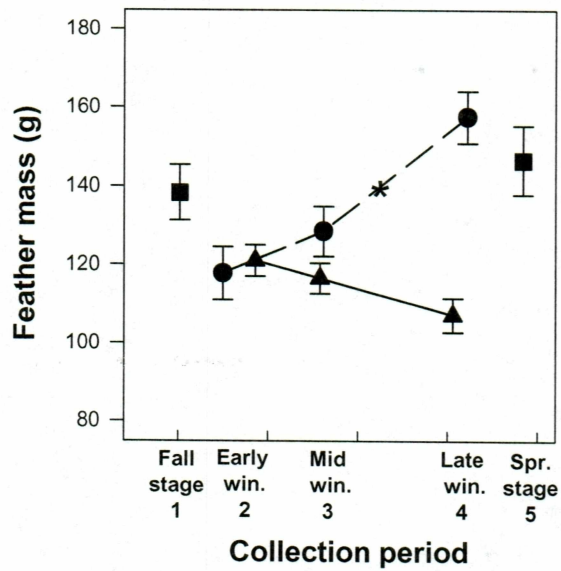


FIG. 1.4. Changes in feather mass ($g \pm SE$) for female Brant during staging (squares) and winter at Izembek (circles, dashed lines) and Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

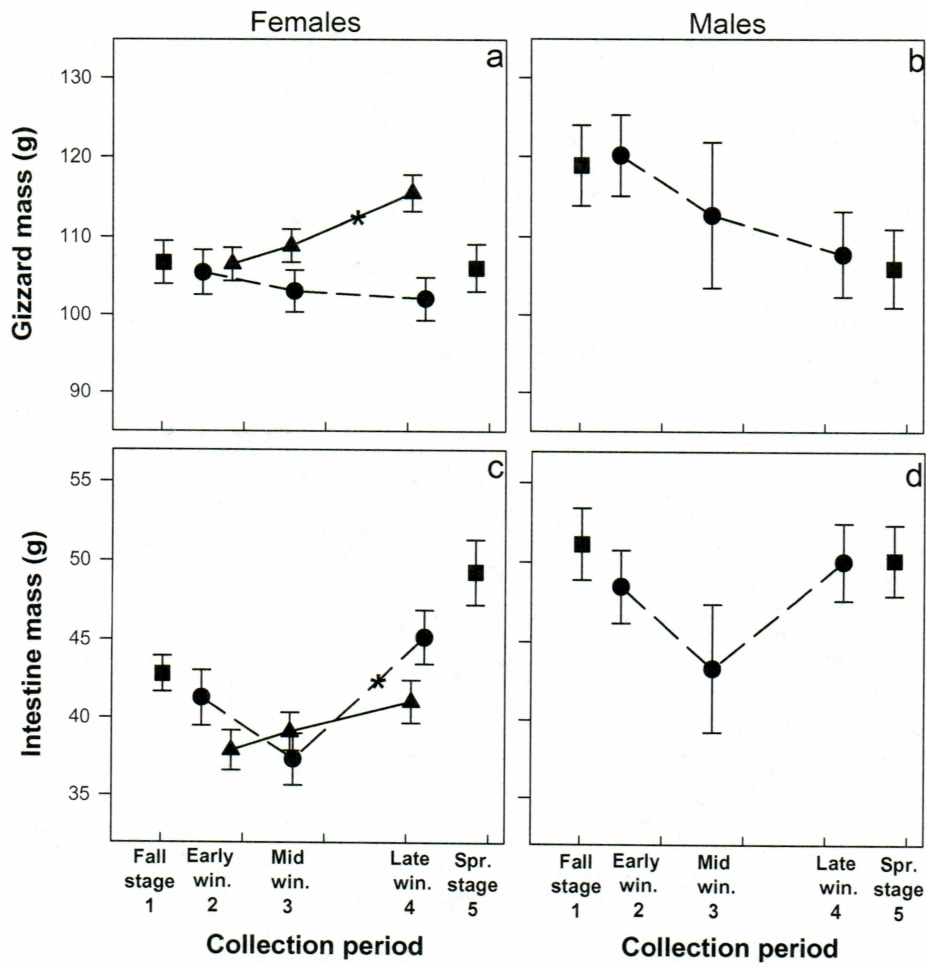


FIG. 1.5. Changes in mass ($g \pm SE$) of gizzards (a-b) and intestines (c-d) for female and male Brant during staging (squares), winter at Izembek (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

CHAPTER 2. NUTRITIONAL CONDITION OF PACIFIC BLACK BRANT AT THE EXTREMES OF THEIR WINTER RANGE¹

ABSTRACT. — Endogenous stores of energy allow birds to survive periods of severe weather and food shortage during winter. We documented changes in lipid, protein, moisture and ash in body tissues of Brant and modeled the energetic costs of wintering. Birds were collected at the extremes of their winter range, in Alaska and Baja California, Mexico. Body lipids decreased over winter for birds in Alaska but increased for those in Baja California. Conversely, body protein increased over winter for Brant in Alaska and remained stable for birds in Baja California. Lipid stores likely fuel migration for Brant wintering in Baja California and ensure winter survival for those in Alaska. Increases in body protein may support earlier reproduction for Brant in Alaska. Predicted energy demands were similar between sites during late winter but avenues of expenditure were different. Birds in Baja California spent more energy on lipid synthesis while those in Alaska incurred higher thermoregulatory costs. Estimated food intakes were similar between sites in late winter; however, feeding time was more constrained in Alaska because of high tides and short photoperiods. Wintering in Alaska may be more advantageous than long distance migration if constraints on foraging time do not impair body condition and increase risk of mortality in late winter.

Keywords: body composition, energy storage, geese, lipid, protein, winter.

¹Prepared for submission in *Condor* as Mather, D. D., P. S. Barboza and D. H. Ward. Nutritional condition of Pacific Black Brant at the extremes of their winter range.

INTRODUCTION

Body condition can be defined as an individual's ability to meet present and future energy requirements (Owen and Cook 1977). Nutritional condition is, therefore, related to the amount of energy stored in the body as lipid and protein. Many species of waterfowl wintering in temperate areas maintain large stores of lipid and protein (Raveling 1979, Moorman et al. 1992); however, winter energy stores are often smaller than pre-migratory stores (Biebach 1996). Adverse winter conditions (low temperatures, frequent storms, short photoperiod, and low food abundance) can inhibit energy storage by constraining food intake and increasing energetic demands (Lovvorn 1994). Winter survival is dependent on balancing energy accumulation and expenditure. Energy expended on activity can be reduced during periods of severe weather or food shortages if birds are able to rely on endogenous energy stored during times of abundant resources (Blem 1990). Conversely, birds that winter in mild climates with abundant resources likely incur lower costs of living and require relatively smaller energy stores to meet energy demands (Castro et al. 1992). Winter survival may be influenced by feeding conditions and energetic demands in the preceding autumn as well as during winter (Haramis et al. 1986). Changes in the nutritional condition of wintering birds may therefore reflect differences in energy demands and constraints on energy accumulation.

Birds in different wintering climates may have different strategies for storing and using energy, but these strategies are rarely considered within species. In the present study we document changes in tissue composition and energy storage for adult female Pacific Black Brant (*Branta bernicla nigricans*, hereafter Brant) wintering at the

extremes of their range to examine the functional significance of changes in body composition. We also use air temperature, estimated time available for foraging and diet quality data to model energetic costs and estimate food intakes for Brant wintering at both sites. Comparisons of energy expenditure between sites will allow us to further examine the relative costs and benefits of each strategy.

Brant are an ideal species for studies of nutritional condition as they rely almost exclusively on a single native food source (*Zostera marina* or eelgrass) throughout their non-breeding range, show high winter site fidelity and exhibit widely divergent wintering strategies (Reed et al. 1998). Wintering populations of Brant are distributed along the Pacific coast of North America between Alaska and Baja California, Mexico (55° to 21°N latitude). Brant from all major Arctic and sub-Arctic breeding areas converge at staging grounds on the Alaska Peninsula in the fall and spring (Reed et al. 1989, Ward and Stehn 1989). Some Brant remain over winter on staging grounds in Alaska, while most migrate an additional 5,000 km to primary wintering areas in Baja California (Reed et al. 1998, Ward et al., in press).

Mather et al. (in review) showed that Brant wintering in Alaska and Baja California maintained similar overall body and visceral fat mass, suggesting that adipose stores should not prevent birds that stage in Alaska from migrating. Changes in body mass, however, varied by location; Brant in Alaska lost mass between early and mid-winter, while those in Baja California maintained mass during the same period of time. Birds at both sites subsequently gained mass in late winter. Mass gains of Brant in

Alaska were due to an increase in mass of nutritional and reproductive organs, whereas birds in Baja California gained visceral adipose (Mather et al. in review).

We predict that winter morphology, such as the mass of the whole body or its component tissues, does not equally reflect stores of lipid, protein and energy at both sites. Furthermore, we predict that lean tissue composition will be conserved as lipid and protein mass change at each site. We also predict that energetic costs and constraints on food intake are higher in Alaska than Baja California and will influence patterns of lipid and energy storage.

METHODS

We collected Brant concurrently in Alaska at Izembek lagoon (IZ) and in Baja California at Bahia San Quintin (BSQ) during the winter of 2002-2003. The timing of collections was based on the average timing of migration and movement of Brant at each location (Reed et al. 1989, Ward and Stehn 1989, Ward and Mather unpubl. data). Birds were collected during three two-week periods: early winter (early December), mid-winter (mid-January), and late winter (late March-early April). Brant were collected by shooting from natural feeding and/or roosting flocks. Decoys were not used during collections because decoys may attract a higher proportion of juveniles or birds in poor condition (Greenwood et al. 1986, Reinecke et al. 1988). We assumed that collected birds would have remained at IZ or BSQ through winter because Brant have high site fidelity during winter (Reed et al. 1998). Changes in body composition of birds at each site were

therefore assumed to reflect responses to local conditions rather than movements of birds during winter.

ENVIRONMENTAL MEASURES

We measured air temperature and estimated time available for foraging at both sites in order to model the energetic costs of wintering for Brant. Air temperatures were obtained from the NOAA weather station in Cold Bay, AK, located approximately 12 km southeast of IZ. Air temperatures at Bahia San Quintin were recorded every 30 minutes on data loggers located at the mouth of the bay (A. Cabello unpubl. data).

Foraging Brant do not dive; food intake is, therefore, restricted by high water level. Most intertidal beds of eelgrass are submerged when the mean tide height is over 1m at IZ (Ward and Stehn 1989, Ward et al. 1997) and at BSQ (Ward et al. 2003). Under the assumption that Brant feed primarily during daylight hours at both locations; we calculated the amount of time available for foraging (foraging window) as the mean number of daylight hours when the mean tide height was $< 1\text{m}$. Water depths were estimated from predicted tides for Grant Point at Izembek Lagoon and for Bahia San Quintin (Tides & Currents 2.1, 1998). Our estimate of foraging window may underestimate total time available for feeding as Brant are known to feed on detrital eelgrass found floating on the surface of the water (Ward and Stehn 1989), and some nocturnal foraging activity has been documented in other locations (Percival and Evans 1997). It is, however, unlikely that nocturnal and surface foraging can totally replace diurnal feeding because food intakes outside the foraging window are probably low.

MEASURES OF BODY COMPOSITION

We weighed freshly killed Brant in the field using an electronic balance (± 0.01 g). Age (adult or yearling) and gender were determined by plumage characteristics and cloacal examination. Gender was later confirmed through internal inspection of reproductive organs. Following methods of Dzubin and Cooch (1992), we measured lengths (± 1 mm) of the total tarsus, head, and total body for each bird. Brant were double wrapped in plastic, sealed in plastic bags, and stored frozen in the field to minimize desiccation and degradation of tissues.

We thawed frozen carcasses in a refrigerator prior to dissection. Feathers were removed with an electric shears (Oster Shearmaster) and by manual plucking. We removed skins to the elbow joint along with adherent adipose tissue to determine the mass of skin and subcutaneous adipose tissue. We dissected pectoralis muscles and the digestive tract from the carcass. Digesta was removed from the tract before analyzing the tissues. Esophageal contents and colonic digesta were stored frozen for subsequent analysis. We combined body tissues into the following three groups for chemical analysis: pectoralis muscle, skin (including subcutaneous adipose), and carcass (all remaining tissues and appendicular skeleton). Tissues were homogenized in a meat grinder with a 4.5mm sieve plate. Homogenates were desiccated in a freeze dryer (carcass and pectoralis) or a forced air oven at 50°C (skin). Water content of the tissues was calculated as mass lost during desiccation. Ash was determined by combustion at 550° C in a muffle furnace for 8 hr. Lipid was extracted with petroleum ether (Dobush et al. 1985) in a modified Soxhlet procedure (Model HT6 Soxtec, Tecator, Foss North

America, Silver Spring Md.). Nitrogen (N) was determined using an elemental analyzer (Model no. CNS 2000, Leco, St Joesph Mich.).

We calculated the mass of lipid, N and ash as the product of dry mass of each fraction (g) and the concentration in dry matter (e.g. g lipid g DM⁻¹). Organic matter (OM) was dry matter minus ash for each body component. Total lipid was subtracted from the dry mass of each tissue to determine lean dry mass. Crude protein content was determined from the ash free lean dry mass (lean OM) with the assumption that all N was associated with this fraction. Crude protein equivalents were determined as the average concentration of N in each fraction: 6.50 gN g⁻¹ lean OM carcass, 5.35 gN g⁻¹ lean OM muscle and 7.50 gN g⁻¹ lean OM skin. We determined the energy content of body tissues by multiplying the gross energy content of lipid (39.3 kJ g⁻¹) and protein (muscle 23.7 kJ g⁻¹, skin 22.5kJ g⁻¹) (Blaxter 1989) by the dry mass of crude protein and lipid contained in each body component. Total lipid and protein were calculated by summing the nutrients contained in the pectoralis, carcass and skin.

DIET ANALYSES

We collected eelgrass samples from three to five locations at each study area during each of the collection periods. We rinsed samples to remove sediments and attached organisms, and removed and discarded the rhizomes. Leaves were stored frozen in plastic bags for analysis. Samples of the diet and of digesta from the esophagus and intestine were thawed and weighed (± 0.001 g) on an electronic balance and then dried at 80° C to a constant mass. We ground dried samples in a Wiley mill (no. 20, 1.25mm wire

mesh) for chemical analysis. Fiber fractions were isolated sequentially (cellulose, hemicellulose and lignin) by the methods of Van Soest et al. (1991). Neutral detergent fiber (NDF) was extracted with Na_2SO_3 and without amylase. Hemicellulose was calculated as the difference between NDF and ADF (acid detergent fiber), and cellulose content as the difference between ADF and lignin. We determined nitrogen (N) content using an elemental analyzer (Model no. CNS 2000, Leco, St Joseph Mich.). We calculated crude protein by multiplying N content by 6.25 (Robbins 1993). The residue of OM after accounting for fiber fractions and crude protein was primarily an estimate of non-structural carbohydrates such as starch because lipid is typically low in leaves of eelgrass (5% of DM; Ward and Stehn 1989).

We calculated digestibility of eelgrass only for birds from IZ because esophageal contents of birds at BSQ were insufficient for chemical analysis. Nutrient digestibility (OM) was calculated from the manganese (Mn) content of digesta from the esophagus and colon as follows; $(1 - ((\text{esophageal Mn/nutrient content}) / (\text{gut Mn/nutrient content})))$. Estimates of dry matter metabolized from Mn balance in captive Brant fed alfalfa was $91 \pm 19\%$ of the dry matter metabolizability determined by direct measurement of dry matter ingested and excreted (P. Barboza unpubl. data). We calculated energy content of the diet from the caloric values of cellulose (17.49 kJ g^{-1}), hemicellulose (17.82 kJ g^{-1}), starch (17.48 kJ g^{-1}) and protein (22.05 kJ g^{-1}) (Blaxter 1989).

MODELING ENERGETIC COSTS AND FOOD INTAKE

We modeled daily energetic costs ($\text{kJ d}^{-1} \text{kg}^{-1}$) for the interval between early and mid-winter and between mid and late winter at each site. We calculated maintenance energy expenditure from average body mass (kg) and the resting rate of metabolism ($567 \text{ kJ d}^{-1} \cdot \text{kg}^{-1}$) of Brant under thermoneutral conditions (20°C) (Sedinger et al. 1992). We assumed an increment of 55% above maintenance for activity costs based on behavioral time budgets of wild Brant at Izembek in October-November (Ward and Stehn 1989). Costs of thermal conductance were based on relationships between body mass (M) and oxygen consumption of non-passerines as follows (Aschoff 1981):

$$\text{Active phase (mLO}_2\text{/h)} = 33.4 (M^{-0.48})$$

$$\text{Passive phase (mLO}_2\text{/h)} = 16.9 (M^{-0.58})$$

Oxygen consumption was converted to energy expended with a respiratory quotient (RQ) that was estimated at $20.92 \text{ kJ L}^{-1} \text{O}_2$ from the composition of eelgrass (Robbins 1993). We assumed that Brant spent equal amounts of time in each diurnal phase of basal metabolism (12 active: 12 passive). Temperature differences (T) were calculated between the mean daily air temperature for each site and interval and 20°C (temperature for maintenance energy expenditure). Daily cost of thermal conductance was calculated as, $\text{Conductance (kJ d}^{-1}) = T (12 (\text{active phase} + \text{passive phase}))$. We calculated total energy flux through the body ($\text{kJ}^{-1} \text{d}^{-1} \text{kg}^{-1}$) as the sum of maintenance, activity, conductance, tissue synthesis, and change in body energy. The cost of adding tissue was the energy content of the tissue (23.7 kJ g^{-1} protein, 39.3 kJ g^{-1} lipid; Blaxter 1989) plus the cost of converting lipid or protein from food to tissue (70% efficiency or $1.43 \times$

energy content; King 1973). We calculated dietary energy intake (kJ d^{-1}) as the energy flux corrected for the net contribution or deposition of energy in the body. We calculated dry matter intake ($\text{gDM d}^{-1} \text{kg}^{-1}$) by dividing dietary energy intake by the digestible energy content of the diet and average body mass. We calculated foraging rate ($\text{gDM h}^{-1} \text{kg}^{-1}$) by dividing dry matter intake by the number of hours in the foraging window during each interval.

STATISTICAL ANALYSES

We assessed effects of site and period on body composition with ANCOVA using three structural covariates (head, tarsus and body length) to standardize for body size. All mass data for body composition (lipid, protein) are presented as adjusted least square means ($\text{g} \pm \text{SE}$) from the ANCOVA and are therefore corrected for structural size. Nutrient concentrations ($\text{g g}^{-1} \pm \text{SE}$) were arcsine-transformed for ANOVA to meet assumptions of normality. Mean energy content (kJ g^{-1}) in the body was compared by ANOVA with site and period as independent factors. We used Bonferroni's adjustment for multiple comparisons among periods. The relationships between dissected tissues and chemically extracted nutrients were assessed through linear regressions. Although we used a cross-sectional design we assumed that changes in body composition represented changes within individuals in the population. All statistical analyses were conducted using SYSTAT 10.2 (Systat Software Inc. 2002) with $\alpha = 0.05$.

RESULTS

ENVIRONMENTAL DATA

Mean monthly air temperature between November and April was 1° C at IZ and 15° C at BSQ (Fig. 2.1a). Range in mean air temperature (maximum – minimum) was greater at BSQ (30° C) than at IZ (3° C). Brant at IZ were, therefore, consistently below 20°C throughout winter. Foraging windows were shorter at IZ than at BSQ from December to March. The duration of the foraging window at IZ decreased from 5.7 hr in October to 1.3 hr in January. Between January and early April, the foraging window increased at both sites reaching > 9 hr in April when birds begin staging at IZ (Fig. 2.1b).

BODY COMPOSITION

The greatest concentrations of lipid were found in the skin and carcass (Tables 2.1, 2.2) which accounted for 52% and 45% of the total body lipid, respectively. Skin mass explained 76% of the variation in total body lipid at BSQ and 80% at IZ (Fig. 2.2a). The pattern of change for total body lipid reflected those in both the skin and carcass at each site (Figs 2.3a-c). Between early and mid-winter, body lipid declined at IZ ($-178 \pm 42\text{g}$, $P < 0.001$) and remained stable at BSQ. Conversely, between mid and late winter, birds at IZ maintained body lipid while those at BSQ gained lipid prior to migration ($+166 \pm 22\text{g}$, $P < 0.001$; Fig. 2.3a). Between mid and late winter, pectoral lipid also declined at IZ ($-3 \pm 1\text{g}$, $P = 0.033$) and increased slightly at BSQ ($+1 \pm 0.4\text{g}$, $P = 0.048$; Fig. 2.3d). The mid-winter period appears to be a pivot point when lipid masses in the whole body, carcass and skin were similar between sites. During winter, the mean overall mass (when

periods were combined) of total body lipid was similar at both sites ($945 \pm 47\text{g}$ BSQ vs. $925 \pm 90\text{g}$ IZ).

The greatest concentrations of protein were found in the carcass and pectoralis (Tables 2.1, 2.2) which accounted for 68% and 19% of total body protein, respectively. Pectoralis mass explained 49% of the variation in total body protein at BSQ and 45% at IZ (Fig. 2.2b). Protein mass in the whole body and carcass increased between early and late winter at IZ ($P < 0.001$), but was similar between periods at BSQ (Figs 2.4a-b). Protein in the skin was similar among all periods at both sites (Fig. 2.4c). Protein in the pectoralis was similar between early and late winter at both sites; however, overall pectoral protein was greater at IZ than at BSQ ($139 \pm 5\text{g}$ vs. $124 \pm 2\text{g}$, $P < 0.001$). Lipid in the pectoralis was also greater at IZ than BSQ in mid-winter ($26 \pm 2\text{g}$ vs. $23 \pm 1\text{g}$, $P = 0.047$) (Fig. 2.3d). Overall protein mass was greater at IZ than at BSQ in the body ($723 \pm 16\text{g}$ vs. $666 \pm 9\text{g}$, $P < 0.001$), and in the carcass ($491 \pm 11\text{g}$ vs. $455 \pm 7\text{g}$, $P < 0.001$), but was similar between sites in the skin.

Composition of lean body tissues remained stable among periods at both sites (Fig. 2.5); therefore, any difference in lean mass was not due to changes in the composition of the fat-free tissue within sites. The overall composition of lean tissues did, however, differ between sites. Concentrations of ash and moisture in the lean body were greater at BSQ than at IZ ($P < 0.026$), and concentrations of OM were greater in at IZ than BSQ ($P < 0.001$).

Lipid contributed 57-77% to total energy in the body (Fig. 2.6), and changes in energy derived from lipid followed patterns for total body energy. Total body energy

decreased at IZ ($P < 0.001$, Fig. 2.6) but increased at BSQ ($P < 0.001$) over winter. Energy from protein increased between early and late winter for birds at IZ ($P = 0.002$) but remained stable for birds at BSQ. The lowest proportion of body energy from lipid (57%) was for birds at IZ in late winter. Overall, total body energy was similar between sites for Brant during the winter. Body mass explained 67% of the variation in total body energy at BSQ and 52% at IZ (Fig. 2.2c).

FOOD MODEL AND ENERGETICS

Eelgrass collected at IZ contained more OM and N ($P < 0.001$) but less hemicellulose than eelgrass collected at BSQ ($P < 0.001$; Table 2.3). The estimated content of gross energy was, however, similar for plants at both sites. Digestibilities of gross energy and OM were estimated at $51 \pm 14\%$ and $47 \pm 17\%$, respectively, based on esophageal and intestinal digesta collected at IZ.

Total energy flux through the body was similar between sites but avenues of energy expenditure were different between IZ and BSQ (Table 2.4). Birds at BSQ spent more energy on tissue (lipid) synthesis between mid and late winter as they prepared for migration; whereas birds wintering at IZ incurred higher cost of thermal conductance throughout winter (Table 2.4). Daily intakes of DM at BSQ ($129, 147 \text{ g d}^{-1} \text{ kg}^{-1}$) were similar to those for IZ ($131, 149 \text{ g d}^{-1} \text{ kg}^{-1}$) within each interval (Table 2.4). Daily intakes were higher after mid-winter at both sites. Concomitant declines in the foraging window increased estimated foraging rates more at IZ than at BSQ before mid-winter.

Consequently, the highest predicted rate of foraging ($44\text{g h}^{-1} \text{kg}^{-1}$) was for birds at IZ during the early and mid-winter interval (Table 2.4).

DISCUSSION

Brant show differences in patterns of nutrient storage and tissue composition, which are apparently driven by a combination of programmed events and differences in environmental conditions. These different patterns influence relationships between body morphology and composition. Changes in skin lipid paralleled changes in carcass lipid and resulted in a highly predictive relationship between the mass of skin and total body lipid. Researchers interested in estimating total body lipid could use skin mass as a predictor of total body lipid (also see Whyte and Bolen 1984). Body mass was a poor predictor of body energy because lipid storage differed between sites and periods. Changes in lipid and protein mass in late winter further confuse the relationships between body mass and lipid or protein. Predictions of body protein from pectoralis mass were also relatively poor because the amount of protein contained in this flight muscle was only a small fraction of total body protein (19%). The use of morphological measures to predict body condition of wintering birds may be best suited to monitoring a population at one site and at one time in the annual cycle.

Declining food resources and deteriorating environmental conditions are often associated with timing of fall migration (Berthold 2001). Movements of Brant at Izembek Lagoon followed both the foraging window and the weather pattern. Mean date of fall departure from Izembek Lagoon (5 November; D. Ward unpubl. data) coincided

with declining air temperature, day length and frequency of low tides for foraging (Fig. 2.1) (also see Ward and Stehn 1989). At Izembek Lagoon, the foraging window was longer in October when peak numbers of staging Brant are present, than in late November when most birds have departed (Fig. 2.1b). During late winter at Bahia San Quintin pre-migratory body mass gains coincided with increases in the foraging window at this site. Migrants also returned to Izembek for spring staging (4 May; D. Ward unpubl. data) when the foraging window was long (> 9 hr). Changes in foraging conditions and decreasing temperatures may also influence patterns of nutrient storage and tissue composition for wintering Brant.

Birds wintering in cold environments have high energy demands, and generally require large intakes of food (Dugan et al. 1981). Thermal conductance measures heat exchange between the body and the environment; as the temperature differential increases in the cold, so does the cost of maintaining core body temperature (McNab 2002). In our study, average daily temperature differed by 14-15°C between wintering sites. Consequently, the cost of thermal conductance for wintering Brant was three- to four-fold greater at Izembek than at Bahia San Quintin. Our estimated cost of thermoregulation is likely low as we did not account for convective losses of energy to wind. Wind speeds at Izembek average 26 kph during winter and are typically much greater than those at Baja San Quintin (12kph; Ward and Stehn 1989). High winds in Alaska would increase not only heat loss but also energy expenditure during swimming and flight.

Total energy flux for Brant was similar between sites even though thermoregulatory costs differed markedly between sites. Low costs for thermoregulation for migrants were partially offset by high costs for pre-migratory lipid storage during late winter. Brant in Bahia San Quintin gained 163g (2.2g d^{-1}) of lipid between mid and late winter; this gain required an additional energy expenditure of 155 kJ d^{-1} which was similar to the cost of thermal conductance (198 kJ d^{-1}) for Brant at Izembek.

High energy expenditure coupled with restricted foraging opportunities may prevent Brant at Izembek Lagoon from maintaining lipid stores in early winter and from gaining lipid in late winter. Food shortages can reduce body mass by 40% in mallards during early winter (Loesch et al. 1992). Our predicted average daily consumption of eelgrass (gDM) for Pacific Black Brant (208g d^{-1}) is greater than estimates for Dark-Bellied Brent (*Branta bernicla bernicla*) geese ($100\text{-}122\text{g d}^{-1}$) in winter and similar to estimates for Brent geese that gain mass during staging (270g d^{-1}) (Drent et al. 1981). We believe that Pacific Black Brant may be foraging near maximum intakes rates during winter and that lipid deposition may be constrained by foraging time. Predictions of high food intakes supported lipid gains for birds at Bahia San Quintin during late winter but only maintained lipid levels in birds at Izembek lagoon during the same time period.

Foraging is compressed into short foraging windows in Alaska in early winter, resulting in an increase of dietary load of DM to $44\text{g kg}^{-1}\text{ h}^{-1}$. It is unlikely that Brant can sustain this foraging rate because fasted Brant only re-feed at $21.9\text{g kg}^{-1}\text{ h}^{-1}$ when held under thermoneutral conditions in captivity (P. Barboza unpubl. data). High rates of food intake can decrease digestive efficiency for fibrous components of the diet. An increase

in food intake by 39% in captive Brant decreased cellulose digestibility by 64% (P. Barboza unpubl. data). Estimates of DM digestibility for Brant from Izembek are similar to metabolizabilities of captive Brant fed alfalfa ($42 \pm 5.8\%$; P. Barboza unpubl. data) or pelleted eelgrass (37% OM; Morehouse 1974). The ability to process large loads of food is ultimately limited by the capacity of the digestive system and the speed of digestion (Karasov 1990, Barboza and Hume 2005). Brant may be able to sustain digestive efficiency by increasing the mass of the intestines or the size of the gizzard (Mather et al. in review).

Brant may be able to extend the amount of time spent feeding outside of the foraging window; however, foraging under less optimal conditions may not be energetically efficient. For example, during extremely cold temperatures waterfowl often reduce activity because costs of foraging exceed energy gains (Paulus 1988). Some birds are known to switch to alternate food sources in order to increase energy intake (McLandress and Raveling 1981) but this is not likely for Brant wintering at these sites because approximately 90% of their diet is eelgrass (Kramer 1976, Ward and Stehn 1989). The depletion of lipid stores between early and mid-winter at Izembek probably reflects under-feeding during short foraging windows. Lipid accumulated in the long foraging window during fall staging and early winter may determine the probability of winter survival in Brant at Izembek (Haramis et al. 1986). Body lipid may vary with environmental conditions even when food is abundant; that is, endogenous regulation of lipid mass in waterfowl can respond to frequency of food supply and inclement weather (Lovvorn 1994, Barboza and Jorde 2002).

Changes in body composition reflect the average energy and nutrient balances of Brant at each site. Brant in Bahia San Quintin gained body energy and were therefore in positive energy balance before migration. Conversely, birds in Izembek lost body energy but gained body protein, that is, negative lipid energy balance was coincident with positive protein balance for Brant in Izembek. Brant at Izembek may have apportioned some of their dietary or endogenous energy to support protein synthesis. Lipid stores of Brant in Izembek lagoon were 13% in late winter and well above the minimal reserve of 5% for geese (Raveling 1979). The higher nitrogen content of eelgrass found in Izembek than at Bahia San Quintin may favor increased protein storage for birds wintering at Izembek. Protein is not, however, likely limiting at either site because N concentrations in eelgrass exceed those required for growth of domestic and wild ducks and geese (Sedinger 1984, National Research Council 1994).

Differences in lean mass between sites reflect both the composition and mass of tissues. Relatively high moisture and low protein content of lean OM in Brant from Bahia San Quintin may indicate differences in the structure of muscles between migrant and resident birds. Migratory flight can change blood perfusion and intracellular composition of pectoralis muscles (Saunders and Fedde 1994). Concentrations of OM in lean tissues remained stable within each site; therefore, protein content was a result of an increase in overall tissue mass. Most of the late winter increase in body protein for Brant in Izembek occurred in the carcass, presumably due to increases in liver and intestinal mass (Mather et al. in review). Protein storage in late winter may indicate early preparation for breeding. Ankney (1984) suggested that Brant nesting in Canada may use

body protein stores for ovarian development in pre-laying females, and contribute up to 70% of the protein in the average clutch of eggs. Brant at Izembek also showed increased ovarian development in late winter (Mather et al. in review) which supports the idea that these birds are beginning to prepare for breeding earlier than birds wintering at Bahia San Quintin.

Despite differences in foraging conditions and energy demands, Brant at both sites appeared to be in good overall body condition. Mean percent body fat for wintering Brant ranged from 14 to 30%, and overall lipid and energy stores were similar between sites. If Brant are able to maintain similar nutritional condition in Alaska and Baja California during winter, why do we see such disparate wintering strategies? Migration should occur when the risks of over wintering are greater than those of migrating (Lack 1968). Comparative data on survival rates for Brant wintering at Izembek and Bahia San Quintin are lacking, but we believe that Brant in Alaska may be more susceptible to increased stress from extended periods with severe weather or disturbance from humans or predators. Because of existing constraints on foraging, Brant in Alaska may not be able to maintain body condition during years of exceptionally harsh winter weather or when ice cover on Izembek lagoon is more extensive. We predict that numbers of wintering Brant in Alaska should continue to increase as long as constraints on foraging time do not impede maintenance of body condition or increase risk of winter mortality. We suggest that wintering in Alaska may be more advantageous than migration to Baja California because migration distance is reduced and birds remain closer to breeding grounds. Management in winter habitats should concentrate on protecting preferred

foraging areas for Brant and limiting disturbance during low tides. Future research should focus on obtaining estimates of survival and activity budgets for Brant wintering in Alaska.

ACKNOWLEDGEMENTS

We would like to thank the following people for their assistance with data collection and logistics: Diana Brann, David Duarte-Etchart, Rolando Duarte, Sergio Duarte-Etchart, Josue Etchart, Alberto "Tiburón" Flores, Kevin and Lisa Fox, Pat Gonzales, Jerry Hupp, Dan Johnson, Jessie Labrador, Arturo Malo, Aaron Martin, Jeff Mason, Jeff Pelayo, Rick Poetter, Andy Ramey, Joaquin Sanchez, Marnie Shepherd, Kate Soetaert, Kristine Sowl, Johann Walker and Jeff Wasley. Alejandro Cabello-Pasini provided laboratory space at the Universidad Autónoma de Baja California, logistical assistance, equipment and temperature data for Bahía San Quintín. We are especially grateful to Marnie Shepherd, Christy Shaw and Desmond Johns for the many long, tedious hours they spent in the lab- almost always with a smile. Mark Lindberg and Ed Murphy provided helpful advice and comments on the manuscript. Financial support was provided by the U. S. Geological Survey-Alaska Science Center, U. S. Fish and Wildlife Service-Region 7 Migratory Bird Management and Izembek National Wildlife Refuge, Angus Gavin Migratory Bird Research Fund, and the Department of Wildlife and Biology, and the Institute of Arctic Biology at the University of Alaska Fairbanks.

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TABLE 2.1. Mean tissue mass ($g \pm SE$) and concentrations ($g\ 100g^{-1} \pm SE$) of moisture, ash, lipid and N in the pectoralis, skin and carcass of Brant wintering at Bahia San Quintin, Mexico. Values with different superscripts within each body component denote a significant difference ($P < 0.05$) in mass or nutrient concentrations between periods.

Tissue	Period	Tissue mass	Moisture	Ash	Lipid	Nitrogen
Pectoralis	Early	200(4.47) ^a	70.8(0.18) ^a	5.83(0.26) ^a	3.91(0.09) ^a	3.81(0.02) ^a
	Mid	210(4.04) ^b	71.3(0.24) ^a	5.50(0.28) ^a	3.42(0.18) ^b	3.81(0.03) ^a
	Late	195(4.17) ^a	69.8(0.24) ^b	5.90(0.33) ^a	4.20(0.14) ^a	3.85(0.03) ^a
Skin	Early	239(6.06) ^a	31.1(1.38) ^a	0.49(0.03) ^a	56.1(1.56) ^a	1.65(0.07) ^a
	Mid	239(9.62) ^a	28.8(1.14) ^a	0.55(0.03) ^{ab}	57.7(1.60) ^a	1.85(0.09) ^a
	Late	315(11.9) ^b	19.9(0.51) ^b	0.42(0.06) ^a	70.8(0.94) ^b	1.19(0.03) ^b
Carcass	Early	795(14.0) ^a	61.1(0.54) ^a	5.20(0.10) ^a	14.9(0.66) ^a	2.89(0.03) ^a
	Mid	803(15.6) ^a	61.4(0.53) ^a	5.27(0.10) ^a	13.9(0.68) ^a	2.86(0.03) ^a
	Late	862(17.6) ^b	56.4(0.65) ^b	4.61(0.19) ^b	22.1(1.10) ^b	2.69(0.05) ^b

TABLE 2.2. Mean tissue mass ($g \pm SE$) and concentrations ($g\ 100\ g^{-1} \pm SE$) of moisture, ash, organic matter (OM), lipid and N in the pectoralis, skin and carcass of Brant wintering at Izembek Lagoon, Alaska. Values with different superscripts within each body component denote a significant difference ($P < 0.05$) in mass or nutrient concentrations between periods.

Tissue	Period	Tissue mass	Moisture	Ash	Lipid	Nitrogen
Pectoralis	Early	212(5.04) ^a	69.0(0.52) ^a	5.63(0.24) ^a	4.76(0.27) ^a	3.85(0.08) ^a
	Mid	227(3.79) ^b	68.0(0.88) ^a	4.58(0.33) ^b	4.22(0.17) ^a	4.12(0.14) ^a
	Late	226(4.69) ^b	70.0(0.48) ^a	5.59(0.30) ^{ab}	2.95(0.25) ^b	3.87(0.05) ^a
Skin	Early	341(21.8) ^a	14.9(1.78) ^a	0.43(0.08) ^a	75.6(2.31) ^a	1.40(0.21) ^a
	Mid	209(7.48) ^b	23.2(2.27) ^b	0.47(0.07) ^a	64.9(2.34) ^b	1.84(0.15) ^{ab}
	Late	215(14.4) ^b	36.3(2.06) ^c	0.53(0.05) ^a	46.0(3.39) ^c	2.31(0.16) ^b
Carcass	Early	875(19.7) ^a	55.4(1.48) ^a	4.15(0.09) ^a	22.3(1.55) ^a	2.76(0.04) ^a
	Mid	802(12.4) ^b	59.1(0.94) ^a	4.89(0.17) ^b	16.1(0.82) ^b	3.10(0.05) ^b
	Late	861(17.4) ^a	64.3(0.70) ^b	4.54(0.17) ^{ab}	10.9(0.92) ^c	3.14(0.05) ^b

TABLE 2.3. Sample size and mean concentration of nutrients (g g^{-1} OM \pm SE), fiber (g g^{-1} OM \pm SE) and energy (kJ g^{-1} \pm SE) in eelgrass (*Zostera marina*) collected during winter at Bahia San Quintin and Izembek Lagoon. An asterisk (*) denotes a significant difference in means between sites ($P < 0.05$).

	Bahia San Quintin		Izembek Lagoon	
	n	Mean	n	Mean
Organic matter*	8	0.72 (0.02)	13	0.81 (0.02)
%Nitrogen*	8	3.18 (0.09)	14	3.97 (0.13)
NDF	7	0.70 (0.01)	14	0.60 (0.04)
ADF	7	0.46 (0.01)	14	0.44 (0.03)
Hemicellulose*	7	0.24 (0.01)	14	0.16 (0.01)
Cellulose	7	0.31 (0.01)	14	0.27 (0.04)
Lignin	7	0.15 (0.02)	14	0.18 (0.01)
Starch	7	0.08 (0.01)	13	0.12 (0.05)
Gross Energy	7	14.15 (0.68)	13	13.65 (0.50)

TABLE 2.4. Energetic costs and predicted intake rates for Brant wintering in Bahia San Quintin, Baja California (BSQ) and Izembek Lagoon (IZ), Alaska.

	<u>Early to mid- winter</u>		<u>Mid to late winter</u>	
	<u>BSQ</u>	<u>IZ</u>	<u>BSQ</u>	<u>IZ</u>
Average body mass (g)	1436	1527	1508	1495
Days elapsed	36	56	74	80
Change in mass (g)	9	-186	136	121
Change in body energy (kJ d ⁻¹)	4	-134	83	-29
Tissue synthesis (kJ d ⁻¹)	3	1	156	2
Resting metabolic rate (kJ d ⁻¹)	818	850	849	892
Activity (kJ d ⁻¹)	450	468	467	490
Thermal Conductance (kJ d ⁻¹)	66	204	47	199
Body energy flux (kJ d ⁻¹ kg ⁻¹)	934	1085	1062	1078
Dietary energy (kJ d ⁻¹)	1340	1389	1602	1554
Daily intake (g DM d ⁻¹ kg ⁻¹)	129	131	147	149
Foraging window (h)	5	3	8	5
Foraging rate (g DM h ⁻¹ kg ⁻¹)	26	44	18	30

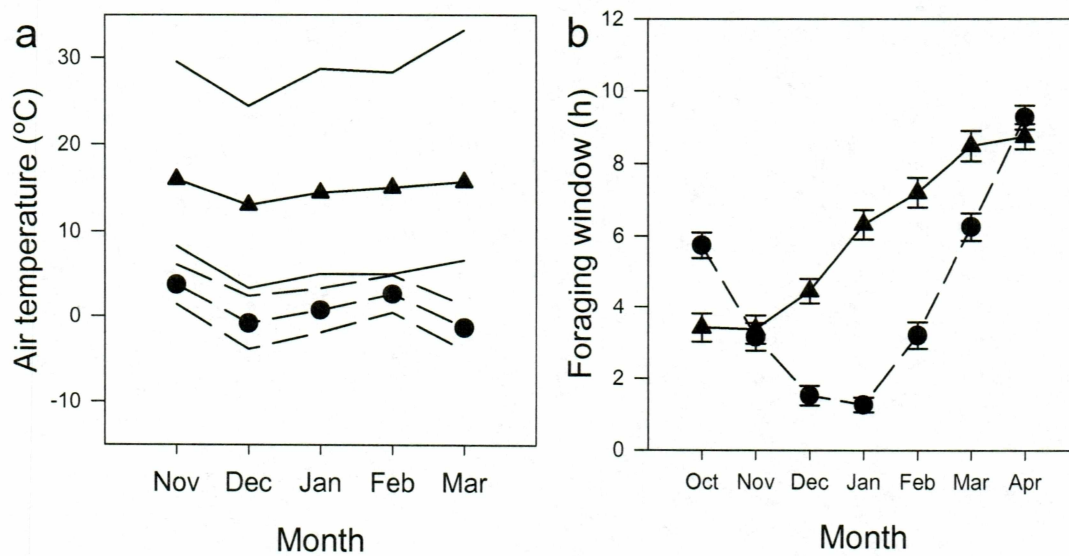


FIGURE 2.1. Mean air temperature ($^{\circ}\text{C}$) with corresponding mean maxima and minima (a) and foraging window (b; daily average of daylight hours when the mean tide height is < 0.9 m) at Izembek Lagoon (circles, dashed lines) and Bahia San Quintin (triangles, solid lines) during the winter of 2002-2003.

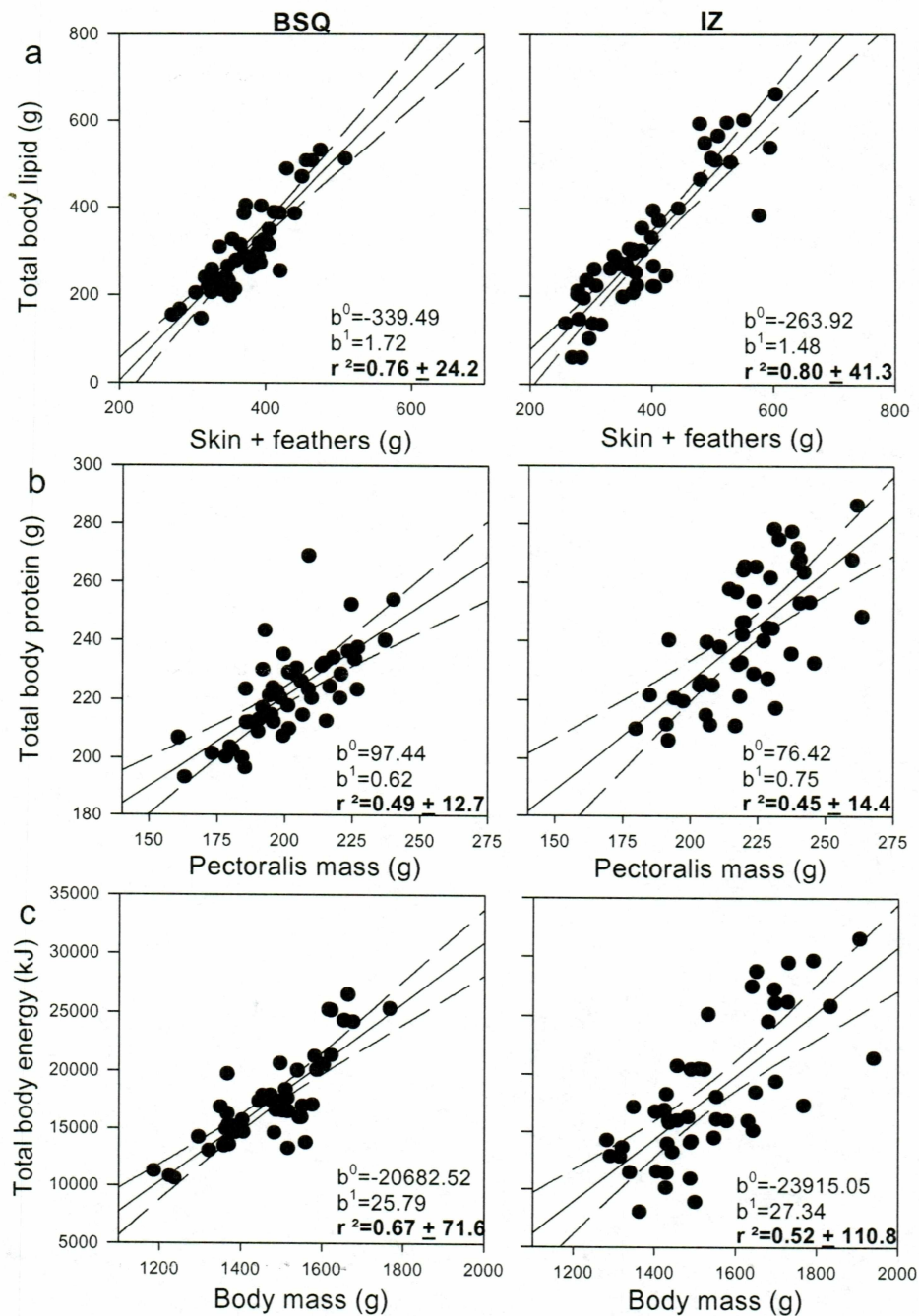


FIGURE 2.2. Relationships between morphological measures and body nutrients. Skin and body lipid (a), pectoralis and body protein (b), and body mass and total energy (c) for female Brant wintering at Izembek lagoon (IZ) and Bahia San Quintin (BSQ).

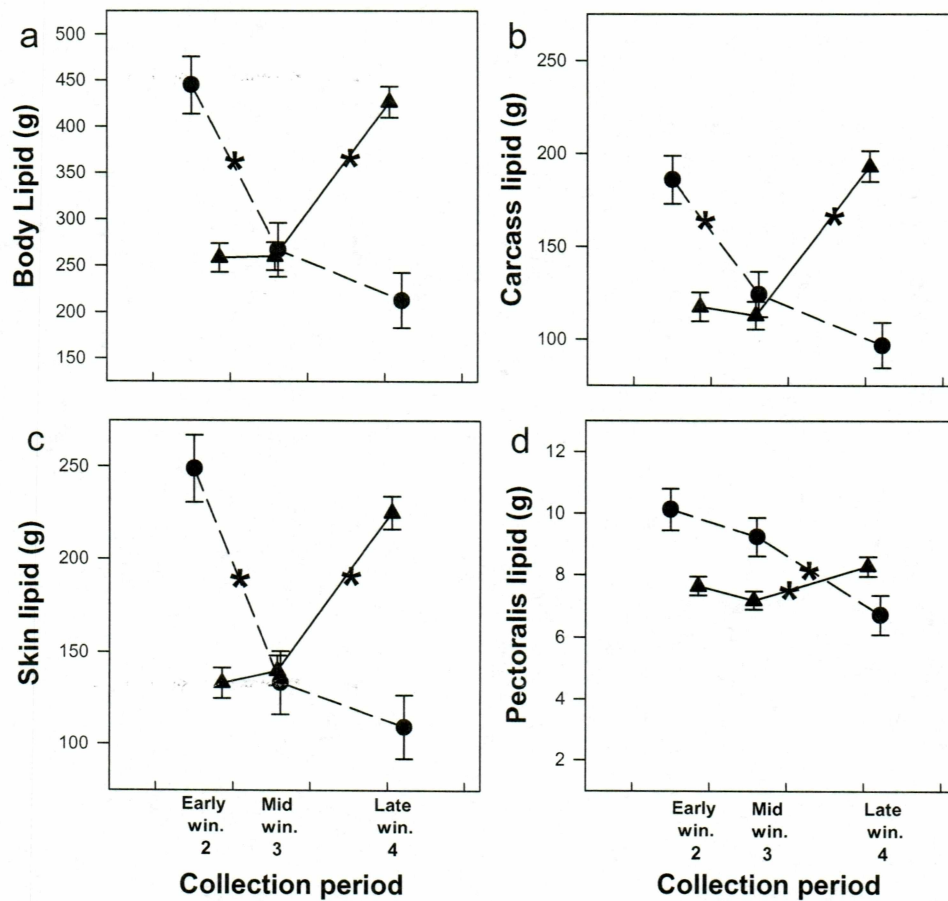


FIGURE 2.3. Lipid mass ($g \pm SE$) in the whole body (a), carcass (b), skin (c) and pectoralis muscle (d) for adult female Brant during winter at Izembek Lagoon (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

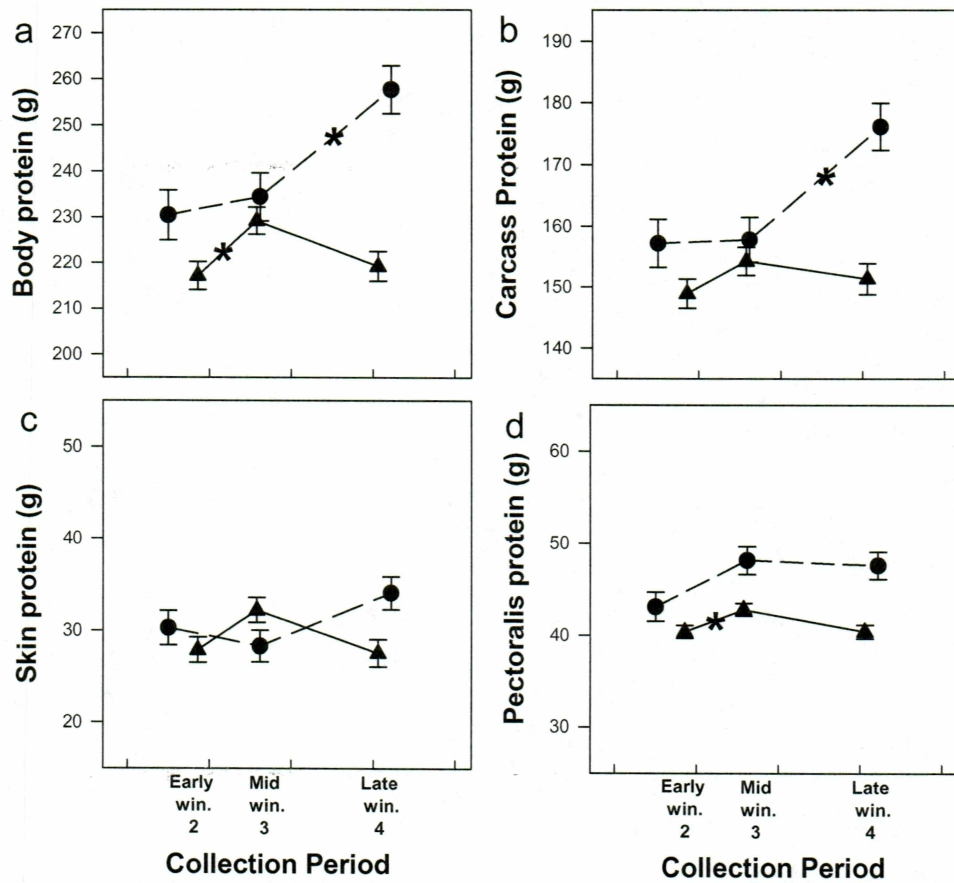


FIGURE 2.4. Protein mass ($g \pm SE$) in the whole body (a), carcass (b), skin (c) and pectoralis muscle (d) for adult female Brant during winter at Izembek Lagoon (circles, dashed lines) and winter at Bahia San Quintin (triangles, solid lines). An asterisk (*) denotes a significant change in mass between consecutive periods within a site ($P < 0.05$).

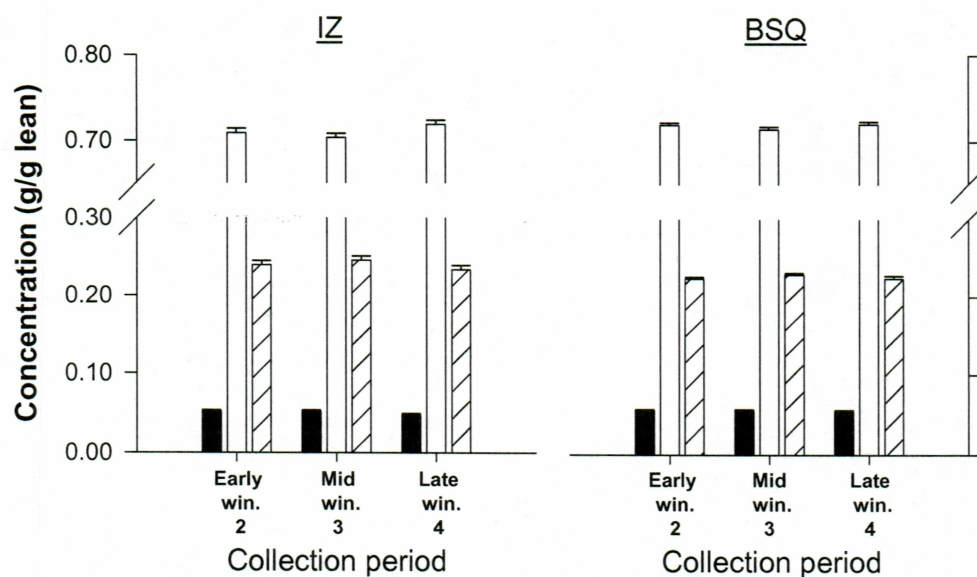


FIGURE 2.5. Whole body concentrations (g g^{-1}) in lean (lipid-free) mass of ash (black bars), moisture (white bars) and OM (hashed bars) for adult female Brant winterring at Izembek Lagoon (IZ) and Bahia San Quintin (BSQ). Concentrations were different between sites ($P < 0.05$) but similar among periods within sites ($P > 0.05$).

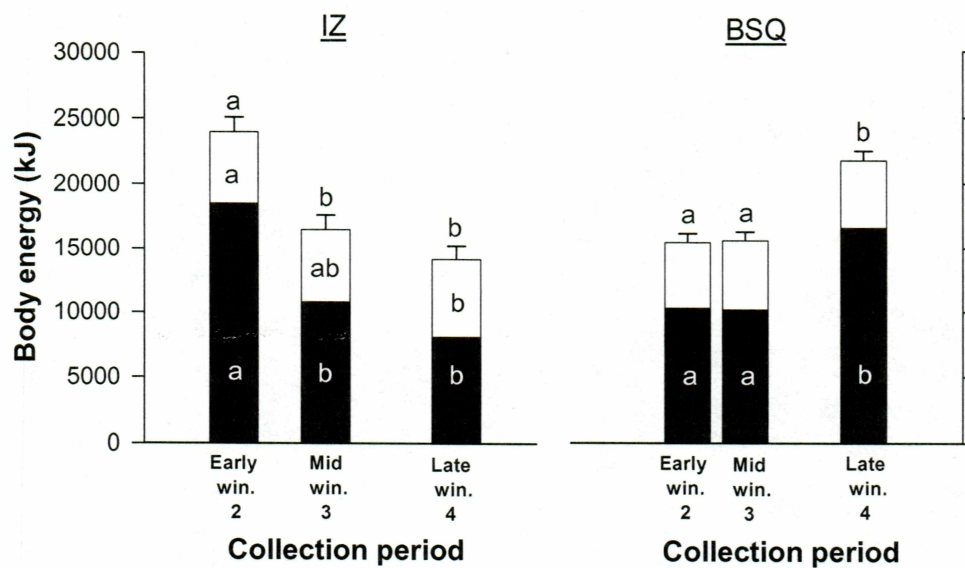


FIGURE 2.6. Total body energy (kJ) allocated to lipid (black bars) and protein (white bars) for female Brant wintering in Izembek (IZ) and Bahia San Quintin (BSQ). Bars with different letters represent a significant difference in energy content between collection periods within sites ($P < 0.05$).

CONCLUSIONS

Brant exhibit differential migration; some individuals migrate short distances between breeding areas and high latitude wintering grounds but most migrate long distances to more southern wintering grounds. Differences in total migration distance for Brant can be as great as 9,000 km. The variations in body morphology and composition exhibited by Brant wintering in Alaska and Baja California indicate that plasticity is a life history trait that enables them to employ two contrasting winter strategies: potentially breeding earlier at the risk of a severe winter versus risks associated with migrating long distances for a mild winter. The flexibility of migratory behavior exhibited by Brant suggests that costs of wintering at high latitudes and long-distance migration are similar.

Brant appear to operate under similar morphological and physiological bounds but adaptive changes in organ mass and nutrient storage took place, seasonally and geographically, within these bounds. Birds wintering in harsh climates are generally expected to maintain larger energy stores than birds in mild climates because energetic demands are less; however, overall body mass and energy storage was similar for Brant wintering in Alaska and Baja California despite dramatic differences in energetic demands. High energetic costs coupled with constraints on foraging for birds in Alaska may have prevented Brant from maintaining larger lipid stores than birds in Baja California. Lipid mass decreased in early winter for Brant in Alaska as the length of foraging window decreased. Alternatively, the high costs of migration may counter benefits of wintering in Baja California. Lipid mass for Brant in Baja California decreased after fall migration and increased before migration in the spring. The seasonal

deposition of adipose appears to favor winter residency and long-distance migration equally. Winter residency demands reliance on energy stores during times of food shortages, whereas migration requires expending energy stores for locomotion. The amount of body lipid stored and the net energy flux through the bodies of Brant were similar for both strategies because Brant in Alaska incurred high thermoregulatory cost over winter and Brant in Baja California incurred high cost of lipid synthesis prior to migration.

In addition to differences in patterns of energetic demand and lipid storage we also documented differences in morphology between sites. Brant wintering in Alaska maintained larger masses of flight muscles, feathers and nutritional organs than Brant wintering in Baja California. These differences in morphology are likely adaptations that allow Brant to survive in Alaska during the winter. Gonadal, hepatic and protein mass also increased in late winter for birds in Alaska but not for those in Baja California; suggesting that birds wintering in Alaska may be able to commence reproduction earlier in the spring than birds wintering in Baja California. Additionally, the high cost of migration may detract from reproductive investment because stored fat provides energy for both locomotion and breeding. Therefore, wintering in Alaska may be more advantageous than migration. Body mass in late winter did not reflect differences in energy storage between sites, these differences would have gone undetected if only body mass was measured.

Differences in the structural size of female Brant and historical band re-sighting data indicate that most of the birds wintering in Alaska may be Arctic-breeding

individuals. Differences in breeding origin alone are not, however, likely to explain the observed differences in body composition or morphology. Changes in tissue and nutrient masses occurred independently of structural size and birds from all breeding areas are known to winter in both Alaska and Baja California. By shortening the total distance traveled birds remaining in Alaska may decrease the risk and energetic cost associated with migration. Both Arctic and Sub-Arctic breeding Brant would likely benefit by shortening migration distance if remaining closer to breeding grounds is reproductively advantageous. Brant wintering in Alaska and breeding on the Yukon-Kuskokwim Delta travel the shortest distance (~900 km) between breeding and wintering areas and may be best suited to develop tissues for reproduction as early as possible if conditions in spring are favorable for nesting.

If survival is similar for birds wintering in Alaska and Mexico the number of Brant in Alaska will likely increase because of potential reproductive benefits of remaining closer to breeding grounds. Increases in the number of birds wintering further north may accelerate if climate change continues to produce more stable and predictable weather at high latitudes or if changes on primary wintering areas in Mexico such as, human development or El Niño events, negatively impact foraging conditions for Brant. Strong reliance on high intakes of a single natively occurring food source may make Brant especially sensitive to changes on wintering grounds. Population growth and winter survival for Brant are contingent on obtaining adequate resources to accumulate energy stores. Results of this study show that differences in the morphology and nutritional condition of Brant wintering in Alaska and Baja California are products of the

timing and magnitude of energetic costs encountered at each site. Understanding how birds cope with energetically demanding events such as migration and over-wintering, is vital in predicting avian responses to environmental change, declining food resources and habitat loss.