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USE OF SUPPLEMENTAL FOOD BY BREEDING ROSS'S GEESE AND LESSER SNOW GEESE: EVIDENCE FOR VARIABLE ANOREXIA

MARK L. GLOUTNEY,[1,4] RAY T. ALISAUSKAS,[1,2] KEITH A. HOBSON,[1,2] AND ALAN D. AFTON[3]
[1]*Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, S7N 5E2, Canada;*
[2]*Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, Saskatchewan, S7N 0X4, Canada; and*
[3]*United States Geological Survey, Biological Resources Division, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, Louisiana 70803, USA*

ABSTRACT.—Recent research suggests that foods eaten during laying and incubation play a greater role in supplying energy and nutrients to arctic-nesting geese than previously believed. We conducted food-supplementation experiments with Ross's Geese (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens*) geese to evaluate: (1) if supplemental food was consumed by laying and incubating geese, (2) how food consumption influenced mass dynamics of somatic tissues of breeding geese, (3) if patterns of mass loss were consistent with fasting adaptations, and (4) whether energetic constraints would cause smaller Ross's Geese to consume more food relative to their body size than would larger Snow Geese. Quantity of supplemental food eaten by both species during laying and incubation was highly variable among individuals. Consumption of supplemental food during laying resulted in differences in overall body composition between control and treatment females. Treatment female Ross's Geese completed laying at a higher mass and with more abdominal fat than controls, whereas treatment female Snow Geese completed laying with heavier breast muscles and hearts. Overall body composition did not differ between control and treatment geese (both sexes and species) at the end of incubation, but treatment geese had heavier hearts than control geese. This suggests that treatment females did not rely to the same extent on metabolic adaptations associated with anorexia to meet energetic costs of incubation as did controls. Stable-nitrogen isotope analysis revealed patterns of protein maintenance during incubation consistent with metabolic adaptations to prolonged fasting. Our prediction that energetic constraints would cause smaller Ross's Geese to consume more food relative to their size than would Snow Geese was not supported. Mass-specific food consumption by Ross's Geese was 30% lower than that of Snow Geese during laying and 48% higher during incubation.
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ARCTIC-NESTING Ross's Geese (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens*; hereafter Snow Geese) have been thought to rely largely on nutrient reserves to meet costs of egg laying and incubation (Ankney and MacInnes 1978, Alisauskas and Ankney 1992). However, recent work with Greater White-fronted Geese (*Anser albifrons*; Budeau et al. 1991), Canada Geese (*Branta canadensis*; Bromley and Jarvis 1993), Greater Snow Geese (*C. c. atlantica*; Gauthier 1993), and Lesser Snow Geese (Ganter and Cooke 1996) suggests that foods eaten during laying and incubation play a greater role in supplying energy and nutrients than was previously thought. Moreover, Gloutney et al. (1999) found that Snow and Ross's geese breeding in a large colony at Karrak Lake, NWT, foraged for more than 7.6 h per day but obtained less than 1.4 g forage (dry mass) per hour while foraging. Thus, two competing paradigms exist concerning the reliance of arctic-nesting geese on local food. We used food supplementation to evaluate which of these paradigms was pertinent to colonial-nesting Ross's Geese and Snow Geese.

Continental populations of Ross's Geese and Snow Geese have increased dramatically in recent years (Ankney 1996); for example, the number of geese breeding at the Karrak Lake colony over the past three decades has increased by 2,000% (Alisauskas 1998). Consequently, geese are depleting available forage at Karrak Lake (Alisauskas unpubl. data) and elsewhere near large colonies (Kerbes et al. 1990, Kotanen and Jefferies 1997). At Karrak Lake, geese commence nesting within a few

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[4] Present address: Ducks Unlimited Canada, P.O. Box 430, #64 Highway 6, Amherst, Nova Scotia B4H 3Z5, Canada. E-mail: m_gloutney@ducks.ca

days of arrival when there is little or no green vegetation. In addition, the tundra habitat at this colony is less productive than the coastal wetlands where geese typically stage for several weeks before laying eggs (Bromley and Jarvis 1993, Gauthier 1993). Given the low food availability and rapid onset of laying once geese arrive at Karrak Lake, we suspected that Ross's Geese and Snow Geese essentially fast from the time they arrive until they leave the colony with goslings.

Metabolic responses to prolonged fasts during reproduction have been well documented for geese, penguins, and petrels (Cherel et al. 1987, 1988; Groscolas et al. 1991; Boismenu et al. 1992). Fasting birds typically enter a period of reduced mass loss, where 93 to 94% of energy is derived primarily from catabolism of lipids, whereas proteins are maintained (Cherel et al. 1988). Furthermore, energetic expenditure during this period typically is diminished by a reduction in locomotor activity and basal metabolic rate (Cherel et al. 1988).

Fasting birds can maintain protein reserves by reducing nitrogen excretion (Cherel et al. 1988). Nevertheless, extensive protein loss can occur to the point where incubating birds die (Ankney and MacInnes 1978). Induced fasting in Japanese Quail (*Coturnix japonica*) and natural fasting by Ross's Geese at Karrak Lake resulted in enrichment in stable-nitrogen isotope ratios in muscle tissue because of a disproportionate loss of the lighter ^{14}N during catabolism compared with equilibrium conditions (Hobson et al. 1993). Thus, measurement of stable-nitrogen isotope ratios can provide insights into the extent of protein catabolism by fasting birds. Furthermore, analyses of stable-carbon isotopes are useful for discriminating between plants with C-3 versus C-4 photosynthetic pathways (Hobson and Clark 1992). Thus, by provisioning geese with a C-4 food in an otherwise C-3 biome, the consumption of the supplemental food can be traced directly.

Smaller body size decreases absolute and relative energy storage capacity as well as fasting endurance (Calder 1974). Ross's Geese are about 20% smaller than Snow Geese (Slattery and Alisauskas 1995) and may need to rely more on local food resources to meet costs of egg laying and incubation than Snow Geese (Ankney 1984, Afton and Paulus 1992, Gloutney et al. 1999). If fasting birds deplete their lipid stores during incubation and reach the point where proteins can no longer be spared, death (Ankney and MacInnes 1978) or nest abandonment (Gloutney and Clark 1991) may result unless the birds resume feeding. Thus, small Ross's Geese should be more likely to forage during reproduction than larger Snow Geese.

Our objective was to investigate the importance of exogenous resources to reproduction in sympatric arctic-nesting geese in order to evaluate current opposing views about the importance of feeding during reproduction. We conducted food-supplementation experiments with breeding Ross's Geese and Snow Geese to evaluate: (1) if supplemental food was consumed by laying and incubating geese, (2) how food consumption influenced mass dynamics of somatic tissues, and (3) whether patterns of mass loss were consistent with fasting adaptations. Furthermore, based on mass-specific differences in metabolic rates, we predicted that energetic constraints would induce smaller Ross's Geese to consume more food relative to their body size than would larger Snow Geese. Experimental food-supplementation studies of precocial birds are few (see Watson et al. 1984), and, to our knowledge, they have not been attempted previously for arctic species.

STUDY AREA AND METHODS

Ross's Geese and Snow Geese were studied at Karrak Lake, Northwest Territories (66°15′N, 100°15′W) in 1995. Detailed descriptions of the study area were given by Ryder (1972) and McLandress (1983). The breeding colony in 1995 consisted of an estimated 212,573 Ross's Geese and 277,886 Snow Geese on 62.6 km^2 of land area (Alisauskas unpubl. data).

Food supplementation: Egg laying.—Six parallel 750-m long transects, 30 m apart, were established in a central location in the colony before geese arrived. Nests were selected along transects at about 30-m intervals, alternating between Ross's Geese and Snow Geese. Transects were checked every second day, during which the date of the first-laid egg at each sample nest was recorded. Territory sizes for Ross's Geese and Snow Geese averaged 225 and 210 m^2, respectively (Gloutney unpubl. data). We recorded number of eggs until no new eggs were laid. Once first eggs were laid, nests were randomly assigned to one of four treatments: (1) control, (2) a mix of cracked and whole corn (1:1 ratio by mass), (3) durum wheat, or (4) shelled rice. We provided a variety of food types in an attempt to increase the probability that at least one of the food types would be consumed. Furthermore, corn is a C-4 plant, whereas the arctic biome is predominantly C-3 (Blake 1991, Hobson 1995); thus, the allocation of nutrients from corn to eggs and somatic tissues can be readily traced isotopically. We placed 250 g of food within 20 cm of focal nests. Food-intake rates were assessed by visually estimating percent disappearance of food between visits and then converting these estimates to mass. When approximately half of the food was consumed, an additional 150 g was added. Observations and stable-isotope analyses (see below) confirmed that resident pairs (vs. intruders or other species) consumed supplemental food.

Food supplementation: Incubation.—Eight transects of variable length (750 to 1,500 m), each at least 30 m apart, were established for the incubation study. We randomly selected nests during laying by checking transects every second day. Focal nests were separated along transects by at least 30 m. At the onset of incubation (i.e. two days after no additional eggs appeared), geese were randomly assigned to either a treatment or control group. Each treatment pair was given 300 g each of corn, wheat, and rice piled separately within 20 cm of each nest. Food was placed in a consistent orientation with respect to the nest, with corn north, wheat west, and rice south. Food consumption was estimated visually every three to four days and replenished as needed.

Behavior.—Thirty-minute observations between 0700 and 1600 CST were used to compare behaviors (behavior of both members of the pair was recorded simultaneously) of control and treatment pairs during laying and incubation to evaluate whether provisioning of pairs with supplemental food increased antagonistic interactions with neighbors. Behavioral data were used to assess whether energy gained by consumption of supplemental food was offset by increased costs of territory defense. Specifically, we examined if supplemental food caused an increase in nest or territory defense, or intensity or frequency of social interactions. We recorded the following behaviors every 10 s: foraging, alert, resting (not including nest attendance), nest attendance, and social interaction (see Gauthier and Tardif 1991, Astrom 1993). Foraging behaviors were recorded when birds held their heads below horizontal, either grazing, grubbing or searching for food (see Gauthier and Tardif 1991) and were primarily observed away from the nest. All observations were made from 150 to 300 m using 15 to 60× spotting scopes. Four levels of social interaction were recorded (head shake, head down threat, chase, and fight). Intensity of social interactions was scored by summing frequency of occurrence of each behavior multiplied by its relative intensity ranked as follows: head shake = 1, head down threat = 2, chase = 3, and fighting = 4. Observations were made by experienced observers. Simultaneous observations by both observers of the same goose pair (n = 10 pairs) revealed no quantitative difference in behavioral assessments, so data from both observers were pooled.

Collection.—We shot a random sample of 21 female Ross's Geese (11 control, 10 treatment [8 corn, 2 wheat]) and 20 female Snow Geese (9 control, 11 treatment [5 corn, 5 wheat, 1 rice]) two days after they had completed laying. We also collected another random sample of 24 female and 16 male Ross's Geese (females, 14 control, 10 treatment; males, 10 control, 6 treatment) and 21 female and 23 male Snow Geese (females, 11 control, 9 treatment; males, 17 control, 6 treatment) within the last four days of incubation. Geese were dissected within 6 h of collection. Mass of abdominal fat, one breast muscle (pectoralis and supracoracoideus), heart, liver, and gizzard were weighed with a precision balance (±0.1 g).

Stable-isotope analysis.—Subsamples of breast muscle and liver were freeze-dried. Lipids were removed using a modified methanol/chloroform extraction technique (Bligh and Dyer 1959). Lipid-free samples were dried and then ground to a fine powder with a mortar and pestle. Isotopic analyses followed protocols outlined in Gloutney and Hobson (1997). All isotope values are expressed in delta (δ) notation relative to the PeeDee Belemnite (PDB) and atmospheric (AIR) standards for carbon and nitrogen, respectively (see Hobson 1995).

As predicted, corn ($-10.57 \pm$ SE of 0.03‰) was enriched in ^{13}C compared with wheat (-24.9 ± 0.1‰), rice (-25.89 ± 0.1‰), and local forage (-29.80 ± 1.6‰ for vascular plants; from data in Blake [1991]). Thus, by comparing stable-carbon isotope ratios in the livers of control versus corn-supplemented geese, we confirmed that geese had consumed corn.

Statistical analyses.—We measured skull height, skull length, keel, and tarsus with precision calipers (±0.1 mm). We used the correlation matrix of these measurements in a principal components analysis (PCA) to derive PC1 as a size index (Reyment et al. 1984). Both species and sexes were combined in this analysis to index size on the same scale. All factor loadings on PC1 were >0.3. Morphological measurements included in the PCA explained 93.3 and 92.1% of the variation in size between species and sexes of geese collected during laying and incubation, respectively. Where appropriate, PC1 scores were used to control for variation in body size (see below).

We used multivariate analysis of covariance (MANCOVA) to analyze overall time budgets as well as intensity of social interactions. All percentages were arcsine-transformed before further analyses (Zar 1984). Analyses were performed independently for laying and incubation experiments. Initial models contained main effects (i.e. treatment, species, sex, number of eggs), covariates (i.e. number of neighbors, Julian date), and two-way interactions. Throughout, we report F-values from MANCOVA based on Wilks' criterion (SAS 1993). If MANCOVA indicated overall differences in behaviors, we used univariate analyses of covariance (ANCOVA) to explore differences in each behavior as recommended by Hatcher and Stepanski (1994). Throughout, MANCOVA and ANCOVA protocols follow hierarchical procedures outlined by Alisauskas and Ankney (1994), with the final model containing only significant effects and interactions. Least-squares means were obtained from reduced models containing significant explanatory variables.

To confirm whether focal geese consumed corn, we used *t*-tests (Zar 1984) to compare $\delta^{13}C$ values of liver from control and corn treatment females at the end of laying and incubation. Our *a priori* assumption was that consumption of corn would result in enriched $\delta^{13}C$ values. To test the prediction that Ross's Geese would consume proportionately more food than Snow Geese, we calculated mass-specific food consumption (MSFC; g) for each female during laying and incubation:

$$\text{MSFC} = \text{total food consumed}/(\text{body mass})^{2/3}, \quad (1)$$

where body mass (g) was the mean mass of control females at the end of either the laying or incubation period.

Use of exogenous resources should have increased as incubation proceeded and endogenous reserves were depleted. Thus, we predicted that consumption of supplemental food would increase as incubation proceeded. Based on up to seven visits (three days apart) to each nest, we calculated the proportion (P_i) of total food (all types) consumed by each pair for each nest between sequential visits:

$$P_i = F_i / F_{total}, \quad (2)$$

where F_i is food consumed between two sequential visits and F_{total} is total food consumed by the pair during the entire experiment. Proportions were arcsine-transformed (Zar 1984). We used these repeated measurements of food consumption in a nested ANOVA with days of supplemental food nested within pair to evaluate temporal changes in food consumption. Food was initially supplied on day 3 (mode, range 3 to 7) of incubation. We used days of supplemental food instead of day of incubation because food was not provided to geese at the same stage of incubation.

We used MANCOVA to test if food supplements affected body composition of females. This procedure allowed for simultaneous evaluation of overall changes in body composition as defined by mass of body, fat, breast, heart, and gizzard. Models were evaluated separately for laying and incubation experiments. Initial models for the laying experiment contained main effects (i.e. treatment, clutch size), covariates (i.e. body size, initiation date), and two-way interactions, whereas the incubation experiment contained main effects (i.e. treatment, clutch size), covariates (i.e. body size, days of exposure to supplemental food) and two-way interactions. When MANCOVA indicated significant differences between experimental groups in any body component, we calculated standardized canonical coefficients. We used ANCOVA to explore effects of food supplementation on each somatic tissue.

We used ANOVA to test for interspecific differences in liver and muscle tissue $\delta^{13}C$ and $\delta^{15}N$ values in control females at the end of incubation. In order to evaluate if food supplementation affected protein utilization during incubation, we used ANCOVA to test for differences between treatments in liver and muscle $\delta^{15}N$ values during incubation. Initial models included main effects (i.e. treatment, species, and period [beginning or end of incubation]) and two-way interactions.

RESULTS

Behavioral observations.—Time budgets did not differ between control and treatment geese during laying (MANCOVA, Wilks' $\lambda = 0.95$, $F = 0.59$, df = 6 and 63, $P = 0.74$) or incubation (Wilks' $\lambda = 0.92$, $F = 1.27$, df = 6 and 91, $P = 0.27$), although sexes differed in time spent resting, attending nests, alert, and in social interactions (Table 1). Sexes also differed in their intensity of social interactions (Table 1). We concluded that food additions during laying and incubation did not increase intensity of inter- and intraspecific interactions.

Supplemental food consumption.—During laying, pairs of Ross's Geese and Snow Geese consumed a mean of 122 ± SD of 203 g (range 0 to 970 g, $n = 34$) and 210 ± 176 g (25 to 760 g, $n = 25$) of supplemental food, respectively. During incubation, Ross's Goose and Snow Goose pairs consumed 341 ± 412 g (0 to 1,465 g, $n = 15$) and 656 ± 908 g (60 to 3,240 g, $n = 17$) of supplemental food, respectively. Although both species consumed food during both periods, food consumption was extremely variable among pairs (Fig. 1). Contrary to the prediction that Ross's Geese would consume proportionately more food than Snow Geese, mass-specific food consumption did not differ between the two species during laying (Ross's Goose, MSFC = 1.0 ± 1.6 g/g body mass; Snow Goose, MSFC = 1.3 ± 1.6 g/g body mass; $t = -0.89$, df = 57, $P = 0.19$) or incubation (Ross's Goose, MSFC = 3.4 ± 4.1 g/g body mass; Snow Goose, MSFC = 2.3 ± 2.9 g/g body mass; $t = 0.86$, df = 39, $P = 0.2$).

At the end of laying, liver $\delta^{13}C$ values were enriched in corn-supplemented females rela-

TABLE 1. Least-squares means (±SE) of percent of time spent in each behavior by control and food-supplemented Ross's Geese and Lesser Snow Geese. *F*-values from ANCOVA calculated from Type III SS testing for treatment effects while controlling for sex and clutch size.

	Least-squares means[a]		*F*-value		
Behavior	Control	Treatment	Treatment	Sex	Clutch size
		Laying period (n = 78)			
Foraging	10.7 ± 4.5	14.2 ± 2.8	0.40	1.2	18.4***
Resting	39.9 ± 5.7	33.2 ± 3.5	1.10	69.6***	0.4
Nest attend	31.9 ± 6.4	35.1 ± 3.9	0.06	97.3***	14.4***
Alert	16.1 ± 3.8	15.8 ± 2.4	0.02	70.3***	4.4*
Social	1.4 ± 0.4	1.7 ± 0.3	0.01	29.7***	10.4**
Social score	5.1 ± 1.4	5.5 ± 0.9	0.06	24.2***	3.9*
		Incubation period (n = 102)			
Foraging	2.5 ± 2.0	7.2 ± 1.8	2.90[b]	12.7***	—[c]
Resting	44.0 ± 2.6	41.9 ± 2.2	0.20	592.0***	—
Nest attend	49.3 ± 0.9	48.4 ± 0.8	1.05	4,452.0***	—
Alert	4.0 ± 1.6	2.1 ± 1.3	0.80	16.7***	—
Social	0.2 ± 0.1	0.4 ± 0.1	2.30	15.7***	—
Social score	0.9 ± 0.5	1.5 ± 0.4	0.80	12.2***	—

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Untransformed percentages.

[b] $P = 0.093$.

[c] Nonsignificant effect excluded from final model.

tive to controls (Ross's Goose, $t = -7.9$, df = 8, $P = 0.0001$; $\delta^{13}C_{control} = -24.4 \pm 0.6‰$; $\delta^{13}C_{supplemented} = -20.6 \pm 0.9‰$; Snow Goose, $t = -2.4$, df = 6, $P = 0.05$; $\delta^{13}C_{control} = -23.1 \pm 0.5‰$; $\delta^{13}C_{supplemented} = -21.5 \pm 1.4‰$). However, at the end of incubation there was no significant difference in $\delta^{13}C$ between livers of control and corn-supplemented geese (Ross's Goose, $t = -1.4$, df = 8, $P = 0.19$; $\delta^{13}C_{control} = -23.9 \pm 1.7‰$; $\delta^{13}C_{supplemented} = -22.7 \pm 0.7‰$; Snow Goose, $t = -0.4$, df = 7, $P = 0.51$; $\delta^{13}C_{control} = -2.7 \pm 1.2‰$; $\delta^{13}C_{supplemented} = -2.4 \pm 1.5‰$). This result supports the fact that during 45 h of observation, we never saw neighboring geese

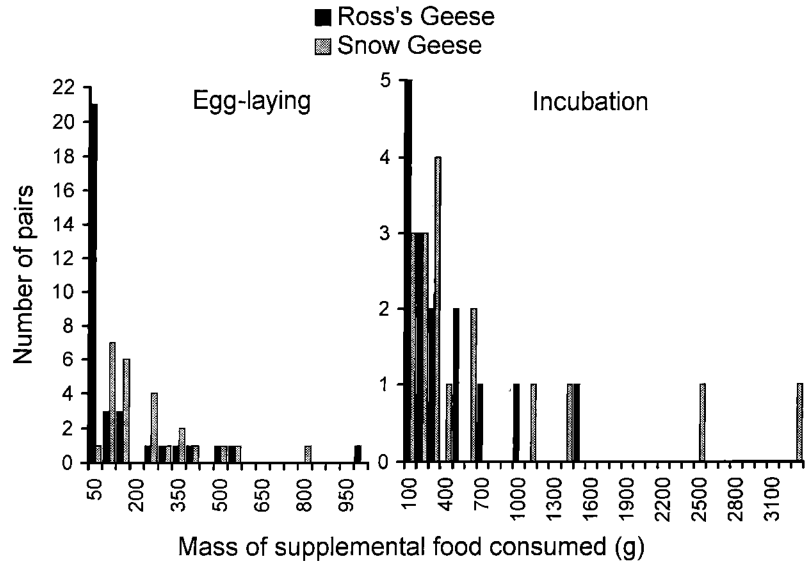

FIG. 1. Mass of supplemental food (g) consumed by pairs of Ross's Geese and Snow Geese during the egg-laying and incubation periods.

TABLE 2. Effects of food supplementation (treatment) on body composition of Ross's Geese and Lesser Snow Geese during egg laying. Shown are F-values from ANCOVA calculated from Type III SS. Initial model contained main effects (treatment, clutch size), covariates (initiation date, body size), and two-way interactions.

	Body mass	Abdominal fat	Breast	Heart	Gizzard
		Ross's Geese			
Model	6.03*	5.07*	0.24	0.38	1.01
Treatment	6.47*	7.59*	ns[a]	ns	ns
Body size	7.16*	ns	ns	ns	ns
Date	ns	4.18*	ns	ns	ns
		Snow Geese			
Model	7.61**	3.33[c]	7.28**	4.76**	8.68***
Treatment	3.55[b]	3.33[c]	6.22*	19.30***	ns
Body size	14.00**	ns	11.20**	ns	ns
Date	ns	ns	ns	5.77*	8.45*
Clutch size	ns	ns	ns	ns	5.48*
Body size × treatment	ns	ns	ns	11.30**	ns
Date × body size	ns	ns	ns	5.09*	ns
Clutch size × date	ns	ns	ns	ns	13.30**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Nonsignificant effect excluded from final model.

[b] $P = 0.077$.

[c] $P = 0.085$.

consume supplemental food and suggests that, at least during laying, treatment pairs consumed most or all of the supplemental corn. Small sample size and high variability in $\delta^{13}C$ likely contributed to the observed nonsignificant differences during incubation. We assume that treatment pairs consumed the supplemental food (corn, wheat, and rice) that disappeared.

Consumption of supplemental food did not change as incubation proceeded (nested ANOVA, Ross's Goose, $F = 0.8$, df = 25 and 30, $P = 0.76$; Snow Goose, $F = 1.0$, df = 33 and 30, $P = 0.45$). However, there was a significant species × stage of incubation interaction ($F = 5.2$, df = 2 and 114, $P = 0.006$), indicating that temporal patterns of food consumption differed between species, with food consumption by female Snow Geese declining through incubation but remaining unchanged for female Ross's Geese.

Body composition: Laying period.—After accounting for variation due to body size, clutch size, initiation date, and clutch size × initiation date interactions, overall body composition of Ross's Geese did not differ between control and treatment females (MANCOVA, Wilks' $\lambda = 0.25$, $F = 3.63$, df = 5 and 6, $P = 0.074$). However, univariate analyses showed that treatment birds were heavier and had more abdominal fat than controls (Tables 2 and 3). Standardized canonical coefficients for body mass, abdominal fat, breast muscle, heart, and gizzard were 1.12, 1.29, −0.97, −0.35, and −0.33, respectively, indicating that treatment and control groups were best distinguished by mass of abdominal fat and body mass in relation to mass of breast muscle.

Similarly, after accounting for variation due to body size, clutch size, initiation date, treatment × size, size × initiation date, and clutch size × initiation date interactions, overall body composition of Snow Geese differed between control and treatment females (Wilks' $\lambda = 0.17$, $F = 7.79$, df = 5 and 8, $P = 0.0061$). Univariate analyses revealed that treatment females had heavier breast muscle and hearts than control females (Tables 2 and 3). Standardized canonical coefficients of −0.4, 1.42, 0.33, 2.08, and 0.62 for body mass, abdominal fat, breast muscle, heart, and gizzard, respectively, indicated that treatment and control groups were best distinguished by mass of abdominal fat and heart.

Body composition: Incubation period.—For female Ross's Geese, after accounting for variance in body size and interactions between body size and treatment, overall body composition of control and treatment birds did not differ (Wilks' $\lambda = 0.57$, $F = 2.1$, df = 5 and 14,

TABLE 3. Body composition of food-supplemented and control Ross's Geese and Lesser Snow Geese. Shown are least-squares mean mass (g) ± SE from ANCOVA in Tables 2 and 4.

	Body mass	Abdominal fat	Breast	Heart	Gizzard
		Female Ross's Geese (laying period)			
Control ($n = 8$)	1,288 ± 26	29.5 ± 1.7	112.5 ± 2.9	12.1 ± 0.5	50.3 ± 2.2
Treatment ($n = 8$)	1,387 ± 29	36.4 ± 1.8	114.7 ± 3.2	11.6 ± 0.6	47.2 ± 2.1
		Female Snow Geese (laying period)			
Control ($n = 9$)	1,998 ± 43	42.0 ± 4.4	162.2 ± 5.2	17.1 ± 0.5	83.3 ± 1.3
Treatment ($n = 11$)	2,107 ± 38	52.9 ± 4.0	179.9 ± 4.7	17.6 ± 0.5	83.6 ± 1.2
		Female Ross's Geese (incubation period)			
Control ($n = 14$)	1,012 ± 14	7.9 ± 1.0	81.4 ± 2.6	10.1 ± 0.3	40.3 ± 1.0
Treatment ($n = 8$)	1,067 ± 19	10.6 ± 1.2	90.3 ± 3.6	10.9 ± 0.4	41.1 ± 1.5
		Male Ross's Geese (incubation period)			
Control ($n = 9$)	1,226 ± 28	2.8 ± 1.0	107.2 ± 3.1	11.5 ± 0.3	54.6 ± 1.7
Treatment ($n = 6$)	1,302 ± 47	5.4 ± 1.5	116.4 ± 5.7	12.9 ± 0.5	52.8 ± 2.5
		Female Snow Geese (incubation period)			
Control ($n = 11$)	1,556 ± 31	10.2 ± 1.8	124.3 ± 3.5	14.4 ± 0.4	72.1 ± 1.7
Treatment ($n = 9$)	1,649 ± 40	13.2 ± 2.6	129.1 ± 4.8	16.1 ± 0.6	73.4 ± 2.1
		Male Snow Geese (incubation period)			
Control ($n = 17$)	1,965 ± 47	1.6 ± 2.0	162.8 ± 4.5	17.3 ± 0.4	114.0 ± 6.0
Treatment ($n = 6$)	2,125 ± 74	16.0 ± 3.2	162.0 ± 7.2	19.2 ± 0.7	108.5 ± 10.0

$P = 0.12$), but univariate analyses revealed that treatment females had greater heart and body mass than did controls (Tables 3 and 4). Similarly, in male Ross's Geese, when accounting for variation in body mass and clutch size, overall body composition of control and treatment geese was not different (Wilks' $\lambda = 0.50$, $F = 1.41$, df = 5 and 7, $P = 0.33$), but univariate an-

TABLE 4. Effects of food supplementation (treatment) on body composition of Ross's Geese and Lesser Snow Geese during the incubation period. Shown are F-values from ANCOVA calculated from Type III SS. Initial model contained main effects (treatment, clutch size), covariates (body size, days of exposure to supplemental food), and two-way interactions.

	Body mass	Abdominal fat	Breast	Heart	Gizzard
		Female Ross's Geese			
Treatment	5.22*	2.61	3.88[b]	7.96**	ns
Body size	9.54**	7.08*	ns	13.00**	ns
Clutch size	ns[a]	7.16*	ns	ns	ns
Body size × clutch size	ns	8.81**	ns	ns	ns
Body size × treatment	ns	ns	ns	7.28*	ns
		Male Ross's Geese			
Treatment	ns	ns	ns	6.27*	ns
		Female Snow Geese			
Treatment	3.30[b]	ns	ns	5.82*	ns
Clutch size	3.89*	ns	ns	ns	ns
		Male Snow Geese			
Treatment	3.21[b]	12.40**	0.01	5.20*	ns
Body size	18.90***	ns	11.05**	15.60***	ns
Clutch size	ns	10.20**	ns	9.33**	ns
Clutch size × treatment	ns	8.62**	ns	ns	ns

*, $P < 0.05$; **, $P < 0.01$; ***, $P \le 0.001$.

[a] Nonsignificant effect excluded from final model.

[b] $P \le 0.087$.

TABLE 5. $\delta^{15}N$ values ($\bar{x}$ ± SD, with n in parentheses) of liver and muscle tissues of control and food-supplemented Ross's Goose and Lesser Snow Goose females at the end of laying and incubation periods.

Species	Treatment	$\delta^{15}N$ (‰) End of laying	$\delta^{15}N$ (‰) End of incubation
		Liver	
Ross's Geese	Control	8.3 ± 0.4 (5)	9.1 ± 0.9 (5)
	Treatment	7.7 ± 0.4 (5)	8.2 ± 0.6 (5)
Snow Geese	Control	8.4 ± 0.2 (5)	9.4 ± 0.5 (5)
	Treatment	7.9 ± 0.9 (3)	8.9 ± 0.9 (4)
		Muscle	
Ross's Geese	Control	7.6 ± 0.1 (5)	7.7 ± 0.5 (5)
	Treatment	7.6 ± 0.5 (5)	7.5 ± 0.5 (5)
Snow Geese	Control	7.7 ± 0.4 (5)	7.9 ± 0.5 (4)
	Treatment	8.0 ± 0.4 (3)	8.2 ± 0.2 (4)

alyses revealed that treatment males had larger hearts than did controls (Tables 3 and 4).

For female Snow Geese, after accounting for variance in body and clutch size, overall body composition of control and treatment birds did not differ (Wilks' $\lambda = 0.59$, $F = 1.7$, df = 5 and 12, $P = 0.21$), but univariate analyses revealed that treatment females had heavier hearts and marginally greater mass than did controls (Tables 3 and 4). For male Snow Geese, when accounting for significant variation in body and clutch size, as well as clutch size × treatment interactions, overall body composition of control and treatment birds was not different (Wilks' $\lambda = 0.58$, $F = 2.0$, df = 5 and 14, $P = 0.14$), but univariate analyses revealed that treatment males had more fat and larger hearts than did controls (Tables 3 and 4).

Stable-isotope analyses.—To explore protein use during fasting and to evaluate effects of supplemental food consumption on protein catabolism, we compared liver and muscle $\delta^{15}N$ values of control and food-supplemented geese collected at the end of laying with corresponding $\delta^{15}N$ values of geese collected at the end of incubation. Liver $\delta^{15}N$ values did not differ between species ($P > 0.16$) but increased during incubation, with control geese having liver $\delta^{15}N$ values that were enriched relative to food supplemented geese (ANCOVA, period, $F = 15.5$, df = 1 and 34, $P = 0.0004$; treatment, $F = 10.9$, df = 1 and 34, $P = 0.0023$; Table 5). Muscle $\delta^{15}N$ values of Snow Geese were enriched relative to those of Ross's Geese, but there were no significant period or food-addition effects (Ps > 0.36; Table 5). The results for liver in combination with the previous interspecific comparison suggest that both species adopt similar protein-maintenance strategies.

DISCUSSION

Extent of food consumption.—Incubating females are faced with a conflict between the need to incubate eggs versus feed themselves (Hogan 1989). Anorexia (fasting when food is available) by incubating females has been suggested for several species (Mrosovsky and Sherry 1980, Sherry et al. 1980, Freed 1981, Gaston and Jones 1989, Hogan 1989). We predicted that there would be an increase in consumption of supplemental food as incubation proceeded and energy reserves were depleted. Contrary to prediction, we found no temporal change in supplemental food consumption by Ross's Geese and Snow Geese; however, temporal patterns of food consumption differed between species, with food consumption declining through incubation in female Snow Geese but remaining unchanged in female Ross's Geese.

We are unsure whether consumption of food on the breeding grounds is facultative (expected in a phenotype with low endogenous reserves) or obligate (expected in a phenotype with anorexia during incubation [see Hogan 1989]), but high variance in food consumption (see Fig. 1) may indicate some genotype-environment interactions in feeding strategies. If this variation is largely genetic, then foraging behaviors may persist because of advantages that would accrue at low population densities, such as shortly after establishment of new colonies by pioneering individuals, when food may be relatively abundant. However, as population sizes increase, as they have over the past three decades at Karrak Lake, anorexic individuals with sufficient nutrient reserves may feed less but increase their nest attendance. Such a strategy may be frequency dependent and will be favored at high population densities if such densities affect inter- or intraspecific competition for nest sites. Our results help to bridge the two current paradigms about the importance of food to egg formation by arctic-nesting geese. These paradigms contend that food is not consumed during laying (Ankney and MacInnes 1978), or that food is consumed by laying geese and is an important component of their reproductive ecology (Gauthier 1993, Ganter and Cooke 1996). We found that Ross's Geese and Snow Geese are highly variable in their consumption of food on the breeding grounds. Some individuals consumed substantial amounts of food, whereas most consumed little or no food (Fig. 1). Therefore, we believe that both genotypes occur at Karrak Lake.

Hobson et al. (1993) reported that $\delta^{15}N$ values for muscle in female Ross's Geese collected at Karrak Lake increased from arrival to hatching and attributed this enrichment to increased catabolism of protein reserves. There was no difference in $\delta^{15}N$ values ($t = -0.74$, df $= 8$, $P = 0.48$) of muscle at the end of incubation between our sample and that of Hobson et al. (1993). In addition, we found no change in $\delta^{15}N$ values of muscle during incubation, but changes in $\delta^{15}N$ were in the predicted direction for Snow Geese. Differences between our results and those of Hobson et al. (1993) may have arisen because our sample did not include the laying period. Laying is a period of rapid and extensive protein mobilization (Alisauskas and Ankney 1992). For example, Ross's and Snow geese eggs contain on average 12.4 and 16.7 g of protein, respectively (Slattery and Alisauskas 1995). Thus, most protein use and, therefore, changes in $\delta^{15}N$ values in body protein reserves may occur during laying. If geese rely on metabolic adaptations during incubation to reduce protein consumption, then changes in $\delta^{15}N$ values due to increases in protein catabolism are expected to be much reduced. Metabolic adaptations to fasting include reduced basal metabolic rates (Cherel et al. 1988). If heart mass is related to metabolic rate (Garland and Else 1987, Daan et al. 1990, Konarzewski and Diamond 1995), then our finding that hearts of treatment Ross's and Snow geese were 8 to 12% heavier than controls suggests that treatment birds did not rely to the same extent as controls on metabolic adaptations to meet the energetic costs of incubation.

Different temporal patterns during incubation in $\delta^{15}N$ values of liver and muscle tissue may relate to the metabolic activity of the two tissues. In Japanese Quail, the isotopic half-life of liver is 2.6 days compared with 12.4 days for muscle tissue (Hobson and Clark 1992). Although values in wild geese may differ somewhat from quail, the incubation period may be of insufficient length for changes in $\delta^{15}N$ values in muscle tissue to become measurable even if geese adopt a protein conservation strategy. However, relatively high metabolic activity of the liver results in patterns of enrichment of ^{15}N consistent with anorexia.

Food supplementation.—Many species of arctic-nesting geese spend time on the breeding grounds before laying, providing an opportunity to replenish reserves (Ely and Raveling 1984, Bromley and Jarvis 1993, Gauthier 1993). Forage in the arctic tundra generally is considered to be sparse and of low quality (but see Fox et al. 1991), and nutrient uptake by geese in this environment may be negligible (Gloutney et al. 1999). When provided with supplemental food, Ross's Geese and Snow Geese depleted reserves to a lesser extent than did control geese. At the end of laying, female Ross's Geese and Snow Geese that were given supplemental food were 98.4 and 109.4 g heavier, respectively, than control females. Additional nutrients ingested during laying may have been used to meet nutritional costs of laying, thereby sparing reserves for incubation. In contrast, Ankney and MacInnes (1978) showed that heavier female Snow Geese had, on average, larger potential clutch sizes, and that females depleted endogenous reserves to similar levels regardless of clutch size. However, we believe that food supplements in our study were provided after females had initiated growth of the last follicle such that changes in clutch size were unlikely (Gloutney unpubl. data).

The body-size hypothesis (Afton 1980) predicts that Ross's Geese should make greater use of exogenous resources than Snow Geese. We found that mass-specific food consumption by Ross's Geese was 30% lower than that of Snow

Geese during laying but 48% higher during incubation. However, differences were not significant during either reproductive period. There were also no differences in time spent foraging by Ross's Geese and Snow Geese during laying and incubation. Apparently, high variance in prevalence and intensity of anorexia within species required sample sizes larger than ours for sufficient power to detect a statistical difference in mass-specific food consumption between species. However, a larger proportion of Ross's Geese consumed little or no food relative to food consumption in Snow Geese (Fig. 1).

Abdominal fat reserves at the end of laying were higher in geese that ate supplemental food than in control geese. However, this difference disappeared by the end of incubation. Thus, both species appeared to deplete reserves to a relatively constant level during incubation regardless of the use of supplemental food. Geese may have used supplemental food to maintain higher nest attendance and thereby potentially decrease overall duration of incubation. Proposed fitness benefits of shorter incubation periods include: (1) reduced risk of egg depredation (Clark and Wilson 1981, Arnold et al. 1987); (2) goslings hatching with a greater proportion of the initial energy invested in eggs as reserves (Williams 1994, Slattery and Alisauskas 1995); and (3) earlier colony departure to foraging areas, which provides goslings more time to attain adult size and acquire sufficient nutrient reserves for migration.

Feeding may be influenced by annual variation in weather. Conditions during incubation in 1995 were cold, windy, and wet (Alisauskas unpubl. data), and benefits of supplemental food may have been substantially higher in 1995 than in other years with more benign weather conditions. Effects of severe weather were apparent for control male Ross's Geese and Snow Geese, both of which had less abdominal fat at the end of incubation than did females (i.e. males were in poorer condition than females). Poor condition may increase frequency of male abandonment of females.

In summary, most evidence suggests that control of reproduction in colonial arctic-nesting geese is under strong environmental control (Ankney and MacInnes 1978, Cooke et al. 1995, Bon 1996). Specifically, variation in reproduction is related to levels of endogenous reserves at the time of arrival at nesting colonies (Ankney and MacInnes 1978, Bon 1996) and to local weather. Our results suggest that the interplay between nutrition and reproduction in Ross's Geese and Snow Geese is also mediated by adaptations to long-term fluctuations in local population size and corresponding effects on local food resources. As suggested by Alisauskas et al. (1988) for wintering Snow Geese, adaptations in morphology, behavior, and physiology may allow breeding Ross's Geese and Snow Geese to function somewhat independently of local food resources. Consequently, adaptations for ample nutrient storage and anorexia apparently enable persistence of these species in breeding areas at immense population sizes.

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