Journal of Wildlife Management 75(2):273–282; 2011; DOI: 10.1002/jwmg.58

Research Article

Time Energy Budgets and Food Use of Atlantic Brant Across Their Wintering Range

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ABSTRACT We conducted extensive behavioral and food sampling of Atlantic brant (*Branta bernicla hrota*) across their winter range and used time–activity budgets for brant to determine daily energy expenditure (DEE). Sampling occurred 1 December–31 May 2006–2008 in 11,225-km^2 sites between Rhode Island and Virginia containing important estuarine and upland habitat. To calculate DEE we used instantaneous scan sampling to estimate time–activity budgets. We also determined foods eaten by brant and energy density of food plants. Last, we quantified body condition of brant, which differed among years, months, regions, and ages, and sexes. Overall DEE for brant was 1,530 ± 64 kJ/day. There was considerable variation in time–activity budgets among years, months, regions, habitat, tide, temperature, and time-of-day, but we detected no significant difference in DEE of brant between years or among regions. However, DEE in January (2,018 ± 173 kJ/day) was nearly double the DEE of brant in May (1,048 ± 137 kJ/day). Brant spent their time feeding (32.3%), swimming (26.2%), resting (16.2%), and flying (14.5%). The percent of brant foreguts sampled contained macroalgae (53%) eelgrass (*Zostera marina*; 18%), salt marsh cordgrass (*Spartina alterniflora*; 17%), and terrestrial grass (*Poa*. sp.) and clover (*Trifollium* sp.; 9%). Energy density differed by vegetation type: macroalgae (12.6 ± 0.1 kJ/g), eelgrass (14.1 ± 0.1 kJ/g), new-growth salt marsh cordgrass (16.9 ± 0.2 kJ/g), and terrestrial grass and clover (17.7 ± 0.1 kJ/g). Atlantic brant exhibited behavioral plasticity thereby allowing modification of daily activity budgets to meet seasonally varying energetic requirements associated with wintering and spring staging. Recognizing a variable DEE can be used along with eventual estimates of food biomass and total metabolizable energy on the landscape to calculate carrying capacity (goose use days) on state, region, or range-wide scales.

KEY WORDS Atlantic brant, *Branta bernicla hrota*, daily energy expenditure, feeding behavior, submerged aquatic vegetation, time–energy budgets.

Current research on wintering migratory waterfowl suggests that the primary factor limiting many populations is availability of food (Owen et al. 1992, Bergan and Smith 1993, Jeske et al. 1994, Clausen et al. 2003, Mini and Black 2009). As habitat loss and degradation affects coastal areas along the Atlantic Coast, there is concern that waterfowl energetic demands may not be met (Stewart et al. 1988). Several joint ventures (JV; Arctic Goose JV, Central Valley Habitat JV, Mississippi Alluvial Valley JV, Gulf Coast JV) have adopted a bioenergetic approach to identify the amount of foraging habitat required to meet waterfowl population objectives, evaluate the extent to which these needs have been addressed on a regional scale, and to help identify areas for priority action (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986).

Atlantic brant (*Branta bernicula hrota*; hereafter brant) populations changed considerably during the 1900s in response to the disappearance of preferred foods at wintering and staging areas (Cottam et al. 1944, Reed et al. 1998). Brant once relied on eelgrass (*Zostera marina*) as a primary food plant (Reed et al. 1998). In 1931–1932 a wasting disease caused by the pathogenic slime mold *Labyrintha zosterae* reduced eelgrass abundance on the North Atlantic coast, which coincided with drastic declines in the brant population (Cottam et al. 1944, Rasmussen 1977). The greatest effect on populations was likely reduced breeding effort and success of malnourished brant (Kirby and Obrecht 1982). A moratorium on brant hunting from 1933 to 1952 occurred until populations of eelgrass and brant recovered (Rogers 1979). According to wintering waterfowl population estimates from the annual Mid-winter Survey, since the 1970s the brant population has fluctuated between 40,825 and 181,631 birds (United States Fish and Wildlife Service Division of Migratory Bird Management 2010). A suite of factors including spatial and temporal variability in reproductive success, harvest, food availability, and severe weather are thought to be responsible for these population fluctuations (Nelson 1978, Rogers 1979, Kirby and Ferrigno 1980). In the past 2 decades, brant have exhibited some plasticity in foraging behavior and food preference enabling birds to

Received: 18 May 2010; Accepted: 22 July 2010

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exploit a variety of food resources throughout the winter (Penkala 1976, Kirby and Obrecht 1980). For example, eelgrass has not recovered to its former extent and brant switched to macroalgae (e.g., *Ulva* sp. and *Enteromorpha* sp.) while expanding to new wintering areas.

Our primary objective was to estimate daily energy expenditure (DEE) of brant calculated from time–activity budgets across the primary Atlantic coast wintering range. We also sought to determine nutritional quality of 4 important foods found in foreguts of harvested and experimentally collected birds across the range, and to determine differences in body condition of brant throughout winter months.

STUDY AREA

Our study took place on the Atlantic coast of the United States between Rhode Island and Virginia (Fig. 1) from December to May of 2006–2008. The mid-Atlantic coastal region is highly urbanized and densely populated by humans. This geographic area is the primary wintering grounds for brant, and provides an array of estuarine habitat types. These habitat types contain important brant food resources (i.e., submerged aquatic vegetation (SAV) including macroalgae (*Ulva* sp. and *Enteromorpha* sp.) and eelgrass (*Z. marina*), new-growth salt marsh cord grass (*Spartina alterniflora*), and terrestrial grass (*Poa* sp.) and clover (*Trifolium* sp.).

METHODS

We designated 11,225-km^2 sites across the winter range in Narragansett Bay, Rhode Island (RI) (41°39′N, 71°19′W), New London, Connecticut (CT) (41°18′N, 72°11′W), Fairfield, CT (41°04′N, 73°23′W), Point Lookout, New York (NY) (40°36′N, 73°36′W), Jamaica Bay, NY (40°36′N, 73°53′W), Barnegat Bay, New Jersey (NJ) (39°39′N, 74°12′W), Atlantic City, NJ (39°24′N, 74°25′W), Cape May, NJ (39°02′N, 74°48′W), Indian River Bay, Delaware (DE) (38°37′N, 75°07′W), Sinepuxent Bay, Maryland (MD) (38°10′N, 75°14′W), and Chincoteague Bay, Virginia (VA) (37°55′N, 75°25′W). We divided the winter range into 4 geographic regions based on latitude and known concentrations of brant from the mid-winter waterfowl survey throughout the Atlantic Flyway. Region 1 contained 3 northern sites in RI and CT, region 2 contained 2 sites in NY, region 3 contained the 3 NJ sites, and region 4 contained one site each in DE, MD, and VA.

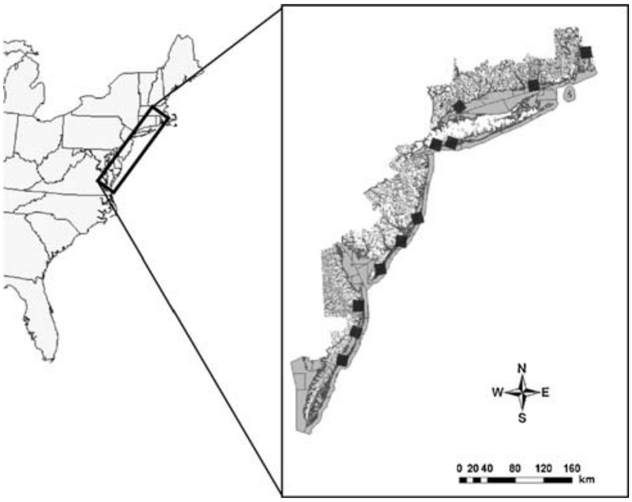

Figure 1. Map of 11,225-km^2 sampling areas distributed along the northeastern Atlantic coast across the wintering range of Atlantic brant in Narragansett Bay, RI (41 °39′N, 71 °19′W), New London, CT (41 °18′N, 72 °11′W), Fairfield, CT (41 °04′N, 73 °23′W), Point Lookout, NY (40 °36′N, 73 °36′W), Jamaica Bay, NY (40 °36′N, 73 °53′W), Barnegat Bay, NJ (39 °39′N, 74 °12′W), Atlantic City, NJ (39 °24′N, 74 °25′W), Cape May, NJ (39 °02′N, 74 °48′W), Indian River Bay, DE (38 °37′N, 75 °07′W), Sinepuxent Bay, MD (38 °10′N, 75 °14′W), and Chincoteague Bay, VA (37 °55′N, 75 °25′W).

We subdivided each of the 11,225-km^2 sites into 1-km^2 plots and alpha-numerically coded them (e.g., A1). For each site we a priori identified plots that contained both estuarine and upland habitat types where brant commonly occur and that were also accessible for land-based observations. We randomly selected plots from within this subset for behavioral data collection and vegetation sampling. We defined 3 habitat types within the Estuarine System (Cowardin et al. 1979): open water, estuarine, salt marsh; we also defined an upland habitat type. Open water habitat type consisted of shallow subtidal embayments. Estuarine habitat type contained intertidal streambeds, rocky shores, unconsolidated shores, and mudflats. Salt marsh habitat type consisted of both irregularly and regularly flooded intertidal emergent wetland dominated by salt marsh cordgrass. We defined the upland habitat type as terrestrial fields, lawns, or areas adjacent to or nearby estuarine habitat.

Estimating Daily Energy Expenditure (DEE)

We reproduced the methods used by Albright (1981) to estimate DEE using the following:

$$\mathrm{DEE} = \sum_{i=1}^{n} \{[(\mathrm{BMR} \times a_i) + C_T] \times T_i\}$$

where BMR is the average basal metabolic rate (kJ/hr), a_i the activity-specific multiple of BMR for the *i*th behavioral activity, C_{T} the cost of thermoregulation (kJ/hr), and T_i the time engaged in the *i*th behavioral activity (hr). We calculated estimates of DEE at 2 spatial and temporal scales. We calculated overall mean DEE on a range wide and season wide scale. Additionally, we calculated DEE for each region and month separately.

We calculated BMR using values for brent geese (*Branta bernicla bernicla*) measured in the zone of thermoneutrality (Stahl et al. 2001). We adjusted values for wintering Atlantic brant with a mean mass of 1.390 ± SE 0.01 kg, yielding a BMR for brant of 17.98 kJ/hr. We calculated the energetic costs for each activity using multipliers (a_i) of BMR for feeding (1.7), resting (sleeping or loafing, 1.6), comfort (preening or bathing, 1.8), walking (1.9), and agonistic (1.9) provided by non-invasive heart rate telemetry calibrated with respirometry of semi-captive brent geese (Stahl et al. 2001). Metabolic multipliers have not been directly measured in brant for swimming and courtship activities so we used values for swimming (2.2) and courtship (2.4) derived from wintering black ducks (*Anas rubripes*; Wooley and Owen 1978). We calculated flight costs from the relationship P_{flight} (W) $= 52.6$ mass$^{0.74}$ (Butler and Bishop 2000), using a mean mass of 1.390 ± 0.01 kg ($\bar{x} \pm$ SE, $n = 1{,}040$) from brant collected across the winter range between December and May of 2006–2008. This allometric relationship predicted energy costs of 67.1 W (241.6 kJ/hr) for flapping flight and thus a multiplier of 13.4 for flight costs relative to BMR.

Given that ambient temperature changed over time during December–May, we estimated C_T and DEE at 2 spatio-temporal scales: range wide (Dec–May 2006–2008) and by region per month. We calculated all thermoregulatory costs using the inverse linear relationship between metabolic rate and ambient air temperature below the lower critical temperature (LCT) of 7.5 °C derived from respirometry studies of Pacific brant (*Branta bernicla orientalis*): $C_T = 1.5 - 0.0365(t)$ (L O_2/hr) calculated from (Morehouse 1974). We converted oxygen consumption of birds using the energy equivalent of 20.1 kJ/hr to 1 L of O_2/hr (Carey 1996). When mean temperatures (temperature data collected during each behavioral observation period, this study) were above the LCT of 7.5 °C we assumed brant had no additional thermoregulatory costs. When calculating range wide DEE estimates we used a mean temperature of 6.8 °C averaged from mean ambient air temperatures at each of the 11 sites between 1 December and 31 May 2006–2008 taken from the National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center to derive a $C_T = 0.51$ kJ/hr (Diamond and Lief 2009).

To estimate the percent time brant engaged in different behavioral activities (T_i) throughout the day, we conducted instantaneous scan sampling of brant at each of the 11 sites, generally once per week, during the study period (Altmann 1974), except that we did not collect data in Delaware during 2006–2007, as that site was added only in 2007–2008. Within each site, we a priori designated plots where brant could potentially occur. From within this subset of plots, we randomly selected plots for observations and distributed them over 3 daytime periods: morning (30 min before sunrise–1,000 hr), midday (1,000–1,400 hr), and evening (1,400 hr–30 min after sunset). To calculate DEE we assumed that diurnal and crepuscular observations were representative of the entire 24-hr period.

Observers completed scans using a 20–60× spotting scope or 10× binoculars depending on the observer's proximity to birds. Once a group of birds was located, a 10-min acclimation period followed. Scan sampling occurred every 15 min for 1 hr or until all individuals left. We assumed that the scans collected every 15 min on the same group of birds ($\leq$4 scans) were not independent of each other, so we averaged them to avoid pseudoreplication. We recorded activities using micro-cassette and digital recorders or using hand counters. We recorded behaviors as feeding, swimming, flying, walking, resting, comfort, agonistic, and courtship. Disturbance impacts may also lead to higher energetic costs. During each scan we also recorded if a disturbance event occurred. We defined disturbance events as times when birds became collectively alert or $\geq$50% of birds took flight. We categorized likely causes of disturbances as 1) anthropogenic, people and dogs; 2) avian sources, raptors or large waders; 3) aircraft, planes, helicopters; 4) boats and jet skis; 5) autos, cars, or trucks; and 6) unknown. We calculated the percent occurrence of disturbances due to each likely cause by dividing the number of disturbance events due to each likely cause by the total number of disturbance events. For each observation, we recorded plot number, date, habitat type (open water, estuarine, salt marsh, or upland), tidal stage (low, flood, full, and ebb), ambient air temperature (°C), and time.

Quantifying Brant Diet and Nutritional Quality

We determined foods in the diet of brant from foregut contents of brant carcasses obtained through hunter-harvested donations and late-season state-issued scientific collection permits. We collected brant in all 11 study sites, as well as in North Carolina, during December–May 2006–2008, and in James Bay on the staging grounds in May 2007. We opened carcasses and removed the entire foregut (including the proventriculus and gizzard) and froze it at −40 °C until processing. In the laboratory, we opened foreguts and removed the contents and identified them as one of 4 food types (macroalgae, eelgrass, salt marsh cordgrass, and terrestrial grass and clover).

To measure food quality we collected plant samples at all sites throughout the study period in areas where we observed brant foraging. We collected live vegetation once every month from randomly selected plots within each site and sorted them into the same 4 categories used for foregut analysis (macroalgae, eelgrass, salt marsh cordgrass, and grass and clover sp.). We clipped upland grass and clover along with salt marsh cordgrass at the soil line and collected SAV by hand while wading in shallow water or in some cases using a D-frame dip net, a metal rake, or by boat. We removed dead plant material and dirt from all samples. We rinsed samples in de-ionized water before identifying them and then dried them for 48 hr at 50 °C. We then homogenized dried samples using a Wiley-mill (Thomas-Scientific, Swedesboro, NJ). We analyzed all samples using a Parr bomb calorimeter to determine energy density (kJ/g).

We calculated a body condition index (BCI) for all individuals with complete body mass (g), un-flattened wing chord (mm), age, and sex data (Table 1). We standardized body mass for structural differences between individuals by dividing body mass by wing chord (Baldassarre and Bolen 1994).

Statistical Analyses

We used univariate analysis of variance (ANOVA, $\alpha \leq 0.05$) to test for differences in DEE among years, months, regions, and ambient air temperatures (listed above). We used ANOVA to assess whether time–activity budgets differed among years, months, regions, habitat type, tidal stage, ambient air temperature categories (<0 °C, 0–7.5 °C, >7.5 °C), and time-of-day (morning, midday, and evening; see above). After testing behavior proportion data for departures from normality and homoscedasticity between

Table 1. Number of Atlantic brant carcasses we collected along northeastern Atlantic coast, USA, during November–May 2006–2008.

Yr	State	Month	No. collected	% ad	% F
2006–2007	RI	Dec	10	70	60
		Jan			
		Feb	9	100	33
		Mar	15	100	40
		Apr	30	47	43
		May			
	CT	Dec	2	100	50
		Jan	20	75	55
		Feb	17	88	65
		Mar	12	100	58
		Apr	10	90	60
		May	11	73	45
	NY	Nov	13	92	54
		Dec			
		Jan			
		Feb	10	100	70
		Mar	10	70	50
		Apr	10	90	70
		May	11	91	36
	NY[a]	Dec			
		Jan			
		Feb	24	67	46
		Mar	5	100	60
		Apr	1	100	100
		May	10	90	50
	NJ	Nov	7	100	43
		Dec	14	107	64
		Jan	17	71	82
		Feb	12	92	75
		Mar	15	40	53
		Apr	7	100	29
		May	5	100	20
	MD	Nov	19	63	47
		Dec	12	83	67
		Jan	22	55	50
		Feb	29	66	31
		Mar	3	67	100
		Apr			
		May			
	VA	Dec			
		Jan	17	88	59
		Feb	22	86	45
		Mar	10	90	30
		Apr			
		May			
	NC	Dec	9	22	78
		Jan	30	73	37
		Feb			
		Mar			
		Apr			
		May			
2007–2008	RI	Dec	14	86	50
		Jan			
		Feb	12	75	33
		Mar	14	64	29
		Apr	14	71	57
		May	15	80	33
	CT	Dec	8	75	63
		Jan	6	50	83
		Feb	15	80	73
		Mar	12	75	58
		Apr	18	67	39
		May	16	50	44
	NY	Dec	22	50	68
		Jan	14	71	43
		Feb	14	100	43
		Mar	7	0	57
		Apr	10	100	40
		May	10	60	50
	NY[a]	Dec			
		Jan	20	40	45
		Feb	20	70	35
		Mar	21	67	48
		Apr			
		May	20	80	40
	NJ	Oct	2	50	50
		Nov	11	82	64
		Dec	13	77	46
		Jan	14	57	43
		Feb	13	69	31
		Mar	15	60	53
		Apr	15	100	47
		May	15	47	40
	DE	Dec	20	60	55
		Jan	9	67	78
		Feb	18	44	50
		Mar	20	55	50
		Apr	20	40	50
		May	11	27	45
	MD	Nov	11	73	55
		Dec	6	33	67
		Jan	14	43	57
		Feb	2	50	50
		Mar	2	50	100
		Apr			
		May			
	VA	Dec			
		Jan	5	80	100
		Feb	10	30	60
		Mar	12	75	58
		Apr			
		May			
Total			1,040		
Mean				70	51

[a] Brant collected through depredation efforts at John F. Kennedy International Airport.

groups, we arcsine transformed data prior to analysis to meet underlying assumptions of normality (Zar 1974). We analyzed energy density values using ANOVA, $\alpha \leq 0.05$ to test for differences among years, months, regions, and vegetation types. We used ANOVA to test for differences in BCI among years, months, regions, age, and sex. When we detected significant main effects and there were $\geq$3 levels of the independent variable, we used Tukey's post hoc tests ($\alpha \leq 0.05$) to determine level of significance.

RESULTS

We completed 1,441 independent behavioral scans, after averaging by observation event, across the study area. Overall mean DEE based on time–activity budget data was 1,530 ± 64 kJ/day. Daily energy expenditure was different among months ($F_{5,102} = 2.44$, $P < 0.05$) but not among years, regions, or temperatures ($F_{1,102} = 2.59$, $P = 0.11$; $F_{3,102} = 0.03$, $P = 0.99$; and $F_{2,102} = 0.55$, $P = 0.58$, respectively). Energy expenditure peaked in January (2,018 ± 173 kJ/day) and declined each month thereafter reaching the lowest energy expenditure in May (1,049 ± 137 kJ/day; Fig. 2).

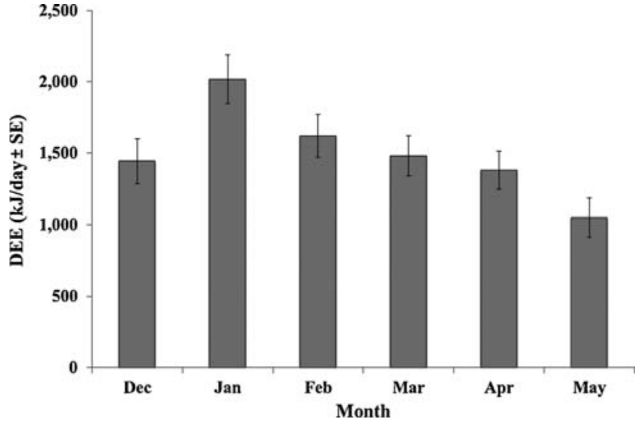

Figure 2. Daily energy expenditure (DEE, kJ/day ± SE) of Atlantic brant by month along the northeastern Atlantic coast, USA, during December–May 2006–2008.

Intrinsically, DEE estimates are driven by cost of thermoregulation and time spent in behavioral activities. Although energy costs associated with thermoregulation were low throughout the study period, brant experienced greater thermoregulatory costs in January and February compared to other months. Thermoregulatory contributions to DEE when mean monthly temperatures were below the LCT of 7.5 °C were on average 4.5% of DEE or 64 kJ/day.

On average, brant were engaged in 32% feeding, 26% swimming, 16% resting, 14% flying, 8% comfort activity, 3% walking, and 0.7% agonistic activity (Table 2). Percent time brant spent in all activities except swimming and walking differed among months, with flight activity being significantly greater in January (24%) compared to all other months (Table 2). We further detected significant differences among years for all behaviors except comfort (Fig. 3), regions (Table 3), and environmental factors including habitats, temperature, tide, and time-of-day (Table 4). Applying energetic costs to each of these behaviors produced relative contributions to yearly DEE of 14–19% feeding, 14–18% swimming, 50–58% flying, 6–11% resting, 4% comfort, 1–2% walking, and <1% agonistic (Table 2).

We calculated the frequency of occurrence of disturbance events for each likely known cause over the entire winter range. We recorded 374 unique disturbance events accounting for 26% of independent sampling events. Disturbances in January accounted for 31% of all scans, which was above the mean for all months. People and dogs caused 25% of disturbances ($n = 93$), birds caused 14% of disturbances ($n = 53$), automobiles caused 10% of disturbances ($n = 36$), boats caused 9% ($n = 32$), aircraft caused 6% ($n = 22$), and hunting was responsible for 2% of all observed disturbances ($n = 6$). However, many causes of disturbance were unknown (36%, $n = 132$; Fig. 4).

Foregut contents from 1,057 carcasses (Table 5) contained mostly macroalgae, which we found in 40–60% of all samples across months and years (Fig. 5). We identified eelgrass in 45% of foregut samples during November of both years but detected it less often in subsequent months. We did not find salt marsh cordgrass in any foreguts during 2006–2007 and it was rare in 2007–2008. We identified grass and clover in more foreguts from brant harvested in spring 2006–2007 (67% of foreguts in May; Fig. 5). Of note, in May 2007 13 of 15 birds sampled on James Bay, a key staging area during migration, had full foreguts containing only terrestrial grasses (family Poaceae, alkalaigrass [*Puccinellia* sp.] and fescue [*Festuca* sp.]).

Average energy density of all vegetation samples ($n = 796$) collected during 2006–2008 was 14.3 ± 0.1 kJ/g, although energy density differed among vegetation types (Fig. 6) but not among years, months, or regions (vegetation type: $F_{3,687} = 71.40$, $P < 0.01$; year: $F_{1,687} = 0.37$, $P = 0.54$; month: $F_{5,687} = 0.82$, $P = 0.54$; and region: $F_{3,687} = 0.35$, $P = 0.79$). Due to differences in energy density, we subsequently tested each vegetation type separately for differences among years, months, and regions. Energy density of macroalgae was on average 12.60 ± 0.10 kJ/g, although it differed among months but not among years or regions (month: $F_{5,452} = 4.42$, $P < 0.01$; year: $F_{1,452} = 0.04$, $P = 0.85$; and region: $F_{3,452} = 0.52$, $P = 0.67$). Energy density of macroalgae in December (13.60 ± 0.30 kJ/g), January (13.30 ± 0.20 kJ/g), and February (13.3 ± 0.3 kJ/g) was greater than in April and May (11.30 ± 0.30 kJ/g and 11.80 ± 0.30 kJ/g, respectively). Energy density of eelgrass varied only as a function of region and not of year or month (region: $F_{3,35} = 4.63$, $P < 0.05$; year: $F_{1,35} = 0.68$, $P = 0.42$; and month: $F_{5,35} = 2.33$, $P = 0.06$). Pair-wise comparisons among

Table 2. Percentage of time ($\bar{x}$ ± SE) Atlantic brant spent in different activities along the northeastern Atlantic coast, USA, during December–May, 2006–2008.

	% time spent per activity													
	Dec		**Jan**		**Feb**		**Mar**		**Apr**		**May**		**Overall**	
Activity	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Feed	27.4	1.8	25.5	1.6	31.4	1.7	30.3	1.5	38.5	1.7	44.2	2.4	32.3	0.7
Swim	26.5	1.7	24.2	1.6	28.2	1.7	27.2	1.7	25.8	1.7	25.2	2.3	26.2	0.7
Fly	13.0	1.8	23.6	2.1	15.3	1.7	13.7	1.7	11.8	1.5	5.2	1.3	14.5	0.7
Walk	2.0	0.3	2.5	0.4	2.5	0.3	2.4	0.3	2.9	0.4	3.1	0.4	2.5	0.1
Rest	18.6	1.5	16.1	1.3	16.8	1.3	18.4	1.3	13.7	1.1	12.8	1.4	16.2	0.5
Comfort	11.8	1.2	7.4	0.8	5.3	0.7	7.0	0.7	6.7	0.6	8.7	1.2	7.6	0.3
Agonistic	0.8	0.1	0.7	0.1	0.5	0.1	0.9	0.2	0.7	0.1	0.8	0.3	0.7	0.1
Courtship							0.2	0.2					0.07	0.04
N	207		272		256		270		289		147		1,441	

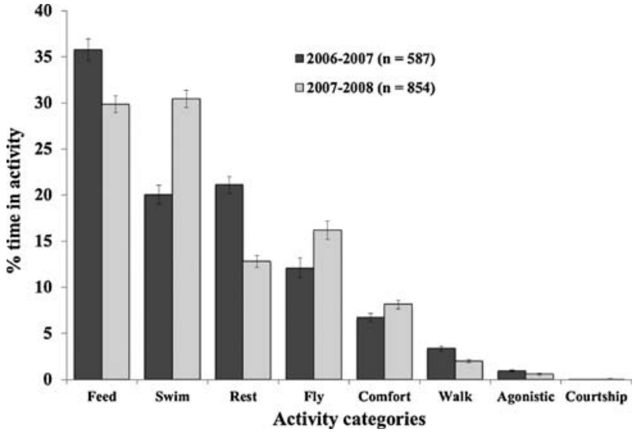

Figure 3. Percentage of time Atlantic brant spent in different activities ($\bar{x}$ ± SE) along the northeastern Atlantic coast, USA, during December–May 2006–2008.

regions did not detect any differences among regions. We detected no differences between years, months, or regions for salt marsh cordgrass (model: $F_{10,52} = 0.25$, $P = 0.99$) or grass and clover (model: $F_{39,148} = 1.14$, $P = 0.28$). Mean BCI calculated from 1,040 individuals was 4.29 ± 0.01 ($\bar{x}$ ± SE). When testing BCI for differences among years, months, regions, ages, and sexes we detected interactive effects among all terms within the model ($F_{161,866} = 1.86$, $P < 0.01$), indicating patterns of BCI between ages and sexes differed among regions, months, and years. In 2006–2007 brant had lower BCI (4.19 ± 0.02) compared to 2007–2008 (4.37 ± 0.02). Values for BCI were greater in after hatch year (AHY) brant (4.42 ± 0.02) compared to hatch year (HY) brant (4.13 ± 0.03). Male brant had higher average BCI values compared to females (4.38 ± 0.02 and 4.20 ± 0.02, respectively). Values for BCI were lower in January, February, and March (4.16 ± 0.03, $\bar{x}$ ± SE) compared to November, December, and April (4.36 ± 0.04, $\bar{x}$ ± SE), and BCI was greatest in May (4.86 ± 0.04). In region 4 brant had lower BCI (4.20 ± 0.03) compared to region 1 (4.35 ± 0.03) and region 3 (4.42 ± 0.03).

DISCUSSION

Wintering Atlantic brant, like other migratory waterfowl, were able to satisfy their energy requirements by adjusting overall time–activity budgets, foraging effort or intake rate, and exploiting different types of available food (Madsen 1985, Prins and Ydenberg 1985, Owen et al. 1992, Rowcliffe et al. 1995, Hassall et al. 2001). The behavioral plasticity of brant allowed them to exploit different foods at different times during the winter and staging periods (Cottam et al. 1944, Kirby and Obrecht 1980, Percival and Evans 1997, Inger et al. 2006, Mason et al. 2007).

Our mean estimate of DEE (1,530 ± 64 kJ/day) was similar to that reported by Tinkler et al. 2009 (1,326–1,556 kJ/day). However, our mean monthly DEE ranged between 1,049 and 2,017 kJ/day. Our DEE estimates were higher than most other previous studies that used time–activity budgets to estimate DEE for brent geese (e.g., 841.4 kJ/day, Riddington et al. 1996; 842 ± 14 kJ/day, Stahl et al. 2001; 1,152 kJ/day, Inger et al. 2006; and 1,013 ± 14 kJ/day, Mini and Black 2009). Riddington et al. (1996), Stahl et al. (2001), and Mini and Black (2009) studied brent geese during late winter and spring staging in salt marsh and pasture habitats. Similar to Tinkler et al. (2009), our study took place over the entire wintering period and included time–activity budget data from the entire wintering period, throughout which we detected significant seasonal variation. Our estimate of DEE for brant also accounts for energy use of brant on a range-wide scale over a large geographic area. Variation in estimates of DEE between European brent geese and Atlantic brant could also result from variation in energetic costs, habitat quality, spatial distribution of food resources between wintering regions and from nocturnal activity of geese.

We found that brant adjusted their behavior between years, presumably in response to annual variation in food abundance and energy demands. In 2007–2008 brant spent a greater percentage of time in costly locomotive flying and swimming activities, compared to in 2006–2007 (Fig. 3). This variation in locomotive behavior corresponds to an increase of 176 kJ/day between years. Brant were able to fulfill these heightened energetic costs in 2007–2008 despite spending less time feeding compared to 2006–2007. When we converted activity budgets to energy budgets, flight behavior constituted 50% of DEE. Wintering European light-bellied brent geese have shown similar behavioral patterns in locomotive activity due to shifts in food abundance, consequent foraging and habitat selection, and engagement in nighttime feeding (Tinkler et al. 2009). Several previous

Table 3. Percentage of time ($\bar{x}$ ± SE) Atlantic brant spent in different activities in 4 regions: region 1 (RI and CT), region 2 (NY), region 3 (NJ), and region 4 (DE, MD, and VA) along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

	Region 1		Region 2		Region 3		Region 4		Overall	
Activity	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Feed	33.3	1.4	33.9	1.5	30.8	1.1	30.4	2.2	32.3	0.7
Swim	24.5	1.5	25.3	1.3	26.3	1.1	31.9	2.6	26.2	0.7
Fly	10.4	1.4	15.5	1.3	16.2	1.3	14.5	2.4	14.5	0.7
Walk	2.2	0.3	3.8	0.3	2.0	0.2	1.9	0.6	2.5	0.1
Rest	21.3	1.3	13.6	0.9	17.0	0.9	9.6	1.4	16.2	0.5
Comfort	6.8	0.6	7.3	0.6	7.3	0.5	11.0	1.5	7.6	0.3
Agonistic	1.3	0.2	0.6	0.1	0.5	0.1	0.7	0.2	0.7	0.1
Courtship	0.2	0.2	0.02	0.01					0.05	0.04
N	328		424		539		150		1,441	

Table 4. Percentage of time ($\bar{x}$ ± SE) Atlantic brant spent in activities among habitat, tide, temperature, and time-of-day factors along the northeastern Atlantic coast, USA, during Dec–May 2006–2008.

		Categories							
		Open water		Estuarine		Salt marsh		Upland	
Factors	Activities	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Habitat	Feed	25.3	0.9	29.1	1.1	45.4	3.2	61.7	2.2
	Swim	31.2	1.1	30.4	1.2	9.1	1.7	3.8	0.9
	Fly	17.7	1.2	11.6	1.1	9.1	2.0	12.3	1.8
	Walk	1.4	0.2	2.3	0.2	2.5	0.5	7.9	0.7
	Rest	17.2	0.8	15.8	0.9	22.5	2.3	10.2	1.3
	Comfort	6.5	0.4	10.3	0.7	11.0	1.7	2.7	0.3
	Agonistic	0.7	0.1	0.5	0.1	0.4	0.1	1.4	0.3
	Courtship								
	N	703		471		90		177	

		Categories							
		Low		Flood		Full		Ebb	
Factors	Activities	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Tide	Feed	35.8	1.6	29.8	1.4	30.6	1.8	33.3	1.2
	Swim	26.4	1.7	28.0	1.4	19.4	1.6	28.2	1.2
	Fly	9.7	1.3	18.0	1.6	14.1	1.7	14.2	1.2
	Walk	2.7	0.3	2.3	0.2	2.3	0.3	2.8	0.3
	Rest	17.3	1.3	14.2	0.9	23.8	1.6	13.3	0.8
	Comfort	6.7	0.6	7.3	0.7	8.8	0.9	7.6	0.5
	Agonistic	1.1	0.1	0.4	0.1	1.1	0.2	0.6	0.1
	Courtship								
	N	255		424		265		497	

		Categories					
		<0		0–7.5		>7.5	
Factors	Activities	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Temp (°C)	Feed	32.2	2.5	30.7	1.2	33.2	1.0
	Swim	24.0	2.2	25.3	1.2	27.1	1.0
	Fly	17.9	2.8	17.1	1.4	12.3	0.9
	Walk	3.1	0.7	2.2	0.2	2.7	0.2
	Rest	17.3	1.9	17.4	1.0	15.2	0.7
	Comfort	4.9	0.7	6.7	0.5	8.6	0.5
	Agonistic	0.6	0.2	0.6	0.1	0.8	0.1
	Courtship						
	N	135		503		803	

		Categories					
		Morning		Midday		Evening	
Factors	Activities	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Time-of-day	Feed	34.8	1.2	30.2	1.0	32.1	2.0
	Swim	23.9	1.1	27.4	1.0	28.4	2.1
	Fly	13.9	1.1	13.8	1.0	18.7	2.4
	Walk	2.6	0.2	2.4	0.2	2.8	0.4
	Rest	16.7	0.9	17.1	0.8	11.9	1.2
	Comfort	7.4	0.6	8.3	0.5	5.7	0.8
	Agonistic	0.8	0.1	0.7	0.1	0.6	0.1
	Courtship						
	N	560		679		202	

studies have also found that waterfowl are active at night and vary their activity under different environmental and physiological stimuli (Morton et al. 1989, Anderson and Smith 1999, Guillemain et al. 2002, McWilliams and Raveling 2004, Rizzolo et al. 2005). Due to inherent difficulty and technological limitations for completing nocturnal observations of brant across the winter range we assumed diurnal and crepuscular energetic costs represented the entire 24-hr period when we estimated DEE. Because it is currently unknown how brant allocate time spent in nocturnal activities, this assumption may introduce bias into our estimates. Investigation of nocturnal activity budgets of brant would improve accuracy in estimates of DEE and carrying capacity.

Disturbance events occurred during 26% of all scans during 2006–2008. Negative impacts due to disturbance have been documented in brant as well as other geese (Belanger and Bedard 1990, McWilliams et al. 1994, Ward et al. 1999, Desmonts 2009). Additional energetic costs associated with

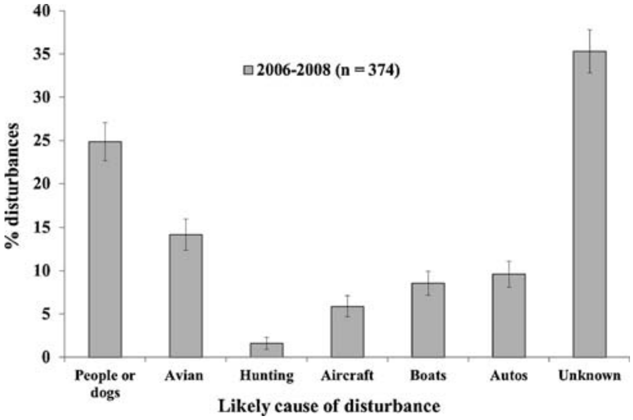

Figure 4. Percentage of likely causes of disturbance of Atlantic brant wintering on the northeastern Atlantic coast, USA, during December–May 2006–2008.

increased flight due to disturbances have been documented in European brent geese in upland pasture and salt marsh habitats where geese may recoup energetic costs associated with disturbance by feeding more at night (Riddington et al. 1996) or by increasing the percentage of time spent foraging in habitats where higher quality food is available (Inger et al. 2008). Although negative impacts from direct disturbance must be considered, broad-scale human impacts resulting in habitat degradation and loss may have an even greater impact on fitness (Desmonts et al. 2009).

Dietary constituents detected from gross foregut content analysis indicate that brant used a combination of SAV species (macroalgae and eelgrass), salt marsh species (*Spartina* sp.), and terrestrial grass and clover. Our results were similar to those from brant wintering in New Jersey (Penkala 1976, Kirby and Obrecht 1980), which indicate brant eat mostly macroalgae in early winter (Fig. 5). European brent geese also select foods based on quality and availability, shifting from macroalgae and eelgrass in early winter to salt marsh cordgrass and upland grass and clover as they become available in late winter (Rowcliffe et al. 2001, Inger et al. 2006). Seasonal variability in macroalgae abundance will impact brant feeding behavior and use of habitats. We observed brant using upland habitat more in 2006–2007 than in 2007–2008. These habitat and food use shifts are most likely in response to seasonal variation in SAV abundance. These results support previous research indicating that brant may shift their diet based on energy content and availability (Hassall et al. 2001, Durant et al. 2004, Inger et al. 2006, Tinkler et al. 2009).

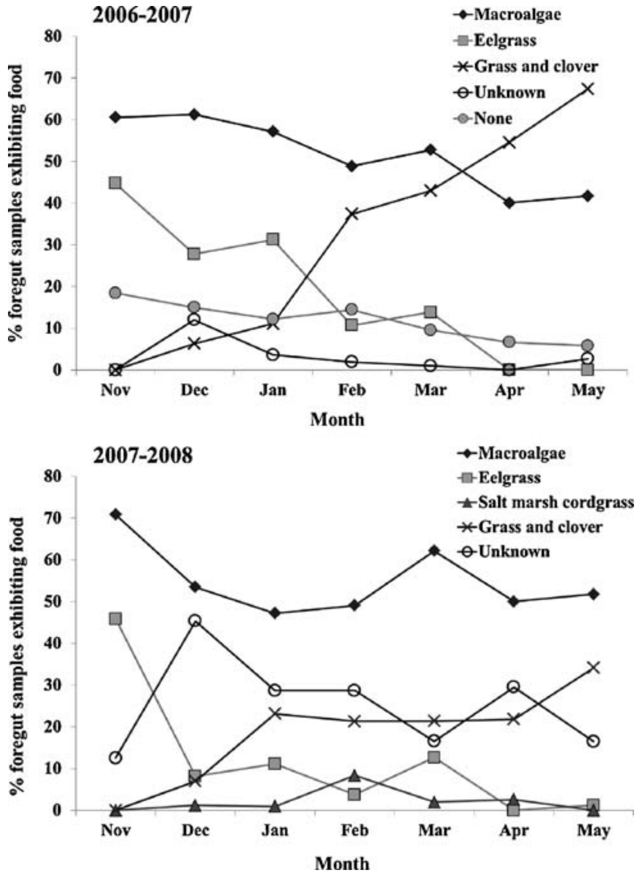

Figure 5. Mean ($\bar{x} \pm$ SE) frequency of occurrence (% of total occurrences) of different food types in foregut samples from Atlantic brant along the northeastern Atlantic coast, USA, during November–May 2006–2008.

Table 5. Foregut samples dissected from 1,057 brant carcasses collected per month along the northeastern Atlantic coast, USA, during December–May 2006–2008.

Yr	Month	*N*
2006–2007	Nov	29
	Dec	47
	Jan	86
	Feb	119
	Mar	73
	Apr	58
	May	51
2007–2008	Nov	26
	Dec	86
	Jan	108
	Feb	108
	Mar	103
	Apr	78
	May	85
Total		1,057

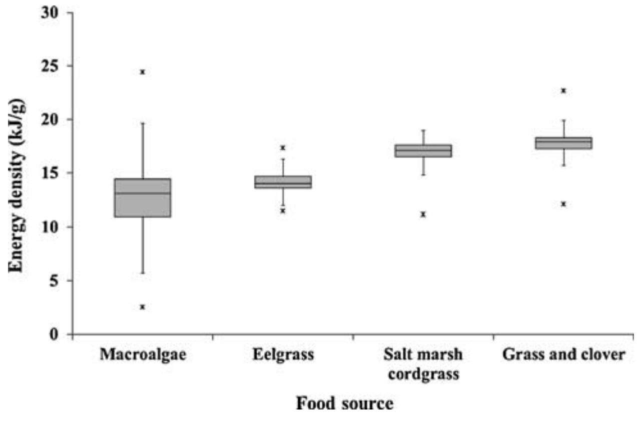

Figure 6. Energy density (kJ/g) of preferred Atlantic brant forage samples (n = 796) collected along the northeastern Atlantic coast, USA, during November–May 2006–2008.

Energy density of foods that brant consume during the winter was similar to foods analyzed by Kirby and Obrecht (1980) including macroalgae (14.6 kJ/g), eelgrass (14.6 kJ/g), and salt marsh cordgrass (17.9 kJ/g; values converted from kcal/g). Interestingly, salt marsh cordgrass and terrestrial grass and clover showed no difference in energy density across years, months, or regions. Conversely, we detected variation in energy density of SAV among months (for macroalgae) and regions (for eelgrass). As macroalgae nutritional quality decreases over winter terrestrial grass and clover become an important dietary component for brant, particularly in late winter prior to migration.

Differences in BCI of brant among months further indicate that brant experience critical periods in early winter when energy expenditure reaches peak levels. During these critical periods brant are susceptible to severe weather events and extreme cold temperatures that can result in higher mortality rates and lowered recruitment (Kirby and Ferrigno 1980). Pacific black brant (*Branta bernicla nigricans*) experience similar patterns of body condition during early winter (Mason et al. 2007). The condition of waterfowl during early winter has also been positively correlated with annual survival (Haramis et al. 1986, Jeske et al. 1994). Additionally, body condition of brent geese during spring staging impacts breeding success (Prop and Deerenberg 1991). Concurrent with lowered energy expenditure during spring staging, brant BCI reached significantly greater levels in May prior to migration.

MANAGEMENT IMPLICATIONS

Atlantic brant exhibited behavioral plasticity thereby allowing modification of daily activity budgets to meet seasonally varying energetic requirements associated with wintering and spring staging. Recognition of a variable DEE, along with eventual estimates of food biomass and total metabolizable energy on the landscape, can be used to calculate carrying capacity (goose use days) on state, region, or range-wide scales. Additionally with recognition of a variable DEE and seasonal carrying capacity estimates, adaptive management could inform annual harvest management decisions for brant throughout the Atlantic Flyway. Future carrying capacity estimates should incorporate terrestrial field habitat acreage when calculating available biomass estimates. We also suggest that remote sensing and predictive modeling techniques be used to estimate seasonal abundances of SAV to aid in the future management of brant.

ACKNOWLEDGMENTS

This work was supported by the Atlantic Flyway Council, New Jersey Division of Fish and Wildlife, Pittman-Robertson Federal Aid to Wildlife Restoration Grant W-68-R, University of Delaware, Edwin B. Forsythe National Wildlife Refuge (NWR), Cape May NWR, and a Washington Brant Foundation grant. We are grateful for the cooperation and support of S. Atzert, H. Schlegel (Edwin B. Forsythe and Cape May NWR, respectively), J. Osenkowski (Rhode Island Department of Environmental Management), M. Huang (Connecticut Department of Environmental Protection), B. Swift, L. Masi, and S. Chan (New York State Department of Environmental Conservation), L. Francoeur (The Port Authority of New York and New Jersey), T. Schneider (Town of Hempstead Department of Conservation and Waterways), T. Nichols (New Jersey Division of Fish and Wildlife), M. DiBona (Delaware Department of Natural Resource and Environmental Control), L. Hindman (Maryland Department of Natural Resources), G. Costanzo (Virginia Department of Game and Inland Fisheries), J. Fuller (North Carolina Wildlife Resources Commission), J. Wortham (U.S. Fish and Wildlife Service), J. Stanton (U.S. Fish and Wildlife Service), K. Winiarski (University of Rhode Island), M. Giles, and a special thanks to D. Cramer. G. Shriver and D. Tallamy provided additional reviews of the manuscript.

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Associate Editor: Bret Collier.