NUTRITIONAL CONDITION OF PACIFIC BLACK BRANT WINTERING AT THE EXTREMES OF THEIR RANGE

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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 adult female Pacific Black Brant (*Branta bernicla nigricans*) 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 daily intake rates of eelgrass were similar between sites in early winter; however, feeding time was more constrained in Alaska because of high tides and short photoperiods. Despite differences in energetic costs and foraging time, Brant wintering at both sites appeared to be in good condition. We suggest that wintering in Alaska may be more advantageous than long-distance migration if winter survival is similar between sites and constraints on foraging time do not impair body condition.

Key words: body composition, energy storage, geese, lipid, protein, winter.

Condición Nutricional de *Branta bernicla nigricans* que se Encuentran Invernando en los Extremos de su Rango de Distribución

Resumen. Las reservas endógenas de energía permiten que las aves sobrevivan condiciones climáticas adversas y de escasez de alimento durante el invierno. Documentamos los cambios en las proporciones de grasa, proteína, agua, y ceniza en el tejido corporal de hembras adultas de *Branta bernicla nigricans*. También modelamos los costos energéticos de la invernada. Las aves fueron muestreadas en los extremos de su rango de invernada: Alaska y Baja California en México. Las grasas corporales disminuyeron durante el invierno en las aves de Alaska pero aumentaron en las aves de Baja California. De manera contraria, las proteínas corporales aumentaron durante el invierno en las aves de Alaska y permanecieron estables en las aves de Baja California. Las reservas de grasa probablemente aportan energía para la migración de las aves que invernan en Baja California y aseguran la supervivencia de las aves en Alaska. Los aumentos de las proteínas corporales podrían permitir la reproducción adelantada de *B. b. nigricans* en Alaska. Los requisitos energéticos predichos fueron similares entre los dos sitios a fines del invierno pero las formas de gasto fueron diferentes. Las aves en Baja California gastaron más energía en sintetizar grasas mientras que las aves en Alaska tuvieron mayores gastos en termorregulación. Las tasas de ingestión diaria fueron similares entre los dos sitios a principios del invierno, pero la duración del periodo de forrajeo fue más restringida en Alaska debido a las mareas altas y a la reducción de las horas de luz durante el día. A pesar de las diferencias en costos energéticos y en tiempo de forrajeo, las aves que se encontraban invernando en ambos sitios parecieron estar en buenas condiciones. Sugerimos que invernar en Alaska podría ser más ventajoso que la migración de larga distancia si la supervivencia durante el invierno es parecida entre sitios y si las restricciones en el tiempo de forrajeo no afectan la condición corporal.

INTRODUCTION

Body condition can be defined as an individual's ability to meet present and future energy requirements (Owen and Cook 1977). Therefore, nutritional condition is related to the amount of energy stored in the body as lipid and protein. Many species of waterfowl wintering in temperate areas maintain large energy stores of lipid and protein (Raveling 1979, Moorman et al. 1992); however, winter energy stores are often smaller than premigration stores (Biebach 1996). Adverse winter conditions (low temperatures, frequent storms, short photoperiod, and low food abundance) can deplete energy stores by constraining food intake and increasing energetic demand (Lovvorn 1994). 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 a low cost of living and require relatively small 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 wintering in different climates may vary their strategy for storage and use of energy. In this study, we document changes in tissue composition and energy storage of 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 estimates of air temperature, time available for foraging, and diet quality to model energetic costs and predict food intake rates for Brant wintering in Alaska and Baja California. Comparison of estimated energy expenditure between sites allows further examination of the relative costs and benefits of wintering at each site.

Brant are an ideal species for studies of nutritional condition because they rely almost exclusively on a single native food source (eelgrass [*Zostera marina*]) throughout their nonbreeding range, and show high winter site fidelity (Reed, Cooch et al. 1998; DHW, unpubl. data). Wintering populations of Brant are distributed along the Pacific coast of North America between Alaska and Baja California, Mexico (55–21°N). Brant from all major arctic and subarctic 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 here to winter, while most migrate an additional 5000 km to coastal bays of Baja California (Reed, Ward et al. 1998, Ward et al. 2005). However, Brant, like some other geese in North America (Abraham et al. 2005, Gauthier et al. 2005), are undergoing a northward shift in winter distribution that appears to be related to changing environmental conditions (Ward et al. 2005). Mather (2005) examined morphometric parameters of Brant wintering in Alaska and Baja California and showed that changes in winter body mass varied by location. Brant in Alaska lost mass from early to mid winter, while those in Baja California maintained mass during the same period. Brant at both sites subsequently gained mass in late winter. Mass gains by Brant in Alaska were due to an increase in organ mass, whereas birds in Baja California gained visceral adipose mass (Mather 2005).

We predicted that winter morphology, such as the mass of the whole body or its component tissues, would not equally reflect stores of lipid, protein, and energy at both sites, and furthermore that lean tissue composition would likely be conserved while lipid and protein mass changed at each site. We also predicted that energetic costs and constraints on food intake would be higher in Alaska than in Baja California and likely have an influence on 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. Only adult females were used in the following analyses; males and juveniles were not included because of small or unequal sample sizes and potential differences in nutritional strategies. Brant were collected by shooting them while they were feeding or roosting. Decoys were not used during collec-

tion because decoys may attract a higher pro-
portion of juveniles or birds in poor condition
(Greenwood et al. 1986, Reinecke and Shaiffer
1988). Birds were collected during three peri-
ods: early winter (IZ: 16–30 November, $n = 16$;
BSQ: 6–15 December, $n = 17$), midwinter (IZ:
12–17 January, $n = 16$; BSQ: 10–17 January,
$n = 17$), and late winter (IZ: 31 March–7 April,
$n = 17$; BSQ: 28–29 March, $n = 14$). The early
winter collection at BSQ began later than at IZ
due to permit delays. We assumed that collected
birds would have remained at IZ or BSQ
because Brant have high winter site fidelity
(Reed, Cooch et al. 1998, DHW, unpubl. data).
Therefore, differences in body composition
among birds collected at each site were assumed
to reflect responses to local conditions rather
than movements of birds during winter. The
timing of collections was based on the average
date of migration of Brant at each location
(Reed et al. 1989, Ward and Stehn 1989; DHW
and DDM, unpubl. data). Average date of peak
fall departure of birds from IZ is 6 November
(95% CI = 4–8 November) and the average date
of spring arrival at IZ is 14 April (95% CI =
10–18 April; C. Dau, U.S. Fish and Wildlife
Service, unpubl. data). The number of late
migrants in our early winter sample was likely
small because fall migration is highly synchro-
nous; the majority of birds depart within days
of each other to take advantage of favorable
wind conditions (Dau 1992). Furthermore, any
effect of late migrants on body composition of
birds in early winter at IZ would be minimal
because mass of the body and visceral adipose
was similar between fall staging (late October)
and early winter at IZ (Mather 2005) and body
mass did not vary significantly with date within
periods (DDM, unpubl. data).

ENVIRONMENTAL MEASURES

Hourly air temperatures for the winter of 2002–
2003 were obtained from the National Oceanic
and Atmospheric Administration weather sta-
tion in Cold Bay, Alaska, located approximate-
ly 12 km southeast of Izembek Lagoon. Air
temperatures at Bahia San Quintin for the
study period were recorded every 30 min with
data loggers located near the middle of the bay
(A. Cabello, Universidad Autónoma de Baja
California, unpubl. data). We calculated mean
monthly air temperatures based on daily
averages.

Brant feed primarily on intertidal eelgrass at
both sites. Foraging Brant do not dive;
therefore, food intake is restricted by high
water levels. Most eelgrass beds are submerged
when tide height exceeds 1 m of mean lower low
water at both sites (Ward and Stehn 1989,
Ward et al. 1997). Under the assumption that
Brant feed primarily during daylight hours at
both locations, we calculated the amount of
time available for foraging (foraging window)
based on the mean number of daylight hours
when the tide height was <1 m of mean lower
low water. Hours of daylight were determined
from predictions of civil twilight at each site
based on the U.S. Naval Observatory website
(⟨http://aa.usno.navy.mil/data/docs/RS_OneDay.
html⟩). Water depths were estimated from
predicted tides for Grant Point at Izembek
Lagoon and for Bahia San Quintin between 1
October 2002 and 30 April 2003 using Tides &
Currents version 2.1 (Nautical Software 1995).
Our estimate of the foraging window may have
underestimated total time available for feeding,
as Brant are known to feed on detrital eelgrass
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). However, it is
unlikely that nocturnal and surface foraging
can totally replace diurnal feeding on exposed
eelgrass because rates of food intake (based on
indirect methods) at Izembek Lagoon were
estimated to decrease by 30%–80% outside the
foraging window (Ward and Stehn 1989).

MEASURES OF BODY COMPOSITION

We weighed freshly killed Brant to 0.01 g using
an electronic balance. Age (adult or yearling)
and sex were determined by plumage character-
istics and cloacal examination, respectively. Sex
was later confirmed through inspection of
internal reproductive organs. Following the
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 at the study site to
minimize desiccation and degradation of tis-
sues.

We thawed frozen carcasses in a refrigerator
prior to dissection. Feathers were removed with
electric shears (Shearmaster, Oster, McMinn-
ville, Tennessee) and by manual plucking. We

removed skins and adherent adipose tissue to the elbow joint and dissected the pectoralis muscles and the digestive tract from the carcass. Contents of the digestive tract were removed and stored frozen for subsequent analysis before analyzing the tissues. 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 4.5 mm 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. Lipid was extracted with petroleum ether (Dobush et al. 1985) using a modified Soxhlet procedure (Model HT6 Soxtec, Tecator, Foss North America, Silver Spring, Maryland). We determined nitrogen content using an elemental analyzer (Model CNS 2000, Leco, St. Joseph, Michigan.). Ash content was ascertained by combustion at 550°C in a muffle furnace for 8 hr.

We calculated the mass of lipid, nitrogen (N), and ash as the product of the dry mass (g) of each fraction and the concentration in dry matter (e.g., g lipid g DM^{-1}). Organic matter (OM) was defined as 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 calculated as the average concentration of N in each fraction: 6.50 g N g^{-1} lean OM (carcass), 5.35 g N g^{-1} lean OM (muscle), and 7.50 g N g^{-1} lean OM (skin). We calculated 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: 22.5 kJ 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 ANALYSIS

We collected eelgrass samples from three to five locations at each study area during each of the collection periods. Our sample size was not

sufficient to evaluate site-specific changes in eelgrass composition, therefore the samples were pooled by location to describe the average composition of the diet at each site. We rinsed eelgrass samples to remove sediments and attached organisms, and removed and discarded the rhizomes, which Brant do not eat (Ward and Stehn 1989, Reed, Ward et al. 1998). Leaves were stored frozen in plastic bags for analysis. Samples of eelgrass and contents of the esophagus and colon were thawed and weighed to ±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, 1.25 mm wire mesh, A. H. Thomas, Philadelphia, PA) for chemical analysis. Fiber fractions were isolated sequentially (cellulose, hemicellulose, and lignin) following the methods of Van Soest et al. (1991). Neutral detergent fiber was extracted with Na_2SO_3 and without amylase. Hemicellulose was calculated as the difference between neutral detergent fiber and acid detergent fiber, and cellulose content as the difference between acid detergent fiber and lignin. We determined N content using an elemental analyzer (Model no. CNS 2000, Leco, St. Joseph, Michigan). We calculated crude protein by multiplying N content by 6.25 (Robbins 1993). The residue of organic matter after accounting for fiber fractions and crude protein was primarily an estimate of starch or nonstructural carbohydrates, because leaves of eelgrass have low lipid content (5% of dry matter; Ward and Stehn 1989, Dawes and Guiry 1992).

We calculated digestibility of eelgrass for birds from IZ only because esophageal contents of birds at BSQ were insufficient for chemical analysis. Nutrient digestibility of organic matter was calculated from the manganese (Mn) content of digestive material from the esophagus and colon as follows:

$$\left(1 - \left(\frac{(\text{esophageal Mn/nutrient content})}{(\text{digestive Mn/nutrient content})}\right)\right).$$

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 used estimates of daily energy expended (kJ day^{-1} kg^{-1}) for body maintenance, activity,

thermoregulation, and net change in body energy between periods to derive rates of food intake for Brant between early and mid winter and mid and late winter at each site. We calculated maintenance energy expenditure from average body mass (kg) and the rate of metabolizable energy ingested by yearling birds during late winter and spring under thermoneutral conditions (567 kJ day^{-1} kg^{-1} 20°C; Sedinger et al. 1992). Predicted costs of maintenance were standardized to the average lean body mass at each site. Activity costs (e.g., feeding, swimming, agonistic behaviors) during each interval were estimated as a percentage above maintenance (75%–78% at IZ; Ward and Stehn 1989, and 67%–85% at BSQ; DHW, unpubl. data) based on daily time activity budgets of flocks of wild Brant from December through March at IZ. Costs of thermal conductance were based on relationships between body mass (M) and oxygen consumption of nonpasserines as follows (Aschoff 1981):

$$\text{Active phase}(\text{mL O}_2 \text{ hr}^{-1}) = 33.4(M^{-0.48}),$$

$$\text{Passive phase}(\text{mL O}_2 \text{ hr}^{-1}) = 16.9(M^{-0.58}).$$

Oxygen consumption was converted to energy expended with a respiratory quotient that was estimated at 20.92 kJ L^{-1} 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) between the mean daily air temperature and 20°C (temperature for maintenance energy expenditure) were calculated for each interval and site. Daily cost of thermal conductance (kJ day^{-1}) was estimated as: T(12(active phase + passive phase)). 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 × energy content; King 1973). We calculated total energy flux through the body (kJ^{-1} day^{-1} kg^{-1}) as the sum of maintenance, activity, thermal conductance, tissue synthesis, and change in body energy. Dietary energy intake (kJ day^{-1}) was estimated as the energy flux corrected for the net contribution or deposition of energy in the body. We calculated dry matter intake (g DM day^{-1} kg^{-1}) by dividing dietary energy intake by the digestible energy content of the diet and by the digestible energy content of the diet and average body mass. We calculated foraging rate (g DM hr^{-1} kg^{-1}) by dividing dry matter intake by the number of hours in the foraging window during each interval.

STATISTICAL ANALYSES

We assessed the effects of site and winter 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 (g ± SE) from the ANCOVA and are therefore corrected for structural size. Nutrient concentrations (g g^{-1} ± SE) were arcsine-transformed to meet assumptions of normality for ANOVA and were not adjusted for structural size. Mean energy content (kJ g^{-1}) in the body was compared using ANOVA with site and period as independent factors. We used Bonferroni's adjustment for multiple comparisons among periods. Although we used a cross-sectional design we assumed that changes in body composition represented changes within individuals in the population. We also assumed that changes in body composition between periods were linear and were average daily changes in composition over the long intervals of winter (36–80 days). Although birds can gain and lose both fat and protein rapidly, these nonlinear changes are typically short-lived (LeMaho et al. 1981, Barboza and Hume 2006) and thus not representative of the longer response to environmental conditions. All statistical analyses were conducted using SYSTAT 10.2 (SYSTAT Software 2002) with significance accepted at α = 0.05.

RESULTS

ENVIRONMENTAL DATA

Mean monthly air temperature between November and April was 1°C at IZ and 15°C at BSQ (Fig. 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. The combination of decreasing day length and frequency of low tides at IZ greatly reduced the length of the foraging window at this site. Only 21% of December low tides occurred during daylight hours at IZ, whereas low tides were more equally distributed between
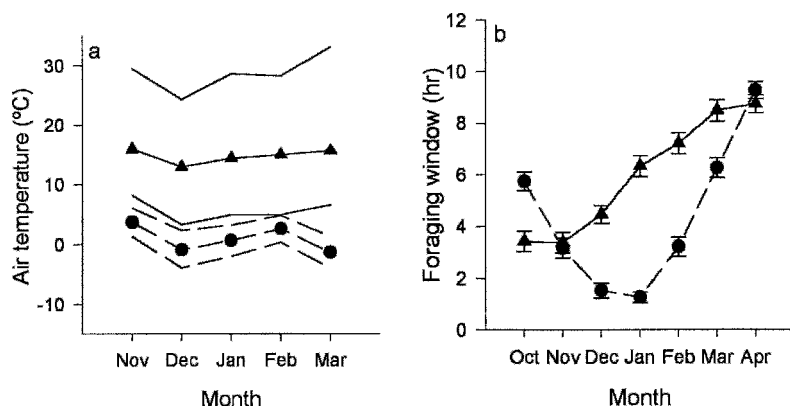
FIGURE 1.   Mean air temperature (°C) with corresponding mean maxima and minima (a) and foraging window (daily average number of daylight hours ±SE when the mean tide height is <1.0 m of mean lower low water; b) at Izembek Lagoon, Alaska (circles, dashed lines) and Bahia San Quintin, Baja California (triangles, solid lines) during the winter of 2002–2003.

night (55%) and day (45%) at BSQ. The duration of the foraging window at IZ decreased from 5.7 ± 0.4 hr in October to 1.3 ± 0.2 hr in January (Fig. 1b). Foraging windows were shorter at IZ than at BSQ from December to March. Between January and early April, the foraging window increased at both sites, reaching >9 hr at IZ in April when birds began staging.

BODY COMPOSITION

The greatest concentrations of lipid were found in the skin and carcass and accounted for 52% and 45% of total body lipid, respectively. The pattern of change in body lipid reflected those in the skin and carcass at each site (Fig. 2a–c). Between early and mid winter, body lipid declined at IZ (-178 ± 42 g, $P < 0.001$, Fig. 2a) and remained stable at BSQ. Between mid and late winter, birds at IZ maintained body lipid while those at BSQ gained lipid prior to migration ($+166 \pm 22$ g, $P < 0.001$). Between mid and late winter, pectoral lipid also declined at IZ (-3 ± 1 g, $P = 0.03$) and increased slightly at BSQ ($+1 \pm 0.4$ g, $P = 0.05$; Fig. 2d). The midwinter period appears to be a pivotal time when lipid masses in the whole body, carcass, and skin were similar between sites. During winter, the mean overall (all periods combined) mass of body lipid was similar at both sites (310 ± 18 g BSQ vs. 301 ± 18 g IZ). However, the variation in mass of lipid stores was nearly two-fold greater for birds at IZ than at BSQ.

The greatest concentrations of protein were found in the carcass and pectoralis muscles, which accounted for 68% and 19% of total body protein, respectively. Protein mass in the body and carcass increased between early and late winter at IZ ($P < 0.001$), but was similar between periods at BSQ (Fig. 3a, b). Protein in the skin was similar among all periods at both sites (Fig. 3c). Protein in the pectoralis muscles was also similar among periods at both sites (Fig 3d); however, the mean overall mass of pectoral protein was greater at IZ than at BSQ (46 ± 2 g vs. 41 ± 1 g, $P < 0.001$). The mean overall mass of lipid in the pectoralis muscles was also greater at IZ than BSQ (9 ± 0.3 g vs. 8 ± 0.6 g, $P = 0.02$; Fig. 2d). Mean overall protein mass was greater at IZ than at BSQ in the body (241 ± 5 g vs. 223 ± 3 g respectively, $P < 0.001$) and in the carcass (164 ± 4 g vs. 156 ± 2 g, $P < 0.001$), but similar between sites in the skin.

Composition of lean body tissues remained stable among periods at both sites; therefore, any difference in lean mass was not due to changes in composition of the fat-free tissue within sites. The overall composition of lean tissues did, however, differ between sites. Concentrations of ash ($5.6\% \pm 0.1\%$ at BSQ, $5.1\% \pm 0.1\%$ at IZ; $P < 0.001$) and moisture ($71.9\% \pm 0.2\%$ at BSQ, $71.1\% \pm 0.2\%$ at IZ; $P = 0.02$) in the lean body were greater at BSQ than at IZ, and concentrations of organic matter were greater at IZ ($23.9\% \pm 0.5\%$) than at BSQ ($22.6\% \pm 0.2\%$; $P < 0.001$).
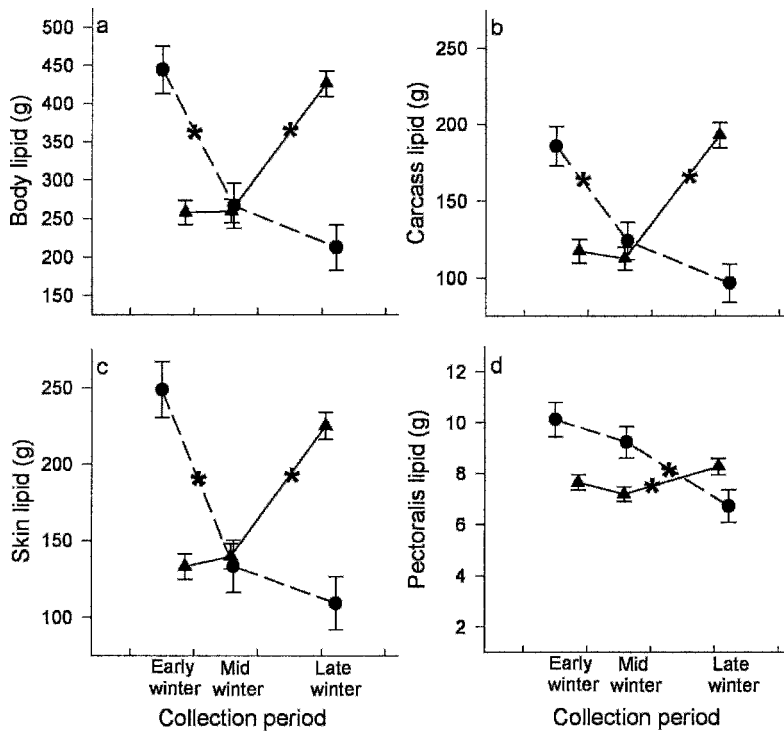
FIGURE 2.   Lipid mass (g ± SE) in the whole body (a), carcass (b), skin (c), and pectoralis muscle (d) for adult female Pacific Black Brant at Izembek Lagoon, Alaska (IZ; circles, dashed lines) and Bahia San Quintin, Baja California (BSQ; triangles, solid lines) during early ($n = 16$ IZ, $n = 17$ BSQ), mid ($n = 16$ IZ, $n = 17$ BSQ) and late winter ($n = 17$ IZ, $n = 14$ BSQ). Gradations of time are marked on the horizontal axes at intervals of 25 days. An asterisk (*) denotes a significant change in mass between consecutive periods within a site (ANCOVA: $P < 0.05$).

Lipid contributed 57%–77% of total energy in the body during winter (Fig. 4). The lowest proportion of body energy from lipid (57%) was for birds at IZ in late winter. Changes in energy derived from lipid followed patterns for total body energy. Total body energy decreased at IZ ($P < 0.001$; Fig. 4) but increased at BSQ ($P < 0.001$) over the winter. Energy from protein increased between early and late winter for birds at IZ ($P = 0.002$) but remained stable for birds at BSQ.

FOOD AND ENERGETICS MODEL

Eelgrass collected at IZ contained more organic matter and nitrogen ($P < 0.001$) but less hemicellulose than eelgrass collected at BSQ ($P < 0.001$; Table 1). The estimated overall gross energy content was similar for plants at both sites. Digestibility of gross energy and organic matter was estimated at 51% ± 14% and 47% ± 17%, respectively, for birds at IZ.

Average body mass was relatively consistent between IZ and BSQ within each interval and resulted in similar predictions of energy required for maintenance of Brant at both sites (Table 2). Total energy flux through the body was similar between sites but avenues of energy expenditure differed between IZ and BSQ. 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 costs of thermal conductance (Table 2). Net loss of body energy at IZ reduced dietary demands for energy throughout winter, while demands for Brant at BSQ were higher during the mid and late winter intervals because of the cost of tissue (lipid) synthesis (Table 2). Predicted daily intake rates of dry matter at BSQ were similar to those for IZ within each interval (Table 2); however, daily intake rates increased after midwinter at IZ. The short foraging window
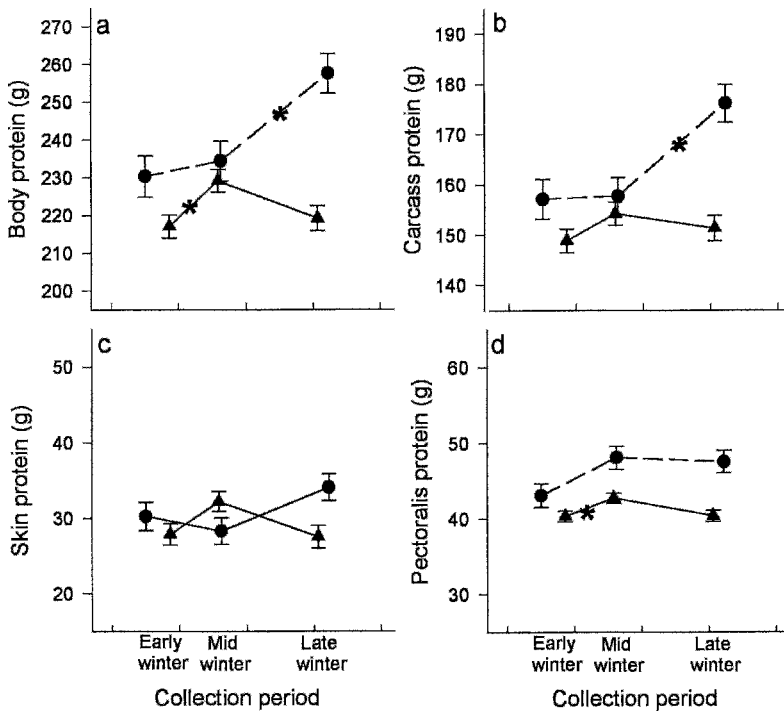
FIGURE 3. Protein mass (g ± SE) in the whole body (a), carcass (b), skin (c), and pectoralis muscle (d) for adult female Pacific Black Brant at Izembek Lagoon, Alaska (IZ; circles, dashed lines) and Bahia San Quintin, Baja California (BSQ; triangles, solid lines) during early (n = 16 IZ, n = 17 BSQ), mid (n = 16 IZ, n = 17 BSQ) and late winter (n = 17 IZ, n = 14 BSQ). Gradations of time are marked on the horizontal axes at intervals of 25 days. An asterisk (*) denotes a significant change in mass between consecutive periods within a site (ANCOVA: $P < 0.05$).
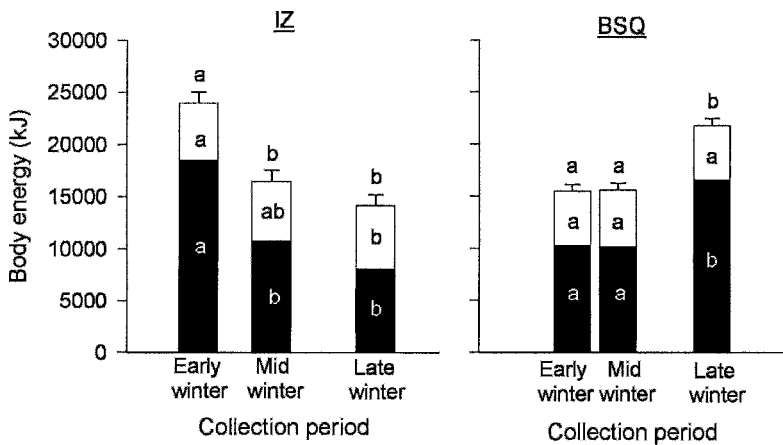
FIGURE 4. Total body energy (kJ) from lipid (black bars) and protein (white bars) for adult female Pacific Black Brant wintering at Izembek Lagoon, Alaska (IZ) and Bahia San Quintin, Baja California (BSQ) during early (n = 16 IZ, n = 17 BSQ), mid (n = 16 IZ, n = 17 BSQ) and late winter (n = 17 IZ, n = 14 BSQ). Bars with different letters represent a significant difference in energy content between collection periods within sites (ANOVA: $P < 0.05$). Spacing of the bars along the horizontal axis reflects the number of days elapsed between collection periods.

TABLE 1.   Sample size (*n*) and mean concentration of nutrients (g 100 g^{-1} OM ± SE), fiber (g 100 g^{-1} OM ± SE), and energy (kJ g^{-1} ± SE) in eelgrass (*Zostera marina*) collected in winter at Bahia San Quintin, Baja California and Izembek Lagoon, Alaska. An asterisk (*) denotes a significant difference in means between sites (ANOVA: *P* < 0.05).

	Bahia San Quintin		Izembek Lagoon	
	n	Mean ± SE	*n*	Mean ± SE
Organic matter*	8	71.9 ± 1.5	13	81.3 ± 2.3
Nitrogen*	8	3.2 ± 0.1	14	4.0 ± 0.1
Neutral detergent fiber	7	70.1 ± 0.9	14	60.0 ± 3.6
Acid detergent fiber	7	45.6 ± 1.4	14	44.3 ± 3.2
Hemicellulose*	7	24.5 ± 0.8	14	15.7 ± 1.1
Cellulose	7	30.9 ± 1.0	14	26.7 ± 3.5
Lignin	7	14.7 ± 2.0	14	17.6 ± 1.3
Starch	7	7.6 ± 0.8	13	12.2 ± 5.5
Gross energy	7	14.15 ± 0.68	13	13.65 ± 0.50

during winter at IZ resulted in higher predicted rates of foraging by Brant at IZ than at BSQ (Table 2).

DISCUSSION

Declining food resources and deteriorating environmental conditions are often associated with timing of fall migration (Berthold 2001). Movements of Brant at Izembek Lagoon coincided with changes in length of the foraging window and weather patterns. Mean date of fall departure from Izembek Lagoon (6 November) coincided with declining air temperature, day length, and frequency of low tides for foraging (Ward and Stehn 1989, this study). At Izembek Lagoon, the foraging window was longer in October when peak numbers of staging Brant

were present than in late November when most birds had departed. Premigratory body mass gains coincided with increases in the foraging window at Bahia San Quintin. Migrants also returned to Izembek Lagoon for spring staging (mean arrival = 14 April) when the foraging window was long (>9 hr).

Predicted costs of maintenance for wintering Brant were similar in Alaska and Baja California; however, the costs of thermoregulation were greater in the consistently cold conditions at Izembek Lagoon than in the relatively mild conditions at Bahia San Quintin. Although convective loss of heat in flowing water or air contributes to thermal demands, the simplest predictor of heat loss is conductance. Thermal conductance measures heat exchange between the body and the environment; as the temper-

TABLE 2.   Estimated energetic costs and rates of food intake for adult female Pacific Black Brant wintering in Bahia San Quintin, Baja California (BSQ) and Izembek Lagoon, Alaska (IZ).

	Early to mid winter		Mid to late winter	
	BSQ	IZ	BSQ	IZ
Average body mass (g)	1436	1527	1508	1495
Days elapsed between collections	36	56	74	80
Change in mass (g)	9	−186	136	121
Maintenance (kJ day^{-1})	818	850	849	892
Change in body energy (kJ day^{-1})	4	−134	83	−29
Activity (kJ day^{-1})	696	637	567	692
Thermal conductance (kJ day^{-1})	66	204	47	199
Tissue synthesis (kJ day^{-1})	3	1	156	2
Body energy flux (kJ day^{-1} kg^{-1})	1105	1196	1129	1213
Dietary energy (kJ day^{-1})	1586	1558	1702	1755
Daily intake (g DM day^{-1} kg^{-1})	153	147	156	169
Foraging window (hr)	6	3	8	5
Foraging rate (g DM hr^{-1} kg^{-1})	26	49	20	34

ature differential increases in the cold, so does the cost of maintaining core body temperature (McNab 2002). During our study, average daily air 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 Lagoon than at Bahia San Quintin. Our estimated cost of thermoregulation is probably biased low as we did not account for convective energy loss. Wind speeds at Izembek Lagoon averaged 26 kph during winter and were typically greater than those at Baja San Quintin (mean = 12 kph). High winds in Alaska could increase not only heat loss but also energy expenditure during swimming and flight.

Despite differences in thermoregulatory demands, dietary energy requirements for Brant were similar between sites within each interval. Low costs of thermoregulation for migrants at Bahia San Quintin were partially offset by high costs of premigratory lipid storage during late winter. Brant in Bahia San Quintin gained 163 g (2.2 g day^{-1}) of lipid between mid and late winter, which required additional energy expenditure similar to estimated costs of thermal conductance for Brant at Izembek Lagoon.

Birds with high energy demands require a lot of food (Dugan et al. 1981). The abundance of eelgrass in both Izembek Lagoon and Bahia San Quintin is high and not likely a limiting factor. Above-ground biomass is higher at IZ (187 g m²) than at BSQ (79 g m²; McRoy 1970, Poumiant-Tapia and Ibarra-Obando 1999); however, foraging conditions at Izembek Lagoon decline from fall to midwinter due to decreasing air temperatures and photoperiod coupled with less frequent low tides. Eelgrass biomass also declines over winter; however, biomass would decline similarly at both sites (McRoy 1970, Cabello-Pasini et. al. 2003). Our predicted average daily consumption of eelgrass (g of dry matter) for Pacific Black Brant (233 g day^{-1}) is greater than estimates for Dark-bellied Brent (*B. b. bernicla*) geese (100–122 g day^{-1}) in winter and similar to estimates for Brent Geese that gain mass during staging (270 g day^{-1}; Drent et al. 1981). We believe that 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.

The ability to process large quantities of food is ultimately limited by the capacity of the digestive system and the speed of digestion (Karasov 1990, Barboza and Hume 2006). In our model, foraging is compressed into short foraging windows in Alaska in early winter, resulting in a very high estimated foraging rate (49 g kg^{-1} hr^{-1}). It is unlikely that Brant can sustain this foraging rate, because fasted Brant only resume feeding at 21.9 g kg^{-1} hr^{-1} when held at thermoneutral conditions in captivity (PSB, unpubl. data). Predicted foraging rates are most sensitive to changes in the length of the foraging window. Brant could increase the amount of time spent foraging by feeding outside our calculated foraging window; however, intake rates would be low (Ward and Stehn 1989) and foraging under less optimal conditions may not be energetically efficient. For example, during extremely cold temperatures waterfowl often reduce activity because the costs of foraging exceed energy gains (Paulus 1988). This may explain why Brant at Izembek Lagoon have been observed rafting together and sleeping during periods of freezing weather and high tides (C. Dau and DHW, pers. obs.). Some birds switch to alternative food sources to increase energy intake (McLandress and Raveling 1981); however, there are no abundant sources of alternative foods for Brant at our study areas (Kramer 1976, Ward and Stehn 1989, Ward et al. 1997). The depletion of lipid stores between early and mid winter in birds at Izembek Lagoon is likely caused by the combined effect of three factors: endogenous regulation, high energy demand, and insufficient feeding time. Waterfowl lose mass in winter when fed ad libitum but cold weather and interrupted feeding often increase mass loss (Lovvorn 1994, Barboza and Jorde 2002). Birds may regain mass when weather conditions ameliorate or foraging time increases (Barboza and Jorde 2001). After losing lipid in midwinter, Brant at Izembek Lagoon may be unable to regain lipid in late winter due to continued cold weather and restricted foraging time. Lipid stores accumulated during fall staging and early winter may ultimately affect the probability of winter survival for Brant at Izembek Lagoon (Haramis et al. 1986).

Changes in body composition reflect the average energy and nutrient balances of Brant at each site. Brant in Bahia San Quintin gained

total body energy and were in positive energy balance before migration. Conversely, birds at Izembek Lagoon lost total body energy but gained body protein, that is, negative lipid energy balance coincided with positive protein balance. The higher nitrogen content of eelgrass found at Izembek Lagoon than at Bahia San Quintin may favor increased protein storage for birds wintering in Alaska. Alternatively, protein storage in late winter may indicate early preparation for breeding. Ankney (1984) suggested that prelaying female Brant nesting in the Canadian Arctic may use body protein stores for ovarian development, and that these stores may also contribute up to 70% of the protein in an average clutch of eggs. Brant at Izembek Lagoon showed increased ovarian development in late winter (Mather 2005), which supports the idea that these birds are beginning to prepare for breeding earlier than birds wintering at Bahia San Quintin. Additionally, levels of body fat were higher for Brant at Izembek Lagoon during late winter (13%; this study) than for prelaying Brant on the breeding grounds (9%; Ankney 1984). Therefore, it appears that Brant at Izembek Lagoon in late winter have sufficient stores of lipid and protein for either migration or breeding.

Despite differences in foraging conditions and energy demands, Brant at both sites appeared to be in good condition. Mean percent body fat for wintering Brant ranged from 13% 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 they have such disparate wintering strategies? Migration should occur when the risks of overwintering are greater then those of migrating (Lack 1968). In addition to climatic differences between wintering sites, there are also differences in predator abundance and hunting pressure. The concentration of eagles is higher at Izembek Lagoon than at Bahia San Quintin; eagles are known predators of Brant and may also indirectly affect survival by increasing energy expended for predator avoidance behaviors (e.g., vigilance and flight). However, sport hunting pressure and human disturbance are higher at Bahia San Quintin than at Izembek Lagoon during winter, which can also increase mortality through direct and indirect effects. Comparative data on survival rates for Brant wintering at Izembek Lagoon and Bahia San Quintin are lacking, and detailed studies of activity budgets and site-specific survival rates are needed to accurately determine how these factors affect survival and energy expenditure of Brant. Nevertheless, we believe mortality risks are likely to be higher for Brant wintering along the Alaska Peninsula because these birds are exposed to a harsher and more uncertain environment. The large variation in lipid stores among individuals in midwinter at Izembek Lagoon may be suggestive of the greater environmental stochasticity of this northern-latitude wintering area. Brant at Izembek Lagoon risk periods of food shortage during midwinter when severe cold weather causes ice to cover intertidal habitats and prevents birds from feeding (C. Dau and DHW, unpubl. data). If food limitations are prolonged and Brant must move to another location or face starvation, the closest beds of ice-free intertidal eelgrass are found on Kodiak and Queen Charlotte islands, 600 and 1800 km away, respectively. Depleted lipid stores prevent birds at Izembek Lagoon from flying such long distances in search of food.

Environmental stochasticity may maintain heritable variation in life-history traits. Brant wintering in Alaska may incur a fitness advantage in some years and a disadvantage in others. Birds may be able to assess this variation and respond accordingly by migrating or remaining in Alaska. Alternatively, the two populations of wintering Brant may be functionally separate and may simply vary in relative abundance in relation to this environmental stochasticity. Our study occurred over a single winter season and during a period of relatively mild climatic conditions in Alaska during the last 25 years (C. Dau and DHW, unpubl. data). If climatic conditions continue to ameliorate and food abundance and availability stays constant, then the energetic cost of wintering at Izembek Lagoon as predicted by our model will likely decline. Management in winter habitats should concentrate on protecting preferred foraging areas for Brant and limiting disturbance during low tides when Brant are most actively feeding.

ACKNOWLEDGMENTS

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