

ENERGETICS AND TIME ALLOCATION OF CACKLING CANADA GEESE DURING SPRING

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Abstract: We compared the observed daily time allocation of cackling geese (*Branta canadensis minima*) during spring with that predicted from estimates of daily energy requirements and measurements of apparent metabolizable energy (AME) and intake rates. Cackling geese gained substantial energy and protein reserves at staging areas in California before migration to Alaska in April and after arrival in Alaska, before egg laying. Cackling geese gained mass during spring by increasing intake rates (g/hr) and by feeding more during the evening and night. During March and April, cackling geese spent 10-12.6 hr each day on feeding fields. We estimated that while cackling geese are on feeding fields they must eat on average 11-18 g dry mass/hr in March and 18-20 g dry mass/hr in April to satisfy daily energy requirements. Diet quality affected intake rates and the amount of time geese spent grazing. When cackling geese were fed a lower-quality forage (pasture grass) they ate 50% less than geese fed a higher-quality forage (alfalfa). AME of the 2 diets was similar (11.3 kJ/g and 10.9 kJ/g). Cackling geese in the wild spent more time feeding when in pasture compared to alfalfa fields, apparently to compensate for reduced intake rates. Temperature had little effect on time allocation except when below -6° C. Compared to larger herbivores, small grazers like cackling geese must eat proportionately more each day and are more likely feeding-time limited. The feeding time of cackling geese during spring was limited primarily by predation risk, daylength, and harvesting and digestive constraints associated with selectively eating leaves.

Key words: Alaska, *Branta canadensis minima*, cackling Canada goose, California, energetics, time allocation.

One key aspect of animal feeding strategies that has attracted little theoretical or empirical attention is the division of total feeding time required per unit time (e.g., a day) into discrete feeding periods (Schoener 1971, Stephens and Krebs 1986). Attributes of the biotic and abiotic environment can affect an animal's energy requirements and the amount of time available for feeding (King 1974). However, few studies have focused on how the duration and division of feeding periods are influenced by both biotic (e.g., growth and reproduction, body size, foraging mode, digestion, competition, predation) and abiotic factors (e.g., weather, light levels). In this paper, we document how an avian grazer allocates its feeding time during spring in relation to such biotic and abiotic factors.

For animals that eat leaves, acquiring sufficient energy is difficult because foliage can be bulky, difficult to digest, and low in energy content (Demment and Van Soest 1985). The virtual absence of folivory among flying animals (Dudley and Vermeij 1992) suggests that

the high energy demands of flight are usually incompatible with the ecological limitations associated with eating leaves (Morton 1978). In general, avian folivores consume relatively large quantities of plant material, have rapid passage rates (McWilliams 1999), and typically digest little if any of the plant's fiber (Mackie 1987, Karasov 1990, Sedinger 1997). Because of their simplified digestive strategy and relatively small size, most avian folivores consume high-quality forage at relatively fast rates (Drent and Prins 1987, Lopez-Calleja and Bozinovic 2000) which, in turn, influences time required for feeding.

We investigated time allocation and energy acquisition strategies of cackling geese during spring. Cackling geese are the smallest race of the Canada goose (ca. 1,500 g versus ca. 5,700 g for the largest race; Bellrose 1980) and are essentially pure grazers during spring (McWilliams and Raveling 1998). Cackling geese increase their body mass 30-50% from mid-winter to spring (Raveling 1979a). Body reserves accumulated by cackling geese during spring are critical for successful breeding (Raveling 1979a). These patterns of spring mass gain and body reserve dynamics have been well documented in many geese including brant (*Branta bernicla*; Ankney 1984, Vangilder et al. 1986), lesser

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snow geese (*Chen caerulescens caerulescens*; Ankney and MacInnes 1978, Alisauskas 1988), greater snow geese (*C. c. atlanticus*; Gauthier et al. 1984a, b), greater white-fronted geese (*Anser albifrons frontalis*; Ely and Raveling 1989, Budeau et al. 1991), and other races of Canada geese (Hanson 1962, Raveling and Lumsden 1977, McLandress and Raveling 1981a, Bromley and Jarvis 1993). However, few studies of geese or other birds have integrated the knowledge of body condition and corresponding energy requirements with observations of time allocation and measurements of energy intake (e.g., Masman et al. 1988, Bedard and Gauthier 1989, Prop and Black 1998).

We predicted how much time cackling geese needed to spend feeding during spring using estimates of daily energetic requirements and measurements of digestive efficiency and intake rates. We compared these predictions with observed time-allocation patterns of cackling geese during spring. This approach allowed us to identify constraints that were important in limiting intake rate and feeding time. We also investigated the effects of weather, phase of moon, duration of daylight, forage quality, and changes in energetic requirements on time allocation of cackling geese during spring.

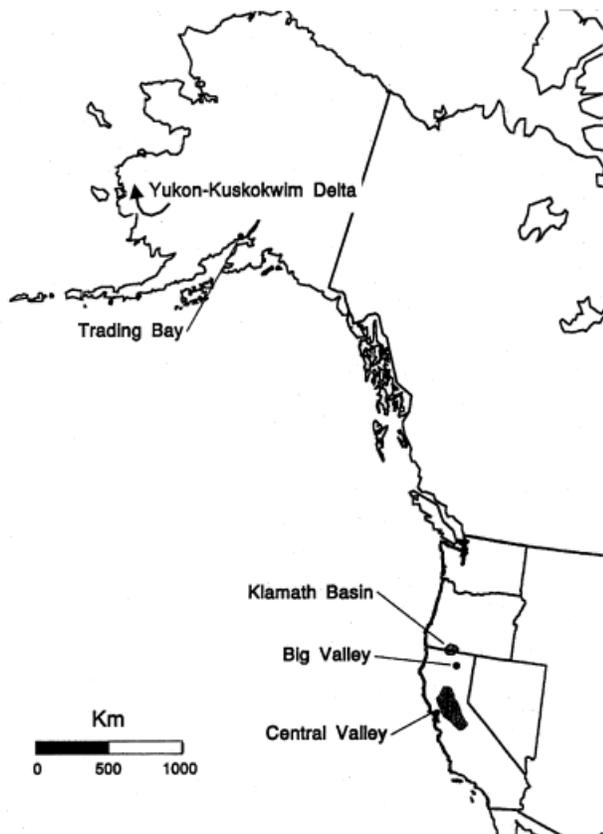


Fig. 1. Locations used by cackling Canada geese throughout the annual cycle.

METHODS

Study Site and Study Period

Between February and late April, up to 75% of the cackling goose population moves from wintering areas in the Central Valley of California to spring staging sites in the intermountain valleys in northeastern California (Fig. 1). Big Valley (41°08' N, 121°04' W), one of the intermountain valleys most used by cackling geese, contains a diversity of habitats including wetlands with mostly native floras (McWilliams and Raveling 1998).

In 1989 and 1990, we began monitoring the abundance, distribution, and activity of cackling geese in Big Valley on 1 March, approximately 1 week after >1,000 cackling geese were counted. In both years, cackling goose populations in Big Valley peaked in early April at about 6,000 individuals. We continued monitoring cackling geese almost daily until they left Big Valley in late April.

Estimate of Daily Energy Expenditure

Daily energy expenditure (DEE) for geese during spring is the sum of daily energy requirements plus the cost of tissue synthesis associated with acquisition of body reserves. We used an equation based on 40 non-passerine species for estimating daily energy requirements of cackling geese: Field Metabolic Rate (FMR; kJ/day) = $8.47 W^{0.704}$, where W is body mass in grams (Williams et al. 1993). Nagy et al. (1999) provided a similar allometric equation (FMR [kJ/day] = $10.5 W^{0.681}$) that was based on 95 species of passerine and nonpasserine birds. The cost of tissue synthesis was estimated using the energy content of the tissue (39.54 kJ/g lipid, 17.99 kJ/g protein; Ricklefs 1974: Table 1) and multiplying by 1.43, assuming a 70% efficiency of energy conversion (King 1973). Thus, DEE for a given period was calculated as:

$$\text{DEE} = \text{FMR (kJ/day)} + \\ ([\text{g lipid added per day}][39.54 \text{ kJ/g}] \\ + [\text{g protein added per day}][17.99 \text{ kJ/g}](1.43))$$

Estimation of Body Composition

We estimated body composition of cackling geese just before their migration from Big Valley to Alaska (hereafter "late spring-staging geese") using body mass of cackling geese ($n = 117$) captured at dawn with rocket nets on 24 April 1989, and body composition data from giant Canada geese (*B. c. maxima*) captured immediately before their spring migration (4–6 Apr; from McLandress and Raveling 1981a). We believe this is a valid calculation because female dusky Canada geese (*B. c. occidentalis*) are intermediate in size between cackling and giant Canada geese and have similar body composition (15% protein, 27% lipid) during the spring staging period (Bromley and Jarvis

1993). Given that cackling geese are smaller in size than dusky and giant Canada geese, these estimates of body composition for cackling geese captured in late April 1989 may overestimate their lipid reserves. In addition, we directly measured body composition of cackling geese that were shot immediately upon their arrival at Trading Bay, Alaska (Fig. 1) on 4 and 6 May 1982 (hereafter "post-migration geese"). Body composition of these geese was measured following methods in Raveling (1979a). We compared these estimates of body composition of late spring-staging geese in California and post-migration geese in Alaska to published estimates of body composition of cackling geese during winter and early spring in California and just prior to egg laying on their Yukon-Kuskokwim Delta nesting grounds in Alaska (Raveling 1979a).

Predicted Feeding Time

The amount of feeding time required to meet the DEE is a function of the (1) energy value of food eaten, (2) digestive efficiency, and (3) intake rate. Apparent metabolizable energy (kJ/g) for a food type provides an estimate of (1) and (2) (Miller and Reinecke 1984, Karasov 1990). We measured AME and intake rates for geese eating alfalfa or pasture grasses using total collection digestibility trials (Robbins 1993) conducted during 12–17 April 1991. The 6 adult male cackling geese used in the trials were captured in Big Valley on 28 March 1991 using rocket nets. Three geese were maintained in enclosures on an alfalfa field and the other 3 on a pasture (grass species composition in McWilliams 1993) for 10 days before the 6-day digestibility trial. During the trial, the 6 geese were confined to adjacent individual cages and fed freshly cut alfalfa or pasture grasses ca. every 2 hr during 0600–2200 hrs. Nutrient composition (% of dry matter) of alfalfa and pasture grasses was 30% and 23% protein, 22% and 34% neutral detergent fiber, 42% and 39% soluble carbohydrates, and 6% and 3% ash, respectively (McWilliams 1993). Some food remained after each 2-hr feeding interval ensuring *ad libitum* conditions. Water and grit (sand) were also provided *ad libitum*. We weighed food provided, food remaining, and collected subsamples (ca. 50 g) from each of the 9 meals provided each day. Every 24 hr we collected and weighed all excreta produced. Vegetation and excreta samples were stored frozen. In the laboratory, samples of forage offered and excreta produced were freeze-dried and then energy density was measured using a Parr bomb calorimeter.

Feeding time (FT) required to meet daily energy requirements was then calculated using:

$$FT \text{ (hr/day)} = (DEE) / (AME_j [I_j])^{-1}$$

where DEE = daily energy expenditure (kJ/day), AME_j = apparent metabolizable energy for diet j (kJ/g), and I_j = intake rate (g/hr) for diet j . We focused on 2 diets, alfalfa and pasture grasses, because cackling geese

during spring in Big Valley spend >90% of their feeding time in these 2 habitat types (McWilliams and Raveling 1998).

We estimated DEE separately for male and female cackling geese because body composition was measured for each gender and because activity budgets during spring often differ by gender. We compared these estimates to measured time-allocation patterns of free-living cackling geese.

Observed Feeding Time

We monitored 2–3 separate flocks of cackling geese almost daily between 1 March and 30 April, 1989 and 1990. Each morning we chose 2–3 fields where previous experience indicated most geese would feed. We arrived at chosen fields ≥ 30 min earlier than geese were first observed the previous day. We recorded the numbers of arriving and departing geese and the time of movement. We estimated the time spent on feeding fields (min) during each morning as the difference between the time when most geese arrived to and then departed from feeding fields. This criterion worked well because individuals in a given flock were usually quite synchronous in their pre-dawn arrival to feeding fields and in their departure to day roosts. McWilliams and Raveling (1998) reported that male and female cackling geese spent 70% of their time actively feeding when in pasture and alfalfa fields in Big Valley. Thus, we estimated time spent feeding during the morning and evening each day by multiplying the time spent on feeding fields by 70%.

In Big Valley, all cackling geese typically spent mid-day at a flooded pasture where they rested on the water and fed along the shore on pasture grasses. During 12 days in 1989 and 29 days in 1990, > 1 observer watched geese continuously on the day roost. For each day, we estimated the time spent by geese at the day roost using the median time of arrival and departure of goose flocks. McWilliams and Raveling (1998) estimated that geese spent on average 45% of their time actively grazing on pasture grasses while at the day roost. Thus, we estimated time spent feeding at the day roost by multiplying the time spent at the day roost each day by 45%.

We recorded the time and number of geese that departed from the day roost and then followed the largest groups to their afternoon feeding field(s). We usually stayed with geese until they departed for a night roost which varied in location but was rarely the favored day roost. We estimated the time spent on feeding fields (min) during each evening in the same way as we estimated the time spent on feeding fields during each morning. When geese did not leave feeding fields within 30 min after sunset we checked these fields at least once by 2200 hr to see if geese were still feeding. If geese were observed in fields at night and were pres-

ent the next morning when we arrived, we assumed geese had spent all night on the feeding fields. If geese were observed at night but were not on feeding fields the next morning when we arrived, we assumed geese had fed only until 2400 hr the previous night (Mayhew 1988). We estimated time spent feeding in the evening and at night by multiplying the time spent on feeding fields by 70% based on the detailed time budgets of these same geese while on feeding fields (McWilliams and Raveling 1998).

We calculated the average time geese spent on feeding fields and at day roosts for ca. 2 week intervals during 1 March–29 April for each of the 2 years. Using the above observation protocol we could account for ca. 70% of the cackling geese in Big Valley every hr of nearly every day with fair weather. Observation of geese on days with rain, snow, or strong winds was more complicated because geese spent little or no time at day roosts. In addition, on days with poor weather the geese were in smaller groups dispersed among many feeding fields. On such days, we attempted to monitor as many geese as possible, but because we often could not account for 70% of the geese in Big Valley we did not include these days in calculations of time spent on foraging fields.

Weather and Lunar Phase

Daily precipitation and temperature data for the Adin Forest Service Ranger Station in Big Valley were obtained from the National Oceanic and Atmosphere Administration (NOAA) (National Climate Data Center, Asheville, NC). We used times of moonrise and moonset, and sunrise and sunset for San Francisco (37° 50' N, 122° 30' W) provided by NOAA. Each day we estimated wind speed as either strong (>20 km/hr) or weak (<20

km/hr), and categorized cloud cover as 10–25%, 25–75%, or 75–100%.

Statistical Analysis

We used 2-way Analysis of Variance (ANOVA) to investigate year and time-period changes in daily time allocation of cackling geese. When interactions between year and time period were significant, we examined the nature of the interaction using a multiple means comparisons test (LSMEANS, SAS Version 6.0, SAS Institute [1988] with Bonferroni adjustments [Rice 1989]). We used Pearson product-moment correlations for all tests of association (SAS Institute 1988).

RESULTS

Body Mass and Composition During Spring

Body masses of male and female cackling geese were 26% and 40% heavier, respectively, just prior to their northward migration from Big Valley compared to wintering cackling geese in Central Valley, California (Table 1). Increased mass of these late spring-staging geese was primarily composed of lipid. Body mass and lipid content of early spring-staging geese was intermediate. Soon after their arrival in Trading Bay, Alaska, cackling geese weighed less and had 50% of the lipid reserves of late spring-staging geese (Table 1). Comparison of body mass of post-migration geese in Alaska on 4 and 6 May 1982 with those of prelaying geese collected during mid-May 1974 on nesting areas in Alaska ($\bar{x} \pm \text{SD}$: males = 1,871 \pm 38 g, range = 1,730–1,995 g; females = 1,890 \pm 9 g, range = 1,860–1,910 g; see Raveling 1979a) suggests that female cackling geese must gain significant mass between arrival in Alaska and the egg laying period. The range of body mass for late spring-staging

Table 1. Body mass (g) and body composition (%) of cackling Canada geese during portions of the annual cycle while in California and Alaska (see Fig. 1 for locations).

Migration stage	Location	Gender	<i>n</i>	Body mass ^a	Body composition (%)		
					Water	Protein	Lipid
Wintering ^b	Central Valley	Male	10	1,398 \pm 33	60	23	5
		Female	5	1,205 \pm 33	60	23	5
Early spring-staging ^b	Klamath Basin	Male	5	1,487 \pm 53	57	22	14
		Female	11	1,295 \pm 47	57	22	13
Late spring-staging ^c	Big Valley	Male	58	1,768 \pm 80	50	21	23
		Female	59	1,683 \pm 71	45	18	29
Post-spring migration ^d	Trading Bay	Male	13	1,673 \pm 26	59	19	12
		Female	13	1,445 \pm 25	57	18	14

^a Mean ingesta-free body mass (g) \pm standard error.

^b Data from Raveling 1979a. Wintering geese were collected on 27 Dec 1973, and early spring-staging geese were collected on 5 Apr 1974.

^c Body mass of late spring-staging geese captured on 24 Apr 1989. Body composition was estimated using percentage of total body mass composed of water, protein, and lipid of giant Canada geese reported in McLandress and Raveling (1981a).

^d Unpublished data for cackling Canada geese collected on 4 and 6 May 1982. Body composition was measured following procedures in Raveling (1979a).

Table 2. Body mass and estimated daily energy expenditure^a (DEE, kJ/day) for cackling Canada geese during winter (27 Dec–5 Apr) and premigration (5–24 Apr).

Time period	Body mass (kg)			Mean daily change ^b			DEE
	Gender	Range	Midpoint	FMR ^c	Lipid	Protein	
27 Dec–5 Apr	Male	1.40-1.49	1.44	1,417	+ 1.4	+0.06	1,498
	Female	1.21-1.30	1.25	1,283	+ 1.2	+0.10	1,353
5–24 Apr	Male	1.49-1.77	1.63	1,546	+10.1	+2.00	2,186
	Female	1.30-1.58	1.49	1,451	+15.8	+0.65	2,365

^a DEE = field metabolic rate + average daily cost of tissue synthesis.

^b Increase in mass (g) of lipid or protein during the time period (from Table 1) divided by the duration of the time period (i.e., 99 and 20 days).

^c Field metabolic rate (FMR, kJ/day) = $8.47(M)^{0.704}$, where M = body mass in grams.

Table 3. Predicted food requirements^a (g dry/day) and feeding time (hr/day) of cackling Canada geese in Big Valley, California, during winter (27 Dec–5 Apr) and premigration (5–24 Apr) given 3 estimates of food intake rate.

Time period	Gender	Intake rate (g dry/hr)	Food required ^a (g dry/day)	Feeding time ^b (hr/day)
27 Dec–5 Apr	Male	25	135	5.4
		18	135	7.5
		11	135	12.3
	Female	25	122	4.9
		18	122	6.8
		11	122	11.1
5–24 Apr	Male	25	197	7.9
		18	197	10.9
		11	197	17.9
	Female	25	213	8.5
		18	213	11.8
		11	213	19.4

^a Food requirements (g dry/day) = (DEE)(AME)⁻¹; where DEE = daily energy expenditure (kJ/day) from Table 2, and AME = apparent metabolizable energy = 11.1 kJ/g for pasture grasses and alfalfa.

^b Feeding time required = (DEE)/([AME][intake rate])⁻¹.

geese (males = 1,410–2,075 g, females = 1,310–1,925 g) included much heavier birds than post-migration geese in Trading Bay, Alaska (males = 1,505–1,828 g, females = 1,289–1,580 g), and many lighter birds than prelaying geese, although maximum body mass was similar for late spring-staging and prelaying geese.

Predicted Feeding Time

DEE (kJ/day) increased 44% for males and 72% for females between winter (27 Dec–5 Apr) and spring (5–24 Apr) primarily due to the cost of lipid synthesis (Table 2). Apparent metabolizable energy for cackling geese fed alfalfa and pasture grasses was 11.3 kJ/g and 10.9 kJ/g intake, respectively. During the 6-day digestibility trial, 5 of the 6 geese increased in mass (\bar{x} = 95 g, SD = 11) while the mass of 1 pasture-fed goose did not change. We estimated intake rates (g/hr) during the digestibility trial using daily intake between 0600–2200

hr. Intake rates of geese eating alfalfa were about twice that of geese eating pasture grasses (\bar{x} ± SD: 65 ± 8 g wet mass/hr or 18 ± 3 g dry mass/hr for alfalfa, 32 ± 4 g wet mass/hr or 11 ± 0.6 g dry mass/hr for pasture grasses). However, these estimates of hourly intake rates include some nonfeeding periods between 0600–2200 hr. Intake rates for cackling geese during active feeding would be 25.7 g dry mass/hr when eating alfalfa and 15.7 g dry mass/hr when eating pasture grasses (assuming 70% of the feeding period is spent actively feeding [McWilliams and Raveling 1998] and using intake rates of 18 g dry mass/hr and 11 g dry mass/hr for alfalfa and pasture grasses measured for the entire daylight period).

We calculated time required for feeding (Table 3) using estimates of intake rates for pasture grasses and alfalfa measured during the digestibility trials (i.e., 11 and 18 g dry mass/hr) and an intake of 25 g dry mass/hr for comparison. This higher intake rate has been used by others for similar calculations (Ebbinge et al. 1975, Raveling 1979b, Prop and Deerenberg 1991). Depending on intake rates, we calculated that cackling geese must feed 5–12 hr/day during March and 8–19 hr/day during April to satisfy DEE requirements (Table 3). Males must feed more per day than females during March (Table 3) primarily because they are heavier (Table 2). In April, however, females must feed more and spend more time eating per day than males because of their higher lipid synthesis (Table 2).

Observed Feeding Time

As daylength increased during March and April, cackling geese arrived on both pasture and alfalfa fields in the morning earlier relative to sunrise (1989: r = 0.81, P < 0.0001, n = 51; 1990: r = 0.3, P = 0.04, n = 49). For example, during 1–15 March 1989 and 1990, cackling geese arrived on feeding fields 20.3 and 22.1 min, respectively, before sunrise. By 16–30 April 1989 and 1990, geese arrived 67.5 and 42.1 min, respectively, before sunrise. Despite the earlier arrival to feeding fields in April, time spent on feeding fields in the morning was similar for all time periods and both years

Table 4. Time (hrs/day) spent by cackling Canada geese on day roosts and on feeding fields during morning, evening, and night in Big Valley, California, during March and April, 1989–1990.

Year	Time period	<i>n</i> ^b	Morning		Day roost		Evening		Evening and night		Hours on feeding fields and day roosts ^a										
			\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	<i>n</i> ^c	w/o night feed		w/ night feed							
1989	1–15 Mar	8	3.8	A ^d	0.5	5.4	A	0.8	3.5	A	0.5	3.5	A	0.5	7	12.7	A	0.9	12.7	A	0.9
	16–31 Mar	12	3.4	A	0.5	6.9	B	1.3	3.4	A	0.6	3.8	A	1.4	8	13.9	B	0.9	14.2	A	1.7
	1–15 Apr	12	3.8	A	0.5	7.6	B	0.5	3.4	A	0.5	3.4	A	0.5	9	14.8	C	0.5	14.8	A	0.5
	16–27 Apr	9	3.9	A	0.4	7.8	B	0.6	3.7	A	0.9	5.2	B	2.5	8	15.5	D	0.4	17.6	B	3.3
1990	1–15 Mar	6	3.4	A	0.8	7.4	A	0.4	2.8	A	1.1	5.6	A	3.0	5	13.5	A	0.7	16.2	A	3.2
	16–31 Mar	12	3.4	A	0.5	8.0	A	1.3	3.0	A	0.7	3.0	A	0.7	10	14.2	A	0.7	14.2	A	0.7
	1–15 Apr	15	3.8	A	0.5	6.6	A	1.1	3.9	B	0.9	5.1	A	2.3	12	14.3	AB	0.6	15.5	A	1.9
	16–27 Apr	10	3.7	A	0.3	7.6	A	0.7	4.1	B	0.3	4.1	A	0.3	4	15.3	B	0.6	15.3	A	0.6

^a Hours between sunrise and sunset were on average 11.7 hr during 1–15 Mar, 12.3 hr during 16–31 Mar, 12.9 hr during 1–15 Apr, and 13.4 hr during 16–27 Apr for both 1989 and 1990.

^b Number of days geese fed in the morning and then went to the day roost.

^c Number of days geese used the day roost and then fed in the evening.

^d Letters indicate whether differences between dates within each year are statistically significant. Means with different letters are significantly different ($P < 0.05$) based on multiple means comparison test with Bonferroni adjustment (Rice 1989).

(Table 4; Year effect: $F_{1,76} = 2.18$, $P = 0.14$; Time effect: $F_{3,76} = 2.78$, $P = 0.06$; Year*Time effect: $F_{3,76} = 0.67$, $P = 0.57$).

In 1989, cackling geese spent increasingly more time on the day roost during March and April (Table 4). This pattern was not apparent in 1990 (Year effect: $F_{1,76} = 1.98$, $P = 0.16$; Time effect: $F_{3,76} = 3.28$, $P = 0.03$; Year*Time effect: $F_{3,76} = 7.24$, $P = 0.0004$) because geese departed earlier from day roosts and spent more time feeding during evening in April than in March. In contrast, evening feeding periods were similar in length for all time periods in 1989 (Table 4; Year effect: $F_{1,76} = 0.02$, $P = 0.9$; Time effect: $F_{3,76} = 3.56$, $P = 0.02$; Year*Time effect: $F_{3,76} = 2.81$, $P = 0.05$). The sum of time spent on feeding fields in the morning and evening plus time spent on day roosts indicates that geese spent more time each day on feeding fields and on day roosts in April than in March in both 1989 and 1990 (Table 4; Year effect: $F_{1,52} = 0.25$, $P = 0.62$; Time effect: $F_{3,52} = 22.79$, $P = 0.0001$; Year*Time effect: $F_{3,52} = 2.28$, $P = 0.09$).

When night feeding was considered, the seasonal increase in time spent on feeding fields and the day roost remained evident in 1989 but not in 1990 (Table 4; Year effect: $F_{1,52} = 1.16$, $P = 0.29$; Time effect: $F_{3,52} = 3.90$, $P = 0.01$; Year*Time effect: $F_{3,52} = 4.70$, $P = 0.006$). Geese increased their daily feeding time during late April 1989 by feeding at night. In 1990, feeding at night did not occur during late April so that the seasonal increase in duration of evening feeding period becomes obscured (Year effect: $F_{1,76} = 1.86$, $P = 0.18$; Time effect: $F_{3,76} = 2.55$, $P = 0.07$; Year*Time effect: $F_{3,76} = 3.21$, $P = 0.03$).

We calculated time spent each day on feeding fields as the sum of time spent on feeding fields in the morning and evening, including night feeding (from Table 4), plus the time spent on feeding fields during

mid-day. In 1989, cackling geese spent 12.6 hr/day on feeding fields in late April compared to only 10 hrs/day in March and 10.6 hrs/day in early April. In 1990, we observed no such seasonal increase in time spent on feeding fields between March (11.1 hr/day), early April (11.8 hr/day), and late April (11.2 hrs/day). Based on our estimates of DEE and AME, cackling geese must maintain intake rates of 11–18 g dry mass/hr during March and 18–20 g dry mass/hr by April.

Effects of Weather and Lunar Phase

Geese remained on feeding fields on all 11 days in 1989 and 7 days in 1990 when it rained or snowed throughout the mid-day. Geese departed from the night roost before sunrise every day except on 10–13 March 1990 when they departed after 1100 hr. These were the only 4 days during March and April, 1989 and 1990, when temperatures at dawn were below -6°C .

Daylength (sunrise to sunset) was correlated with both minimum daily temperature (1989: $r = 0.3$, $P = 0.019$, $n = 61$; 1990: $r = 0.45$, $P = 0.0005$, $n = 55$) and maximum daily temperature (1989: $r = 0.54$, $P = 0.0001$; 1990: $r = 0.44$, $P = 0.0008$), so we used partial correlations to analyze associations between temperature and feeding variables while holding daylength constant. We found no significant partial correlations between minimum daily temperature and arrival time to feeding fields in the morning (1989: $r = 0.02$, $P = 0.91$, $n = 51$; 1990: $r = 0.06$, $P = 0.70$, $n = 45$) or time spent at feeding fields in the morning (1989: $r = 0.08$, $P = 0.62$, $n = 40$; 1990: $r = 0.28$, $P = 0.09$, $n = 38$).

Cackling geese fed in pasture and alfalfa fields during 4 of 34 nights in 1989 and 6 of 42 nights in 1990 when there was no rain and less than 75% cloud cover at night (Fig. 2). When cackling geese fed at night, they always remained on feeding fields throughout the night except on 22 March 1989 when they departed for the

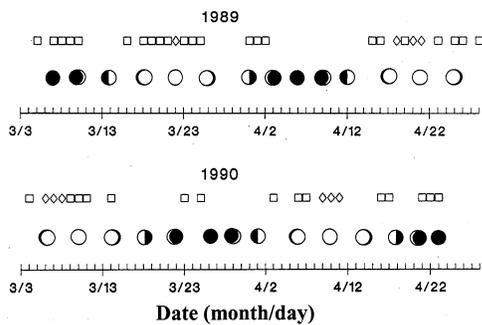


Fig. 2. Phases of the moon (open circle = full moon), incidence of cackling Canada goose feeding activity at night (diamonds), and incidence of >75% cloud cover or rain (squares) during Mar–Apr 1989 and 1990 in Big Valley, California. Cackling geese fed on 4 nights in 1989 and 6 nights in 1990, but never fed during rainy nights or when there was >75% cloud cover.

night roost by 2000 hr. During 1989 and 1990, geese fed at night on 10 of the 24 nights when the moon was at least 75% full and the moonrise occurred within 2 hr after sunset. Poor weather (i.e., clouds, rain, snow, cold) occurred on 11 of the 14 nights when geese would have had sufficient moonlight but did not feed at night (Fig. 2).

Diet and Feeding Time

Cackling geese that fed in pastures during the morning departed for day roosts later (an average of 43 min in 1989 and 36 min in 1990) than geese that fed in alfalfa fields on 13 of 14 days in 1989 and 13 of 17 days in 1990 for which we had departure times for both habitats on the same day. During this additional time feeding in pastures, cackling geese gained 72–86 kJ (at intake rates of 11 g/hr and 10.9 kJ/g AME) or 19% more total energy than if they departed at the same time of day as geese feeding in alfalfa fields.

DISCUSSION

Body Mass and Composition During Spring

Raveling (1979a) suggested that cackling geese gained little or no body mass before migration to Alaska. However, we found that cackling geese had reached close to peak mass (and probably lipid content) for the annual cycle by late April while still on staging areas in California; only male and female cackling geese in Alaska just prior to egg laying had higher average body mass (Raveling 1979a).

A second period of mass gain and lipid reserve acquisition probably occurs in early May after arrival at stopover sites in Alaska and before arrival on the Yukon-Kuskokwim Delta nesting areas. Female and male cackling geese were 31% and 12%, respectively, heavier in mid-May 1974 upon arrival on nesting areas compared to 4 and 6 May 1982 at a stopover site in Alaska. Arctic-

nesting geese vary annually and individually in the timing and extent to which they gain body mass during spring (e.g., Gauthier et al. 1984a, c; Alisauskas 1988). Consequently, the relative importance of this second period of body mass gain for cackling geese in a given year remains unclear.

The pattern we observed of geese accumulating substantial reserves on staging areas in California prior to migration to Alaska which are then used during migration and the reproductive season was also found in female dusky Canada geese that breed in southeastern Alaska (Bromley and Jarvis 1993) and in greater white-fronted geese that breed on the Yukon-Kuskokwim Delta (Ely and Raveling 1989). In contrast, arctic and subarctic nesting geese that migrate through interior North America (e.g., lesser snow geese [Ankney and MacInnes 1978, Alisauskas 2002]; Ross's geese [*Chen rossii*, Barry 1967]; and interior Canada geese [*B. c. interior*, Raveling and Lumsden 1977]) gain body mass primarily later during spring migration when they are closer to their nesting areas. These interspecific differences in phenology of body mass gain are probably adaptive responses to differences in the availability of high-quality foods on staging areas during spring migration (also see Bromley and Jarvis 1993, Gloutney et al. 2001).

Cackling Goose Time Allocation During Spring

Raveling (1979b) estimated that cackling geese subsisting on only a leafy diet during the spring fattening period would require 338–408 g dry mass of food each day and 13.5–16.3 hrs to obtain it. We estimated that cackling geese during this period required no more than 250 g dry mass of a leafy diet but still required at least 11 hr and perhaps as much as 24 hr (depending on intake rates per hour) of feeding time to achieve this daily intake requirement. The differences in estimates of food and time required to meet DEE occur because Raveling (1979b) assumed cackling geese metabolize only 6.23 kJ/g of a leafy diet and that they are capable of 25 g/hr intake rates. We found that cackling geese fed diets *ad libitum* ate at most 11 g dry/hr of pasture grasses or 18 g dry/hr of alfalfa and that they metabolized 10.9–11.3 kJ/g of these diets.

In general, geese rarely metabolize more than 11.0 kJ/g when eating forage (Owen 1972, 1980; Madsen 1985; Sedinger et al. 1989; Prop and Deerenberg 1991; Prop and Vulink 1992). Because plants allocate more resources to less digestible cell wall components as they grow (Osbourne 1980), geese feeding on a sward that is growing often experience a decline in AME over time (Prop and Deerenberg 1991). During spring, geese compensate for this decrease in plant quality by selecting higher quality plant parts (e.g., McLandress and Raveling 1981a, McWilliams 1993), by increasing intake rates (Prop and Deerenberg 1991, Prop and Black 1998),

and by spending more time feeding (Alisauskas and Ankney 1992, Ely 1992, this study).

Intake rates of wild cackling geese may be higher than those we measured using wild-caught geese in cages fed freshly cut alfalfa or pasture grasses. However, intake rates >25 g dry/hr for geese eating leaves are unusual (e.g., Ebbinge et al. 1975, Harwood 1975, Prop and Black 1998). Intake rates are limited by digestive capacity and higher intake rates are associated with more rapid passage rates and reduced digestive efficiency (Prop and Vulink 1992). In addition, geese fed *ad libitum* have fewer constraints on intake rates than wild geese in terms of searching and selecting a diet. Thus, cackling geese in the wild may increase intake rates in response to increased energy demands in spring, but because of digestive tradeoffs and harvesting constraints increases in food intake may be limited.

Cackling geese spent 70% of their time actively feeding when in pasture and alfalfa fields throughout March and April (McWilliams and Raveling 1998). Cackling geese accomplished mass gain during spring by increasing the time directly allocated to feeding. For example, they increased their feeding time during late April by feeding at night when the moon was close to full (as in 1989) or by spending more time feeding in the evening before sunset (as in 1990). Cackling geese fed nearly every night that weather conditions and light levels allowed, suggesting they are feeding-time limited (Belovsky 1981, Hixon 1982) and, thus, are energy or nutrient maximizers (Schoener 1971).

If cackling geese are feeding-time limited, why do they spend about 50% of their time during mid-day not feeding? Congregating on water during mid-day provides time for resting, drinking, maintenance, and social interactions. It may also allow geese to remain cool during the warmest period of the day. In general, however, cackling geese are most likely congregating on water during mid-day to reduce predation risk. Golden eagles attacked flocks of cackling geese on average once every 3–4 days in Big Valley (McWilliams et al. 1994). Roosting on water during mid-day with most other geese in Big Valley reduced the risk of eagle attack (McWilliams et al. 1994). On rainy days, eagles were less active (McWilliams et al. 1994) and cackling geese usually spent the entire daylight period on feeding fields and did not use the day roost.

Annual Differences in Time Allocation

Cackling geese increased the time they spent on feeding fields from March to late April in 1989 but not in 1990 (Table 4). Plants initiated growth earlier in 1990 compared to 1989 (McWilliams and Raveling 1998) and this may have allowed cackling geese to initiate body mass gain earlier in 1990. Annual differences in plant phenology and food availability can directly affect the timing and extent of body reserves acquired by geese

during spring (Owen 1981, Alisauskas 1988, Prop and Deerenberg 1991, Prop and Black 1998).

Effects of Weather and Lunar Phase

When skies were cloudy, cackling geese arrived later to feeding fields in the morning and departed earlier for the night roost (also see Owen 1972). Thus, incident light affects timing of feeding in cackling geese as is also the case for other geese (Raveling et al. 1972, Owen 1980, Alisauskas and Ankney 1992, Ely 1992) and sheldgeese (Summers and Grieve 1982).

Night feeding occurred only when there was adequate moonlight (i.e. the moon was at least 75% full and there was little cloud cover) that occurred soon after sunset. Night feeding by barnacle geese (*B. leucopsis*) during winter was similarly restricted to nights when the moon was nearly full (Ebbinge et al. 1975, Ydenberg et al. 1984). Owen (1972), Raveling et al. (1972), and Madsen (1998) noted that European greater white-fronted geese (*A. a. albifrons*), interior Canada geese, and pink-footed geese (*A. brachyrhynchus*), respectively, fed at night under bright moonlight or when heavily disturbed.

Temperature had little quantitative effect on cackling goose time allocation except when temperatures were below -6° C. This is close to the lower critical temperature at which LeFebvre and Raveling (1967) predicted a small goose like the cackling goose would become inactive. The behavior of wintering geese and other waterfowl is often not affected by temperature (reviewed by Baldassarre et al. 1988, but see McLandress and Raveling 1981b). In contrast, non-avian herbivores generally modify their activity in response to relatively small changes in air temperature (e.g., Belovsky and Slade 1986).

Diet and Feeding Time

Cackling geese spent more time on pasture than alfalfa fields during the morning. Our digestibility trial results suggest that this difference occurred because geese eating pasture grasses have lower intake rates than geese eating alfalfa and so must increase time spent feeding to achieve similar daily energy intake. Other studies of geese also suggest that the nutritional or energetic value of a given food and the rate it can be acquired and processed influence time spent feeding each day (Prop and Black 1998, Hassall et al. 2001). For example, the higher energy density of cereal grains allows geese to spend much less time feeding than when feeding on green leaves (Raveling et al. 1972, Drent et al. 1978, Madsen 1985, Ely 1992). Tubers of marsh plants are also relatively energy rich (Alisauskas et al. 1988), although geese must spend considerable time and energy extracting and processing the tubers (McIlhenny 1932, Bedard and Gauthier 1989) so that

their feeding time each day was similar to cackling geese eating a leafy diet.

During spring, increased nutrient and energy demands require geese to spend more time feeding. Lesser snow geese spent about 2.1–2.4 hr/day eating corn during winter (Frederick and Klaas 1982, Davis et al. 1989). As fat storage rates increased in April and May, lesser snow geese ate corn for 4.8 hr/day (Alisauskas and Ankney 1992). Similarly, greater white-fronted geese eating cereal grains and potatoes increased their time spent feeding from 1.8 hr/day during winter to 5.1 hr/day in spring (Ely 1992).

Geese that eat primarily leaves instead of roots or seeds also increase their time spent feeding during spring. Barnacle geese eating grass leaves fed for 7.4 hr/day during winter, 9.0 hr/day during April, and 12.9 hr/day during May (Prop and Vulink 1992). European greater white-fronted geese spent nearly 10 hr/day grazing during winter (Owen 1972). By spring, white-fronted geese had doubled their intake rates and increased their feeding time compared to winter (Owen 1980). We found that cackling geese spent 10–12.6 hr/day on feeding fields during March and April and that, in 1989, they increased the time spent on feeding fields from March through April. Comparisons with predicted feeding time suggested that increases in intake rates were also necessary for cackling geese to meet DEE during late April.

Allometrics of Goose Feeding

Like many other grazing herbivores, geese must spend appreciable amounts of time feeding because of the relatively poor quality of herbage (Belovsky and Slade 1986, Drent and Prins 1987, Karasov 1990). In addition, smaller herbivores tend to eat more food per day, as a proportion of body mass, than larger herbivores (Owen-Smith 1988). As relatively small herbivores, geese during winter eat 6–10% of their body mass in food each day (Table 5) compared to 4% for small

antelope and about 1% for elephants (Owen-Smith 1988: 75). When only geese that graze during winter are compared, smaller geese like cackling geese eat proportionately more food per day than larger geese (Table 5). Our estimates suggest that cackling geese during April must increase daily intake rates to $\geq 13\%$ of their body mass to satisfy their high daily energy requirements (Table 5).

Drent et al. (1978) and Summers and Grieve (1982) suggested mass-specific rate of food intake was similar between species of geese. When daily food intake is converted to g dry matter per metabolic body mass ($\text{kg}^{0.75}$), the rate of food intake is roughly similar across species of geese although mass-specific food intake of cackling geese during spring is exceptional (Table 5). Thus, the higher mass-specific rates of food intake of smaller geese may not simply compensate for their higher specific metabolic requirements. When provided food *ad libitum* during the digestibility trials, cackling geese ate 326 ± 56 g dry mass of alfalfa and 201 ± 3 g dry mass of pasture grasses per day which represents 22% and 16%, respectively, of their body mass. During the digestibility trial, cackling geese were able to increase daily food intake significantly above that predicted for their body size and metabolic requirements in part because they fed throughout the day on already harvested forage. This suggests that cackling geese in the wild encounter harvesting constraints that directly limits instantaneous intake rate to levels below those we measured in captive geese. Daily food intake of wild geese was also limited because they did not feed during nights without moonlight, and because geese fed less during mid-day compared to the morning and evening to reduce predation risk.

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Table 5. Body mass (g), daily food intake (g dry), and mass-specific food intake^a for certain species of grazing waterfowl during winter (prior to body mass gain) and spring (during body mass gain).

Season	Species	Body mass(g)	Daily food intake (g dry per day)			Authority
			g day ⁻¹	% live mass	Mass-specific ^a	
Winter	<i>Anas penelope</i>	700	92	13.1	120	Mayhew 1988
	<i>Branta canadensis minima</i> ^b	1,345	129	9.6	103	This study
	<i>B. bernicla</i>	1,350	135	10.0	108	Drent et al. 1978
	<i>Chloephaga rubidiceps</i> ^b	1,650	143	8.6	99	Summers & Grieve 1982
	<i>B. leucopsis</i> ^c	1,800	145	8.2	95	Owen et al. 1992
	<i>Anser albifrons</i>	2,300	175	7.6	95	Owen 1972
	<i>A. brachyrhynchos</i>	2,500	159	6.4	81	Madsen 1985
	<i>C. picta</i> ^b	3,350	249	7.4	102	Summers & Grieve 1982
Spring	<i>B. c. minima</i> ^b	1,560	205	13.1	148	This study
	<i>Chen atlantica</i>	3,000	218	7.3	92	Bedard & Gauthier 1989

^a Mass-specific daily food intake = $\text{g day}^{-1} (\text{M}^{0.75})^{-1}$, where M = body mass in kg.

^b Average of body mass (Table 2) and daily intake (Table 3) estimated separately for males and females.

^c Average of body mass and daily intake estimated separately for Jan and Feb.

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