Activity budgets, daily energy expenditure and energetic model of Black Brant *Branta bernicla nigricans* during winter and spring along the Lower Alaska Peninsula

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Abstract

Black Brant *Branta bernicla nigricans* have one of the most specialised of goose diets during the non-breeding season, utilising coastal habitats to up-end and feed on dense beds of intertidal Common Eelgrass *Zostera marina*. Past studies suggested that Black Brant may not reach energetic requirements during diurnal foraging on eelgrass beds and must use alternate, less energetically beneficial foraging strategies (*e.g.* searching for and consuming sparse drifting eelgrass and night-time eelgrass bed foraging) to meet energy demands. Time-activity budgets and daily energy expenditure (DEE) were quantified and use of alternate foraging strategies during periods of limited food availability were described for Black Brant along the Lower Alaska Peninsula in Kinzarof and Izembek Lagoons during winter (February–March) and spring (April–May) 2011. Based on 577 instantaneous flock scans across seasons and tide stages, predominant Black Brant activities were vigilance (41%), foraging (33%), comfort (16%) and locomotion (8%). Estimated mean DEE across months and locations was 1,181 ± 110 kJ/day. Flight costs accounted for an estimated 23–46% of expended energy in winter and spring, roosting 22–27%, thermoregulatory costs 13–18%, foraging 8–15% and vigilance 10–17% in spring. Black Brant only met daily energetic requirements by employing alternate foraging strategies, particularly nocturnal foraging, which offset their DEE by 21–43% in winter and 17–28% in spring.

Key words: Black Brant, eelgrass, foraging, Izembek Lagoon, Kinzarof Lagoon, thermoregulation, *Zostera marina*.

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Breeding success of arctic-nesting geese is dependent on nutrient reserves acquired at spring staging sites (Ryder 1967; Vangilder *et al.* 1986; Black *et al.* 2007). Prior to migration to the breeding range, geese must deposit body reserves of fat, protein and minerals, which are metabolised to provide the energy and nutrients needed to complete migration, to form eggs and fuel incubation (Ankney 1984; Prop & Deerenberg 1991; Bromley & Jarvis 1993; but see Hupp *et al.* 2018). Meeting these high metabolic requirements can be problematic for geese because many plants are low in essential nutrients and high in structural components that are indigestible (Buchsbaum *et al.* 1996). Unlike large vertebrate herbivores, which have large and complex digestive tracts, the digestive tracks of geese are relatively small and simple, resulting in the birds needing to process large amounts of plant material to extract energy and nutrients for their daily requirements (Prop & Vulink 1992; Prop & Black 1998). One of the smallest and potentially most constrained of the goose species, the Brent Goose *Branta bernicla* has a specialised diet in that it feeds primarily on intertidal eelgrass *Zostera* sp. in coastal habitats during the non-breeding and pre-breeding seasons (Einarsen 1965; Jones 1970; Baldwin & Lovvorn 1994; Moore *et al.* 2004; Lewis *et al.* 2013). Previous studies suggest that the Black Brant *B. b. nigricans* subspecies which migrates along the Pacific Flyway of North America may have difficulty meeting its daily energy requirements because of limited tidal access to eelgrass meadows (Einarsen 1965; Baldwin & Lovvorn 1994; Moore & Black 2006). Elkinton *et al.* (2013) showed that foraging Black Brant could reach eelgrass beds only when tides are below 0.9 m of water depth (mean lower low water; MLLW), which occurs for < 65% of the day in Alaska during winter, whereas foods of geese foraging on land are not restricted and are constantly available. Black Brant may compensate for a potential energetic "shortfall" by utilising alternate foraging strategies, such as feeding on dislodged drifting eelgrass during tides above 0.9 m MLLW (hereafter drift-feeding; Elkinton *et al.* 2013), and on exposed eelgrass beds at night when access is unfavourable during daylight periods (hereafter nocturnal foraging; Ward & Stehn 1989). Studies calculating daily energy expenditure and nutrient intake for Black Brant, however, have not accounted for these additional strategies to acquire eelgrass (Moore *et al.* 2004; Mason *et al.* 2006).

In the Atlantic Flyway, where the eelgrass abundance and distribution has steadily declined since the 1930s outbreak of the wasting disease (Renn 1934; Short & Wyllie-Echeverria 1996; Short & Short 2003), Brent Geese (*B. b. bernicla* or *B. b. hrota)* engage in alternative foraging strategies and use alternative habitats to meet daily energetic demands when eelgrass beds are unavailable for grazing. Brent Geese in England feed at night especially on colder nights (Lane & Hassall 1996) and drift-feed during high tides (Percival & Evans 1997) to achieve their energy requirements. As eelgrass beds are depleted by grazing in late winter and spring, Brent Geese shift to nearby foraging habitats such as salt marshes, algal mats and inland pastures (St Joseph 1979; Vickery *et al.*

1995; Ladin *et al.* 2011; Clausen *et al.* 2013) to meet energy demands. Such alternative foraging habitats are less abundant and rarely available to Pacific Flyway Black Brant (Moore *et al.* 2004; Ward *et al.* 2005), especially in Alaska where foraging is restricted to marine habitats, and food intake barely meets daily energy expenditure (Mason *et al.* 2006; Ward *et al.* 2009).

In this study, time-activity budgets and daily energetic requirements of Black Brant were derived in winter and spring along the lower Alaska Peninsula, where > 75% of the Pacific Flyway population of Black Brant stage during migration (Ward & Stehn 1989; Lewis *et al.* 2013) and a growing portion (currently 30%) of the population now winters (Ward *et al.* 2009). Of particular interest was how Black Brant meet their daily energetic demands during periods of reduced access to food and increased energetic costs during winter and spring. Common Eelgrass *Zostera marina* is locally abundant in this region of Alaska (Hogrefe *et al.* 2014), but climatic conditions may be harsh and access to eelgrass challenging when availability is reduced by ice and biomass is at its seasonal lowest (Ward *et al.* 2009; Petrich *et al.* 2014). Short winter day length, increasing low tide water depths and low tide frequencies in the hours of darkness, further reduce access to eelgrass (Mason *et al.* 2007; Ward *et al.* 2009). These environmental constraints ameliorate slightly in the spring as day length, frequency of daylight low tide cycles and temperatures increase, and the mean water depth during low tide cycles decreases. Nevertheless, access to eelgrass beds may still restrict the abilities of Black Brant to acquire necessary body stores for successful reproduction, because shoot lengths and biomass of eelgrass increases little (*c.* 15% on average) between winter and spring.

Given the energetic challenges that Black Brant may face in obtaining sufficient nutrition during winter and spring, we sought to: 1) quantify time-activity budgets for Black Brant during winter and spring, 2) estimate daily energy expenditure from these activity budgets, 3) create an energetic model for the subspecies, and 4) describe alternate foraging strategies during periods of limited food availability. Understanding activity budgets and energy expenditures of Black Brant will allow managers to determine more effectively the ecological and nutrient requirements for their survival during winter and spring in Alaska.

Methods

Study area

The study was carried out near the southwest tip of the Alaska Peninsula in 2011, at Kinzarof Lagoon (55.29°N, 162.64°W) from 28 January–15 March (winter) and at Izembek Lagoon (55.32°N, 162.84°W) from 28 March–25 May (spring). Kinzarof Lagoon (2,055 ha) is a critical overwintering site for Black Brant when ice covers their primary eelgrass beds in the much larger Izembek Lagoon (34,167 ha; Ward *et al.* 2009; Wilson & Dau 2016). Kinzarof Lagoon contains one of the most substantial intertidal eelgrass beds on the Pacific side of the Alaska Peninsula (Hogrefe *et al.* 2014) and is frequently ice-free when Izembek Lagoon is frozen over, providing foraging opportunities for the geese. Situated on the Gulf of Alaska (south) side of the Alaska Peninsula, Kinzarof Lagoon is influenced by warmer sea temperatures than Izembek Lagoon on the Bering Sea (north) side of the peninsula (Hogrefe *et al.* 2014, Fig. 1). In 2011, a significant portion of Izembek Lagoon was covered by ice in February–March and about 5,000 Black Brant wintered in Kinzarof Lagoon (Bollinger 2012; Petrich *et al.* 2014; Daniels 2014). As spring progressed in 2011 and climatic conditions ameliorated, most Black Brant moved to Izembek Lagoon, which is consistent with previously reported trends of use of this site by the geese (Ward & Stehn 1989; Lewis *et al.* 2013). The late April 2011 estimate of the Black Brant population wintering in Alaska was 45,000 birds, with 86% of Black Brant at Izembek Lagoon (Dau & Mallek 2012).

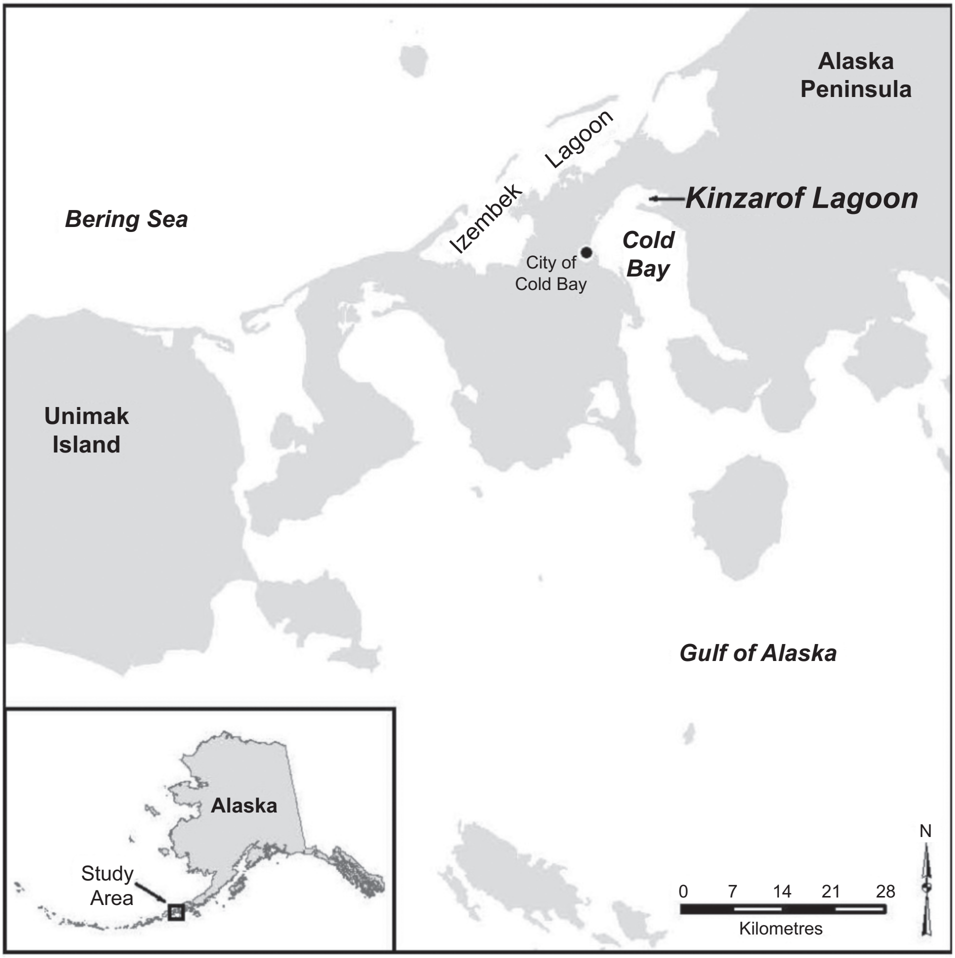

Figure 1. Location of Kinzarof and Izembek lagoons on the lower Alaska Peninsula, Alaska.

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Eelgrass is predominantly intertidal, covering about 60% of the area of each of the lagoons (Hogrefe *et al.* 2014). During our 2011 study, the above-ground biomass of eelgrass at Kinzarof Lagoon (mean range = 150–210 g dry weight mass) was comparable to that at Izembek Lagoon (mean range = 120–205 g dry weight mass; Hogrefe *et al.* 2011). The tides are generally semi-diurnal, with asynchronous high and low tides at Kinzarof and Izembek Lagoons (U.S. Department of Commerce 1980).

Black Brant, Steller's Eider *Polysticta stelleri* and Emperor Geese *Anser canagica* are abundant avian taxa in the study area during winter (Wilson & Dau 2016). Bald Eagles *Haliaeetus leucocephalus* are also common and disturb Black Brant (Ward *et al.* 1994). The most common human disturbance of Black Brant during autumn is low altitude (< 305 m) over-flying fixed-wing aircraft, which occur a couple of times a week (Ward *et al.* 1994), but this disturbance was rare (recorded only once) during winter and spring of our study. Black Brant were hunted infrequently (< 10 days) during the local subsistence hunting season, which in 2011 occurred between 1 April and 15 June (Daniels 2014).

The climate is maritime, with a mean monthly air temperature of 1°C between January and March (Mason *et al.* 2006) and 83% annual mean daily cloud cover (Brower *et al.* 1988). During this study, winds averaged 23 ± 1.1 km/h with a range of 0.0–108 km/h (NCDC 2011).

During winter, the duration of time Black Brant spent in Kinzarof Lagoon day or night was determined by recording the time when geese first arrived and last departed the lagoon during observations from elevated shoreline bluffs near its entrance that allowed full views of the lagoon. During spring, Black Brant were assumed to remain 24 h/day in the Izembek Lagoon. This was a reasonable assumption because aerial surveys of Black Brant on the lower Alaska Peninsula detected 98% of the population in Izembek Lagoon in spring 2011 (Dau & Mallek 2012) and 24 h tracking of radio-marked individuals in autumn indicated that birds remained in the lagoon through the night (Ward & Stehn 1989).

Diurnal activities

Daily activity budgets of Black Brant were calculated during winter and spring using ten instantaneous scans of flocks (Martin & Bateson 1993) per daylight hour per month. Sampling was limited to three scans per flock within a 1 h period with a > 10 min break between scans (Black & Owen 1988). Observations were restricted to flocks of > 100 birds because smaller flocks rarely occurred during our study and individuals may behave differently when in small groups than in larger flocks (*sensu* Inglis & Lazarus 1981). Similar numbers of geese per flock were sampled at each lagoon (mean ± s.e.; Kinzarof: 185 ± 5.6, *n* = 192; Izembek: 219 ± 4, *n* = 416). During each scan, we recorded whether birds were on land or in water and categorised their behaviours as: 1) foraging (actively feeding with head-up, head-down or up-ending); 2) vigilant (head-up relaxed or alert); 3) locomotion (walking, swimming); and 4) comfort (preening, wing flapping, resting or bathing; Daniels 2014).

Flying birds were not usually recorded

during flock scans of birds on the water, so flying birds were underestimated by using these scans. Hence, we conducted separate scans to determine the proportions of birds flying based on counts of total numbers of Black Brant in the field of view of the observer when on land, water, or flying. These counts of birds in flight were standardised across observations because the area viewed through the telescope differed between sites (range of view: Kinzarof = *c.* 325 ha; Izembek = *c.* 550–1,000 ha). We recorded the apparent cause of a disturbance when > 50% of the flock flew during a scan, as well as the number of courtship display flights which were characterised as three birds flying in synchronous, twisting flight (Barry 1967). To determine the overall activity budget during daylight hours, the number of minutes an average Black Brant spent flying in a day was calculated from flight scans. The remaining period of "non-flying" time was then apportioned to non-flight activities (*i.e.* foraging, vigilance, locomotion and comfort) based on the results from flock scans.

Nocturnal activities

On nights when water depth was below 0.9 m MLLW, we conducted flock scans with night vision scopes to determine night-time foraging when eelgrass was available. Due to scope capabilities and our inability to approach flocks to classify individual behaviours without disturbing birds, flocks were classified only as feeding (> 50% of flock feeding) or not feeding.

Nocturnal foraging costs were calculated during winter and spring based on the number of nights when tides were low enough for birds to feed on rooted eelgrass (hereafter referred to as bed-feeding) in each of the lagoons. Flocks were assumed to forage only at tide levels of < 0.9 m MLLW (Elkinton *et al.* 2013). On nights when tidal conditions were above 0.9 m MLLW we assumed no foraging and that all birds roosted.

The proportion of moon illumination during each night of the study was determined based on the crescent moon light visible from the US Naval Observatory (2011). The greater percentage of visible moon, the more ambient light is reflected (Foster & Roenneberg 2008). Percent moon visible was used as a predictor to model foraging behaviour in geese.

Activity based metabolic rates

Daily energy expenditure was estimated by summing the energetic costs of daily activities (based on data from activity scans) with thermoregulatory costs (Stock & Hofeditz 1997). Activity-specific energy costs were calculated using multipliers of basal metabolic rate (BMR) based on literature values: costs of foraging (1.7× BMR), vigilance, (1.7×), preening (1.8×), resting (1.6×), walking (1.9×) and interacting (1.9×) were derived from semi-captive Brent Geese (*B. b. bernicla;* Stahl 2001); cost of swimming (2.2) was derived from Black Ducks *Anas rubripes* (Wooley & Owen 1978). Flight costs (13.4× BMR) were derived from an allometric equation of the cost of flight in Light-bellied Brent Geese (*B. b. hrota*; Ladin 2010). Basal metabolic rate (Lasiewski & Dawson 1967) was calculated using body mass values from Black Brant (mean mass = 1,410 g; *n* = 46: 18 males, 14 females, 14 juveniles) harvested at the study sites in April and May 2011 (Daniels 2014) resulting in a BMR of 17.5 kJ/h.

Estimated thermoregulatory costs (Ct) were based on a similar-sized (1,400 g) Cackling Goose *Branta hutchinsii* that showed a loss of 1.272 kJ/hour/°C whenever temperature fell below the lower critical temperature (LCT; LeFebvre & Raveling 1967) with a known LCT for Black Brant of 6°C (Irving *et al.* 1955). Ct was calculated as:

$$Ct = 1.272 * N * \Delta t$$

where 1.272 was the loss of energy measured in kJ/h/°C, N was the number of hours per day the ambient temperature was below 6°C, and Δt was the average number of degrees below 6°C (Clausen *et al.* 2012). This calculation, however, assumed the bird was on land and only exposed to air, which in our study occurred infrequently when the bird was standing or flying. Therefore, when birds were floating on the water the cost of thermoregulation was calculated based on both air and water temperature, assuming the proportion of the body in contact with water and air was 33% and 67%, respectively (van Sant & Bakken 2006).

Daily energy expenditure was expressed as:

$$DEE_{[kJ/day]} = \sum (BMR * a_i * t_i) + (Ct_{air/water} + Ct_{air})$$

where a_i is the activity multiplier, t_i is the time spent performing the activity, $Ct_{air/water}$ is the cost of thermoregulation while floating on water as expressed as the proportion of a birds body in contact with water (33%) and exposed to air (67%), and Ct_{air} is the thermoregulatory cost of birds exposed only to air (100%) in kJ/day (modified from Stock & Hofeditz 1997). Because of activity-created heat, Ct_{air} was considered null for the proportion of time birds were in flight. DEE was calculated as the expended energy (kJ) per goose in a 24 h period.

Eelgrass and faecal matter nutritional quality

Samples of eelgrass were collected for nutrient content from beds grazed by Black Brant in Kinzarof and Izembek Lagoons. Collections were made at three eelgrass beds every two weeks for a total of eight sampling weeks. We also collected detached, drifting eelgrass in a plankton net that was towed from a boat along two transects located at or near one of the entrances to each of the lagoons. Concurrently with eelgrass sampling, we collected Black Brant faecal matter from three separate eelgrass beds after foraging observations. All eelgrass and faecal matter was placed in individual plastic bags and later cleaned and stored frozen until drying. Nutrient analyses were conducted at the Washington State University's Habitat and Nutrition Laboratory.

Eelgrass and faecal matter were analysed for acid detergent fibre (ADF), nitrogen content (N), carbon (C), ash content, and caloric content with bomb calorimeter. ADF, which is assumed to be a valid measure of crude fibre, is negatively correlated with digestibility (Van Soest 1994). ADF is a reliable marker for constituents of the cell walls during winter (Drent *et al.* 1980) and was used as an indigestible marker. To estimate crude protein in the eelgrass we used the Kjeldahl method and multiplied nitrogen content by a factor of 6.25 (Kjeldahl 1883). To calculate assimilation rate of nutrients, the proportion of nutrients in faeces was subtracted from the proportion of nutrients in the eelgrass. All nutrient values were corrected for an ash-free weight.

Environmental factors

Tide stage, water depth and water temperature were collected hourly using *in situ* time-depth loggers (Onset HOBO Water Level) placed in a channel near the mouth of Kinzarof Lagoon, and at Grant Point in Izembek Lagoon. The time-depth loggers recorded water temperature and absolute pressure, which was converted to water depth (metres, MLLW) by calibrating readings to another time-depth logger placed nearby on land that measured atmospheric pressure and standardising readings to a known tidal depth location in each lagoon. We used these water depth estimates to predict bed- and drift-feeding for Black Brant.

Hourly measurements of air temperature and wind velocity were obtained from the National Oceanic and Atmospheric Administration National Climatic Data Center for Cold Bay weather station (NCDC 2011), located approximately 9 km from Kinzarof Lagoon and 13 km from Izembek Lagoon. We used the climate data to calculate the number of hours that air temperatures were below LCT for each day during the study.

Daily number of daylight hours were determined from predictions of civil twilight at Cold Bay (US Naval Observatory 2011).

Energetic intake

To predict if Black Brant were on average reaching daily energetic requirements each month, we calculated an assimilated energy intake model for bed, drift and nocturnal feeding. A low-tide, daylight only energetic model for bed-feeding was based on the assimilated caloric content (kJ/g) of bed eelgrass from this study, hours foraging during this study, and an estimated high foraging rate of 34 g/h for mid-to-late wintering Black Brant at Izembek Lagoon from Mason *et al.* (2006). To model the energy intake from drift-feeding we used the assimilated caloric content of drifting eelgrass collected during this study, time spent drift-feeding from activity budgets during this study, and an intake rate of 9.6 g/h (from Elkinton 2013) during drift-feeding. Lastly, an energetic intake model was calculated for nocturnal foraging using the assimilated caloric content of bed eelgrass collected during this study, the duration (hours) eelgrass beds were available for foraging at night during this study, and an intake rate of 13.6 g/h. This intake rate was calculated by taking the average difference between diurnal and daily intake of eelgrass by Brent Geese between January and March (40%; Tinkler *et al.* 2009) and multiplying it by the intake rate used for daytime bed-feeding (34 g/h; Mason *et al.* 2006).

Data analyses

The proportion of time that birds were engaged in the five primary behaviour categories was compared across flocks during daylight hours using generalized liner models (GLM) and also Mann-Whitney U-tests to account for non-normality. Differences in proportion of birds flying and proportion of birds foraging within a flock were assessed using GLM. We accounted for over-dispersion by refitting the model using a quasi-binomial error distribution. Estimate coefficients from GLMs were back transformed into probabilities (p), and are meant to be compared between parameters. Independent variables included: 1) tide stage (high, low, flood, ebb), 2) month (February, March, April, May), and 3) study site (Kinzarof and Izembek).

Eelgrass bed availability, eelgrass nutritional quality, and the cost of thermoregulation in water and the air/water interface were assessed using ANOVA and student *t*-tests. Independent variables included: 1) tide stage (high, low, flood, ebb), 2) month (February, March, April, May), and 3) season (winter and spring).

To examine the influence of duration of time that eelgrass beds were accessible for foraging (tide height < 0.9 m MLLW) during the previous 12 hours, and the predicted visibility of the moon the night before on the probability of bed-feeding during the day, we developed a candidate set of logistic regression models. The response variable was a matrix of the number of birds foraging and not foraging within a flock, while the duration that forage had been available in the previous 12 hours (Prior12) and the percent predicted visibility of the moon (Moon) were the predictor variables. Models contained both additive and interactive combinations of these explanatory variables. We accounted for over-dispersion by refitting the models using a negative binomial error distribution.

Elkinton *et al.* (2013) determined 0.9 m MLLW was the average tide height at which the majority (> 50%) of Black Brant switch to drift-feeding from bed-feeding in Humboldt Bay, California. We observed a similar response in feeding behaviour of Black Brant in Alaska at this same tide height and defined low tide when water depth was below 0.9 m MLLW, high tide when water depth was above 1.2 m MLLW, and flood (incoming) and ebb (outgoing) tides when water depth between 0.9 m and 1.2 m MLLW. Eelgrass was assumed to be available to Black Brant at water depths below 0.9 m MLLW when swimming and below 1.2 m MLLW when up-ending.

Data analyses were conducted in Program R (R Core Team 2016). Tests were considered significant when estimates were $< \alpha = 0.05$, and estimated values were reported as means ± 1 s.e.

Results

Diurnal activities

Black Brant were present in Kinzarof Lagoon for a mean 11.25 ± 0.25 h/day (n = 14 days) and assumed to be present in Izembek Lagoon for 24 h/day (n =31 days).

Five hundred and seventy-seven diurnal flock scans were conducted at the two study sites during the four-month study period. Observed flock sizes were similar across tide stages: low tide bed-feeding (mean = 214 ± 4.0 birds/flock; n = 393 flocks); high tide drift-feeding (212 ± 8.5 birds/flock, *n* = 75 flocks), and flood and ebb tides bed- or drift-feeding (ebb: 217 ± 11 birds/flock, *n* = 85 flocks; flood: 177± 12 birds/flock, *n* = 24 flocks). On average across months and tide stages, Black Brant engaged more in foraging (33%) and vigilance (41%), than in locomotion (8%) and comfort (16%) behaviours (Table 1).

The probability of birds foraging during low tide differed significantly from the other three tide stages, with little difference between ebb, flood, and high tides in the probability of foraging (low: p = 0.44; ebb: p = 0.13; flood: p = 0.14; and high: p = 0.16; $t_{3,576} = -7.57$, $P < 0.05$), whilst the proportion of foraging birds was higher during low tide compared to other tide stages (Fig. 2). The proportion of the flock foraging varied by season (W = 43644,

Table 1. Mean (x̄ ± s.e.) proportion of individuals in flocks of Black Brant engaged in four behaviour categories during daylight hours on the lower Alaska Peninsula, February–May 2011.

		February (*n* = 67)		**March** (*n* = 138)		**April** (*n* = 157)		**May** (*n* = 215)	
Behaviour category	**Activity**	x̄	s.e.	x̄	s.e.	x̄	s.e.	x̄	s.e.
Foraging	Head-up forage	0.01	0.01	0.00	0.01	0.00	0.00	0.00	0.00
	Head-down	0.17	0.10	0.15	0.30	0.11	0.24	0.20	0.12
	Standing head-down	0.02	0.03	0.03	0.06	0.10	0.22	0.14	0.14
	Tip-up	0.05	0.06	0.09	0.17	0.02	0.05	0.04	0.07
Vigilant	Head-up	0.29	0.13	0.45	0.84	0.20	0.38	0.24	0.12
	Standing head-up	0.02	0.03	0.03	0.05	0.12	0.21	0.06	0.05
	Alert	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.01
Locomotion	Swim	0.06	0.07	0.06	0.11	0.05	0.09	0.07	0.05
	Walk	0.00	0.00	0.01	0.02	0.03	0.05	0.02	0.02
	Flying[a]	0.26	0.03	0.08	0.02	0.18	0.05	0.07	0.01
Comfort	Preen	0.04	0.03	0.05	0.10	0.03	0.06	0.03	0.04
	Stand preen	0.03	0.04	0.03	0.05	0.09	0.18	0.09	0.08
	Rest	0.03	0.04	0.02	0.03	0.02	0.02	0.02	0.04
	Stand rest	0.00	0.00	0.00	0.00	0.02	0.04	0.02	0.03
	Bathe	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01

[a] Flying was calculated during a separate scan (see Methods).

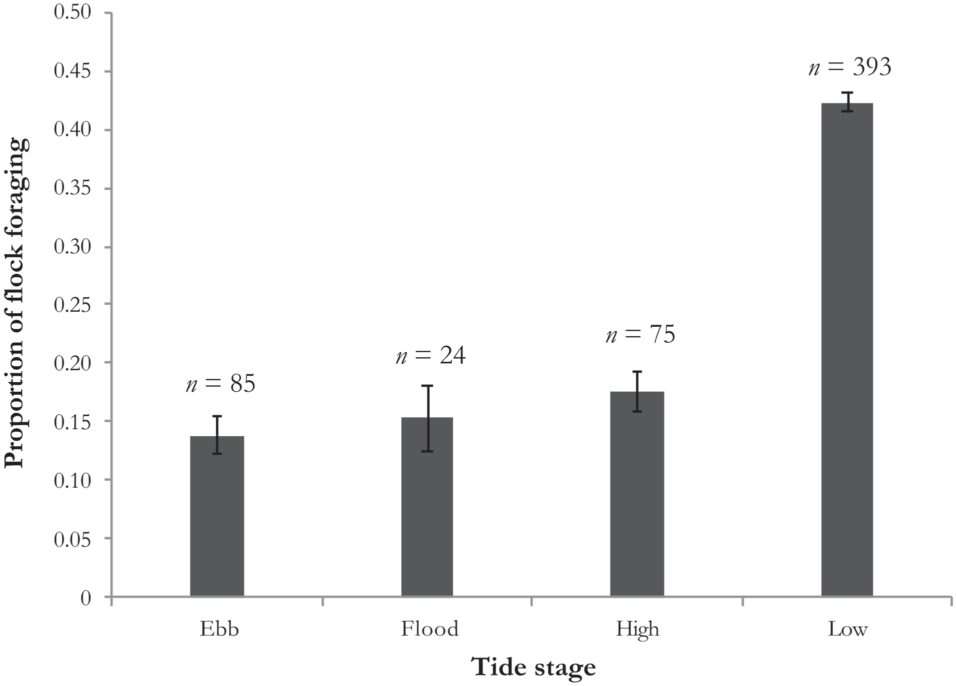

Figure 2. Mean (± s.e.) proportion of flocks of Black Brant foraging across tide stages, February–May 2011.

$P \leq 0.005$) and the probability of foraging in May was significantly greater than the other three months (February: $p = 0.31$, March: $p = 0.30$, April: $p = 0.33$, and May: $p = 0.39$; $t_{3,576} = -8.97$, $P < 0.05$). Eelgrass beds were predicted to be exposed for longer time periods and therefore available to the birds to forage upon more often during daylight hours in spring (11.7 ± 0.5 h) than in winter (5.3 ± 0.4 h; $t_{1,93} = 11.7$, $P \leq 0.001$).

The proportion of Black Brant foraging was best described by the number of hours the bed was available in the previous 12 h and the predicted percent moon visible the previous night (Table 2). The interaction between the two factors had no explanatory weight and was statistically insignificant.

Black Brant were less vigilant during spring (36.0 ± 1.0; $n = 372$) than winter (52.0 ± 1.0; $W = 17142$, $n = 205$, $P \leq 0.001$).

Black Brant performed locomotion behaviours more often during spring (9.0 ± 3.0, $n = 372$) than during winter (6.0 ± 0.5; $W = 48027$, $n = 205$, $P \leq 0.001$). There was no statistical difference in the probability of birds swimming among tide stages (low: $p = 0.06$; ebb: $p = 0.06$; flood: $p = 0.07$; and high: $p = 0.08$; $t_{3,576} = -11.50$, $P > 0.05$, n.s.). However, Black Brant spent a greater proportion of their time walking during ebb tide (4.0% ± 0.6) when eelgrass beds become exposed, compared to high tide (2.0% ± 0.8) when geese congregated on gritting bars. The probability of Black Brant

Table 2. Coefficient estimates for the top candidate model describing factors influencing proportion of Black Brant foraging during the day on the lower Alaska Peninsula, February–May 2011. Prior12 = duration of forage availability in the previous 12 h; Moon = predicted percent visibility of the moon.

Model	Parameter	Estimate	95% CI	
			Lower	Upper
Moon + Prior12	Intercept	–1.23	–1.306	–1.154
	Moon	–0.28	–0.369	–0.191
	Prior 12	0.06	0.05	0.07

walking was significantly different during ebb tide than the other 3 tides (low: p =0.01; ebb: p = 0.03; flood: p = 0.01; high: p = 0.01; $t_{3,576} = –22.69$, $P < 0.05$).

The percentage of Black Brant flying recorded during flight scans ranged from 0–100% (mean = 14 ± 1.2, *n* = 602 scans). Greatest numbers of flying Black Brant followed an aircraft disturbance in spring (21,000 birds). During 602 flight scans, Black Brant took flight for courtship displays (819 events), human disturbance (5 events), avian predators (12 events), and to relocate within the lagoons, presumably for further foraging opportunities. The probability of Black Brant flying was similar between February and April (February: p = 0.26; April: p = 0.22; $t_{3,576} = –15.10$, $P < 0.05$), and March and May (March: p = 0.08; May: p = 0.07; $P < 0.05$), with more flying occurring during spring months (W = 44038, $P < 0.05$). No statistical differences were found for the probability of the flock in flight among tide stages (low: p = 0.11; ebb: p = 0.13; flood: p = 0.14; and high: p = 0.14; $t_{3,576} = –3.88$, $P > 0.05$, n.s.; Fig. 3).

There was no statistical difference between the proportion of Black Brant flocks performing comfort behaviours between winter (0.12 ± 0.01, *n* = 168) *versus* spring (0.18 ± 0.01; W = 37922, , *n* = 414, $P = 0.91$, n.s.).

Nocturnal activities

Assessments of nocturnal foraging were made on 16 occasions. Black Brant flocks were present and feeding on 42% of the nights during winter (*n* = 12) and 100% of nights during spring (*n* = 4). On the nights when flocks were not present during winter, the birds were assumed to be roosting.

Eelgrass nutritional quality

Caloric quality (kJ/g) of eelgrass did not differ between samples collected from beds during winter (16.10 ± 0.13 kJ/g) or spring (16.27 ± 0.10 kJ/g; $t_{1,49} = –1.07$, $P = 0.29$, n.s., Fig. 4). Percent nitrogen content of eelgrass from beds was greater in winter

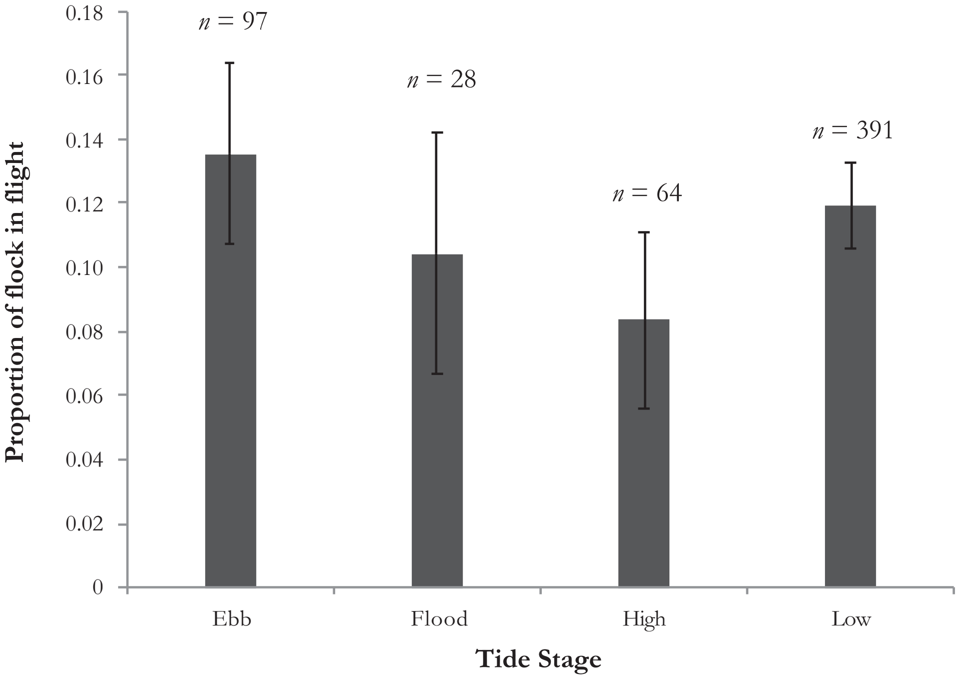

Figure 3. Mean (± s.e.) proportion of flocks of Black Brant engaged in flight across tide stages, February–May 2011.

(18.14% ± 0.58) than spring (15.77% ± 0.27; $t_{1,33}$= 3.73, $P < 0.05$). Percent ADF content in eelgrass was greater during spring (25.58% ± 0.67) than winter (23.09% ± 0.26; $t_{1,46}$= –3.45, $P = 0.001$), and carbon content was greater in spring (37.63% ± 0.47) than winter (36.20% ± 0.46; $t_{1,57}$= –2.17, $P = 0.03$, Fig. 4).

In general, percent nitrogen and carbon were greater in drifting eelgrass than rooted eelgrass collected from beds, but ADF was greater in rooted eelgrass (Table 3). Because of low sample size of drifting eelgrass (1 per sample period), statistical comparison could not be made as all drifting eelgrass samples had to be combined for nutritive analyses.

Activity-based metabolic rates

The cost of thermoregulation was estimated to be significantly greater in winter than in spring ($t_{1,59}$ = 7.66, $P < 0.05$). Cost of thermoregulation in water (air/water interface) differed among months ($F_{3,106}$= 104.3, $P < 0.001$) and generally decreased from February through May (Fig. 5). Cost of thermoregulation was highest for birds in water across all months except April (Table 4). Cost of thermoregulation when standing and exposed to air differed between months ($F_{3,106}$ = 43.55, $P < 0.001$) and was highest in April (Fig. 5).

Estimated mean DEE across months and study sites was 1,181 ± 110 kJ/day and was highest in February at 1,396 kJ/

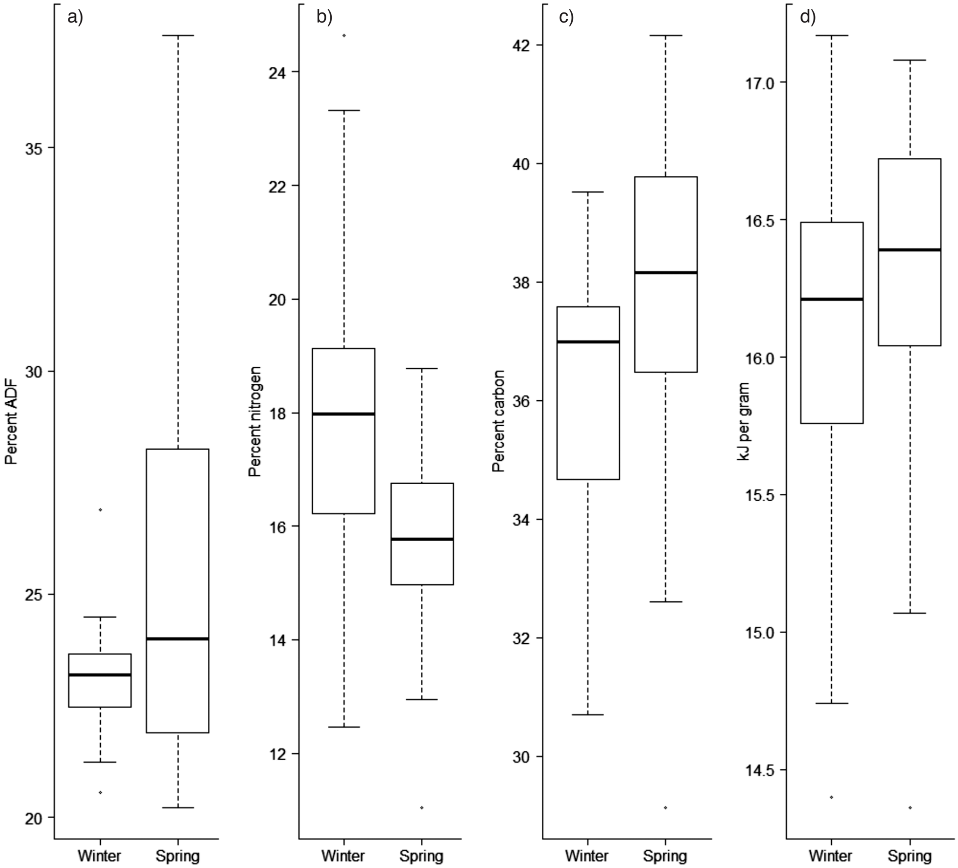

Figure 4. Median, 50 and 75 percentiles, and 95% CI for: a) acid detergent fibre (ADF), b) nitrogen, c) carbon and d) kilojoules (kJ) in a gram of eelgrass, February–May 2011.

day, and lowest in May at 893 kJ/day (Table 5).

Flying was predicted to be the most energetically expensive activity, accounting for 23–46% of the estimated expended energy during the study. The next most energetically expensive activities were roosting (22–27%) during winter, and foraging (8–15%) and vigilance (10–17%) during spring. Cost of thermoregulation for February, March, April, and May accounted for 11%, 18%, 9%, and 4% of daily energy expenditure, respectively.

Cost of thermoregulation was predicted to be higher in all months except May when the cost of thermoregulation was calculated using air temperatures only (Table 5). There was no statistically significant difference between methods used for calculating the cost of thermoregulation ($t_{1,218} = 1.79$, $P = 0.07$, n.s.).

Energetic intake

Energetic intake increased from February–May as eelgrass beds became more available to birds for foraging during daylight hours

Table 3. Mean percentage of nitrogen, acid detergent fibre (ADF), carbon, and (kJ) of rooted (bed) or detached (drift) eelgrass leaves collected on the lower Alaska Peninsula, February–May 2011.

	Bed				**Drift**			
Date	**Nitrogen**	**ADF**	**Carbon**	**Energy content (kJ/g)**	**Nitrogen**	**ADF**	**Carbon**	**Energy content (kJ/g)**
07/02/2011	15.09	27.78	33.23	15.63	19.33	33.61	43.03	15.15
23/02/2011	19.63	28.53	36.92	16.16	–	30.13	26.99	15.38
07/03/2011	18.70	27.43	37.47	16.32	20.88	23.55	–	16.50
23/03/2011	16.39	28.71	35.49	16.05	15.00	28.27	45.00	16.21
01/04/2011	14.52	–	42.16	–	–	25.20	45.23	16.32
09/04/2011	15.94	25.58	39.07	16.51	–	25.20	–	–
17/04/2011	16.77	25.34	40.49	16.77	18.56	24.82	–	16.30
02/05/2011	15.77	31.86	37.71	16.40	–	26.07	–	15.83
17/05/2011	14.69	38.77	35.62	15.91	–	32.27	42.51	15.51

Table 4. Estimated daily cost of thermoregulation (Ct; kJ/day) for a Black Brant standing on land (Ct_{air}) and sitting on water ($Ct_{air/water}$) compared to the cost of thermoregulation using only air temperatures, February–May 2011. See methods for formula calculations.

	Daily cost of thermoregulation (kJ)			
Month	Ct_{air}	$Ct_{air/water}$	Total Ct	Ct calculated with air temperatures only
February	7	153	160	198
March	14	180	194	213
April	65	64	129	163
May	14	24	38	37

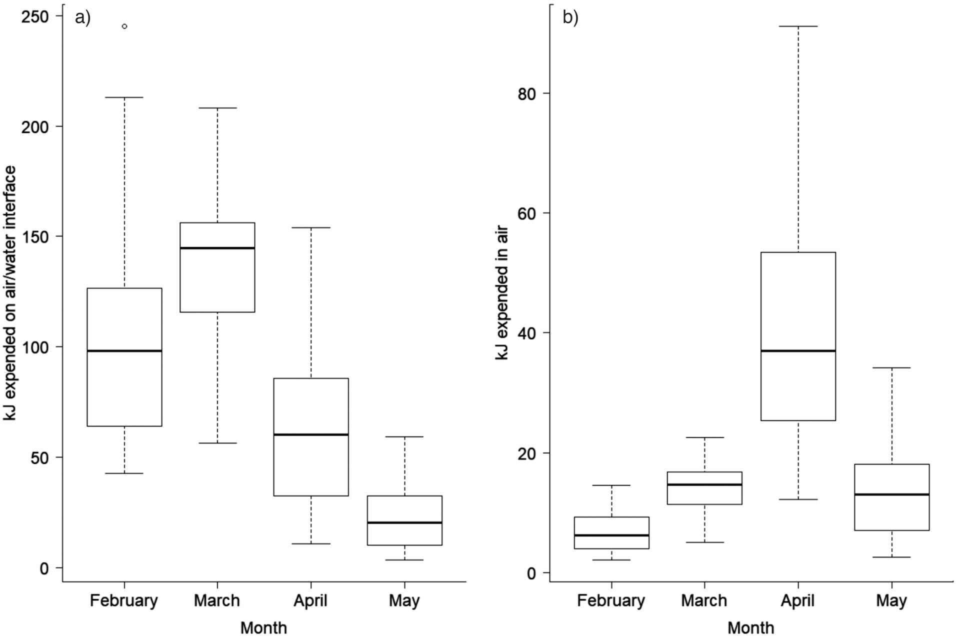

Figure 5. Median, 50 and 75 percentiles, and 95% CI for daily cost of thermoregulation (kJ) for the proportion of a bird exposed to: a) air/water interface while sitting on the water, and b) air while standing, February–May 2011.

(Table 6). Drift-feeding accounted for < 1% kJ/h intake for every month, and nocturnal foraging in February provided 75% of the energy acquired during the day and estimated 21–40% more energy in the other three months. Without use of alternate foraging strategies, Black Brant were predicted to be unable to reach daily energy expenditures except in May; however, employing alternate foraging strategies reduced the deficit in all months, and exceeded energetic expenditure in March (Table 6).

Environmental factors

Daily mean water and air temperatures were below the lower critical temperature threshold for Black Brant (6°C) during both seasons. During winter, mean water temperature (0.58 ± 0.003°C) was lower than mean air temperature (2.26 ± 0.185°C). In spring, mean air temperature (2.9 ± 0.07°C) was predicted to account for greater thermoregulatory demand than water temperature (4.5 ± 0.09°C). Mean wind speeds were similar across seasons with average wind speed slightly lower in winter (27 ± 1.5 km/h; range = 0–88.5 km/h), than in spring (35 ± 0.8 km/h; range = 0 – 77.25 km/h).

Discussion

Diurnal activities

Recent studies have determined activity budgets of wild Brent Geese in their

Table 5. Estimated mean daily energetic expenditure (kJ/day) for seven main behavioural activities and the cost of thermoregulation for Black Brant on the lower Alaska Peninsula, February–May 2011.

	February	**March**	**April**	**May**
Diurnal Foraging	83	109	125	134
Nocturnal Foraging	89	24	73	51
Vigilant	97	126	146	155
Comfort	32	41	47	51
Locomotion	25	33	38	41
Fly	602	247	633	255
Roost	308	286	183	176
Cost of Thermoregulation	160	194	128	32
Total	1,396	1,059	1,374	893

modified and alternative terrestrial habitats (Riddington *et al.* 1996; Ladin *et al.* 2011; Clausen *et al.* 2013), but few have occurred exclusively in their natural marine environment in winter and spring (Kramer 1976; Elkinton 2013). Brent Geese using these modified and alternative foraging habitats regularly adjust their activity and foraging strategies to meet energy demands while splitting foraging effort among marine habitat types along salinity gradients or terrestrial habitat types of inland areas (St Joseph 1979; Prop & Loonen 1989; Prop & Deerenberg 1991; Vickery *et al.* 1995; Ladin *et al.* 2011; Clausen *et al.* 2013, Elkinton *et al.* 2013). We show that Black Brant foraging in their natural marine environments in Alaska also adjust their behaviours to changing environmental factors in winter and spring by foraging over a greater portion of the day, including during high tides and at night, and foraging when eelgrass beds become available at low tide.

In comparison to our study, Ladin *et al.* (2011) found that Brent Geese spent a similar amount of time foraging on eelgrass and saltmarsh plants during winter and spring in Delaware. When activity budgets from this study are compared with those of Brent Geese in Denmark (Clausen *et al.* 2013), which use marine environments at a similar latitude, Black Brant in Alaska spent less time foraging (Denmark: 70% *vs.* Alaska: 33%), were more vigilant (Denmark: 1% *vs.* Alaska: 41%), but performed comfort and locomotion activities at a similar proportion (Denmark: 18% *vs.* Alaska: 6%). We suspect the disparity in foraging and vigilance between the two locations may be explained by differences in

Table 6. Estimated energetic intake of eelgrass by Black Brant when feeding on rooted (bed) and detached (drift) Common Eelgrass shoots during daylight hours or rooted shoots at night on the lower Alaska Peninsula, February–May 2011.

		Month			
Foraging strategy		**February**	**March**	**April**	**May**
Bed-feeding	Dry g consumed/hour (Mason *et al.* 2006)	34	34	34	34
	No. hours foraging in a day (based on activity budgets)	3.17	3.97	4.85	6.75
	Assimilated energetic value of eelgrass (kJ/g; this study)	4.14	6.47	4.83	5.15
	Energy intake (kJ/day)	**446**	**873**	**797**	**1,182**
Drift-feeding	Dry g consumed/hour (Elkinton 2013)	9.6	9.6	9.6	9.6
	No. hours foraging in a day (based on activity budgets)	0.17	0.16	0.12	0.20
	Assimilated energetic value of eelgrass (kJ/g; this study)	3.60	6.62	4.51	4.69
	Energy intake (kJ/day)	**6**	**10**	**5**	**9**
Nocturnal feeding	Dry g consumed/hour (Tinkler *et al.* 2009)	13.6	13.6	13.6	13.6
	Mean number of hours available in a night bed	6.00	2.82	4.83	3.46
	Assimilated energetic value of eelgrass (kJ/g; this study)	4.14	6.47	4.83	5.15
	Energy intake (kJ/night)	**338**	**248**	**318**	**243**
Total	Assimilated energy intake (kJ/day)	790	1,131	1,119	1,434
	Energy expenditure (this study)	1,396	1,059	1,374	893
	Net daily energy intake (kJ/day)	**–606**	**72**	**–255**	**541**

exposure to disturbances. In Denmark, there are few predators and virtually no hunting of Brent Geese (Clausen *et al.* 2013), while on the lower Alaska Peninsula Black Brant are hunted both by Bald Eagles and humans and dedicate more time towards vigilance than foraging. We often observed Black Brant flocks feeding, then taking flight, flying for a few minutes, and landing on the same eelgrass bed to resume foraging presumably in response to a perceived predator. As a result, flight and vigilant activities accounted for large proportion of the energy budget of Black Brant during our study.

Bald Eagles gather in high densities on the lower Alaska Peninsula in late autumn and remain there through the winter and early spring, when they prey on waterbirds (Ward *et al.* 1994; Daniels 2014). Bald Eagles were the most frequent disturbance of Black Brant during our study. Eagles were particularly abundant in Kinzarof Lagoon possibly because this lagoon is small and Black Brant are concentrated on intertidal eelgrass beds close to the elevated shoreline bluffs where eagles can perch and stoop on flocks from relatively short distances. We found that Black Brant did not remain in Kinzarof Lagoon at night or during daylight high tides, but instead moved to Cold Bay, where this much larger embayment presumably provided greater safety for roosting (Daniels 2014). Eelgrass is sparse and grows deeper in this bay (Hogrefe *et al.* 2014), providing little to no foraging opportunity for Black Brant.

Black Brant moved less often in winter than in spring. Thermoregulation demands were highest in winter and birds were likely conserving energy during the colder temperatures. Black Brant also foraged less often in winter than in spring, presumably because eelgrass availability and abundance was more restricted due to the shorter length of shoots and lower above ground biomass of eelgrass, fewer hours of daylight access to beds, and increased ice cover (Ward & Stehn 1989; Petrich *et al.* 2014; Bollinger 2012; current study).

Black Brant flew during all tide stages and participated in three-bird courtship flights. Birds partook in three-bird courtships flights more regularly in spring than winter, likely to form, strengthen and test pair bonds prior to departing for the nesting grounds. Flight was also a greater energetic demand in April as Black Brant migrated into Izembek Lagoon throughout the month and we suspect our data captured some of the energetic demand associated with migration during this month, resulting in an energy shortfall.

We found that Black Brant foraged more often during daylight hours when rooted eelgrass was less accessible during the previous 12 hours, and the percent moon visible was greater the previous evening. We propose the mechanism to describe this behaviour to be when tides allowed for foraging within the previous 12 hours with visible light, Black Brant were able to engage in other activities during low tide, possibly because birds acquired sufficient energy to meet energy expenditures more readily. When rooted eelgrass was not available during the previous 12 hours, Black Brant appeared to maximise their energy intake to meet their daily energy expenditure by foraging on the first beds exposed and then dispersing to other newly exposed beds near channels that have the highest quality forage (Moore & Black 2006).

Our data suggest that nocturnal foraging may be a critical source of energy intake for Black Brant overwintering in Alaska given that individuals may obtain up to half of their daily expenditure by feeding at night (this study). This alternate foraging strategy is likely most critical for their survival between December and March when nearly all low tide, bed-feeding opportunities occur at night and the cost of thermoregulation is highest. Mason *et al.* (2006), who measured changes in body composition of overwintering Black Brant at Izembek and Kinzarof Lagoons, also found this period to be most energetically demanding. Birds used lipid reserves obtained in autumn to offset periods of food shortages in winter. Mason *et al.* (2006) showed that Black Brant do not begin to gain body mass and store body reserves until May, which is consistent with our finding that the greatest increase in gross energy intake occurred in this month. Black Brant must rapidly gain body reserves for migration and reproduction over a short (average two weeks) period in spring (Lewis *et al.* 2013) to keep pace with advancing phenology on the breeding grounds (Ward *et al.* 2015). This period of rapid energy intake is enhanced when birds employ both daytime and nocturnal foraging strategies. We found that nocturnal feeding can supplement daily gross energy intake by 21–40% in spring.

Lane & Hassal (1996) and Percival & Evans (1997) documented Brent Geese feeding at night in England when disturbed during the day. Human (< 1% of scans) and Bald Eagle (< 2% of scans) disturbances were low during our 4-month-long study, and thus, were not a main factor leading to nocturnal feeding. Instead, we believe that nocturnal feeding was largely a response to the timing of low tides facilitating bed foraging.

Drift-feeding accounted for only a small (< 1%) fraction of the overall gross energy intake in any month of our study, and thus, likely plays only a minor role in offsetting energy expenditures. This is likely, in part, because eelgrass productivity and abundance are at a minimum between December and April on the lower Alaska Peninsula (McRoy 1970). We suspect that nearly all drift eelgrass available to Black Brant at high tide were shoots pulled-up by these birds but not eaten during the previous low tides.

Activity-based metabolic rates

To the best of our knowledge no other study of Black Brant has considered an air/water interface model for determining cost of thermoregulation. Our estimates of Ct were similar to those of Mason *et al.* (2006), who calculated thermoregulation costs based on allometric metabolic equations for Black Brant wintering in Alaska in early winter (November–January; 204 kJ/day) and late winter (January–April: 199 kJ/day) with similar air temperatures overall during the two studies. Ladin *et al.* (2011) found a much lower average Ct (64 kJ/day) for Atlantic Brant during winter and spring, using an equation in Stock & Hofeditz (1997) that did not consider the cost of thermoregulation with contact to the water. The average reported by Ladin *et al.* (2011) was for a three year period, and encompassed the cost of thermoregulation in both winter and spring. Ladin *et al.* (2011) also used an LCT of 7.5°C, whereas this study used LCT of 6°C, which invalidates comparisons. This study used the in-depth model to calculate cost of thermoregulation to reduce bias in calculations, although the calculations may still be biased low since the equation did not account for convective energy loss from birds' legs in the water. However, we believe this energy loss to be negligible due to counter-current exchange. This study was also unable to account for convective heat loss from wind, due to inability to measure accurately the amount of wind the birds were experiencing.

Expectedly, the predicted cost of thermoregulation for birds exposed to the air/water interface decreased from March to May as air and water temperatures increased and the difference between LCT and the ambient temperature decreased. The increased cost of thermoregulation in April when exposed to air was likely caused by colder temperatures, including a 2-week period of below freezing temperatures during the middle of that month.

The overall mean estimated DEE for Black Brant overwintering in Alaska (1,181 ± 110 kJ/day) was similar to estimates reported for Brent Geese wintering in Delaware (1,238 kJ/day; Heise 2012). Ladin *et al.* (2011) assumed nocturnal activities of Brent Geese were equal to that of daytime activities. Our estimates of overall mean DEE were also similar to the estimates for Brent Geese foraging in Ireland (1,326–1,556 kJ/day, Tinkler *et al.* 2009), but higher than estimates for Brent Geese in the Netherlands (828 kJ/day, Stahl 2001; 841 kJ/day, Drent *et al.* 1978) and Black Brant in Alaska (892 kJ/day; Mason *et al.* 2006). Daily energy expenditure differences between Mason *et al.* (2006) and our study could be attributed to differences in time budgets and costs of thermoregulation between the studies (both higher in this study), despite similar air temperatures between studies (1°C; November–April *vs.* 2.6°C February–May, respectively).

Variation in estimates of DEE among Brent Goose populations in the Atlantic and Pacific flyways could result from variation in annual changes, energetic costs, habitat quality, and spatial distribution of food resources between wintering regions and from nocturnal activity of geese. Except for the recent studies of Mason *et al.* (2006), Ladin *et al.* (2011) and Heise (2012), previous studies did not deduct the cost of thermoregulation, and thus comparisons of DEE values would not be valid.

Understanding Black Brant activity budget and energy expenditure allows managers better to determine the ecological requirements of the species and to manage the population more effectively for sustainable yield. During years with heavy ice cover, Black Brant require embayments outside of Izembek Lagoon to meet their energy requirements even with little human disturbance. Black Brant also appear able to switch behaviours and foraging strategies to modify energy intake and meet changing daily energy needs. Further research to increase our understanding of Black Brant habitat sustainability would include assessments of food availability relative to sea level rise (Shaughnessy *et al.* 2012) and an evaluation of Black Brant foraging rates (g/day) during bed- and drift-feeding. Information from such studies would inform future research exploring the conditions leading to nocturnal foraging, which would enhance our understanding of how Black Brant survive winters in Alaska and exceed daily energy expenditure in spring for migration and reproduction.

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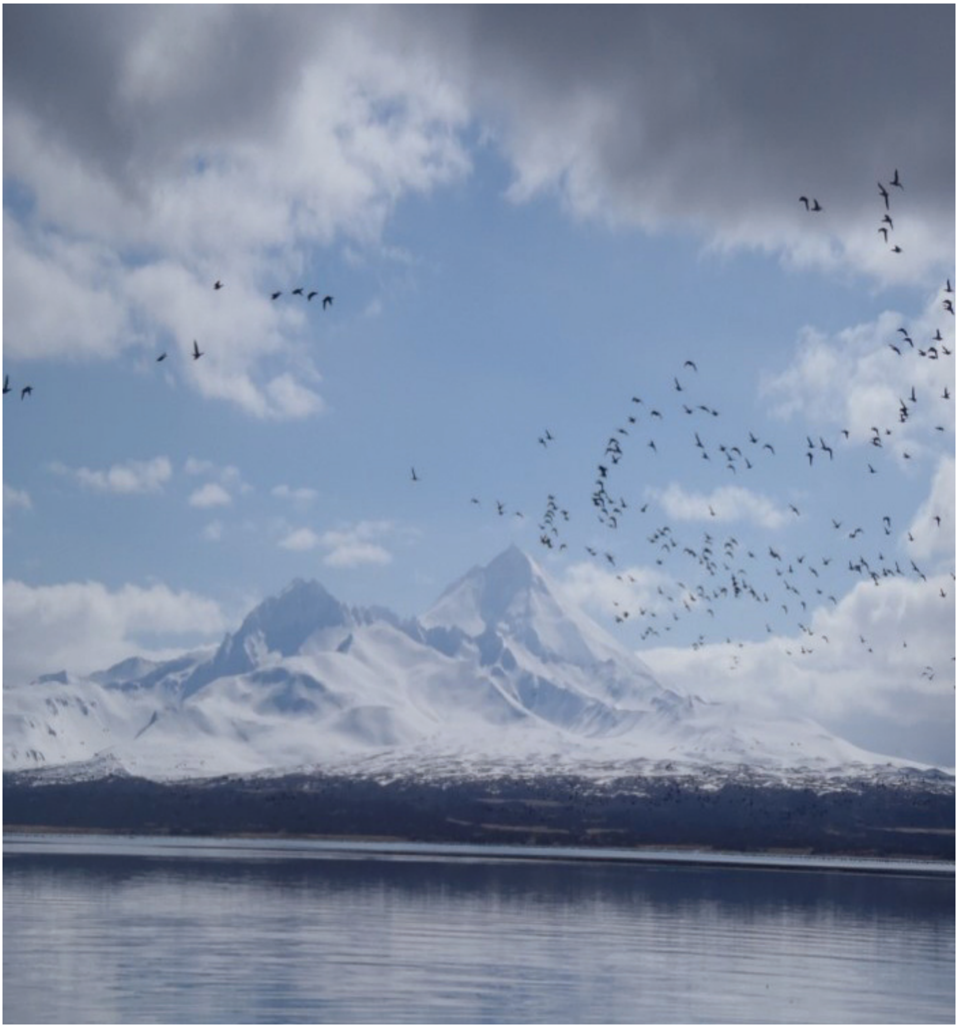

Photograph: Black Brant flying at high tide on the Izembek Lagoon, Alaska, in April 2011, by Bryan Daniels.

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