BODY RESERVE AND FOOD USE BY INCUBATING CANADA GEESE

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ABSTRACT.—During incubation, female Canada Geese (*Branta canadensis moffitti*) nesting near Brooks, Alberta, derived 87% of their energy requirement from body reserves, more than that used by any other subspecies of Canada Goose studied to date. The use of exogenous food was negligible during early incubation, but it appeared to be important to many individuals during the final week of incubation. *Received 13 May 1988, accepted 22 March 1989.*

FEMALE Canada Geese (*Branta canadensis*) incubate their clutches without assistance from males. High levels of incubation attentiveness are essential to ensure maximum success. Absence from the nest results in higher rates of egg predation (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977) and may interfere with normal embryonic development (Harvey 1971, MacInnes et al. 1974, Aldrich 1983). The high levels of attentiveness, typical of Canada Geese (Cooper 1978, Aldrich 1983, Bromley 1984), reduce significantly the time that females can feed. Incubating females reconcile the time constraints of incubation with their own nutrient demands by catabolizing body reserves. This use of body reserves is controlled ultimately by the trade-off between increased fecundity in a particular year and continued survival of the individual (Aldrich 1983, Thompson and Raveling 1987). At the proximate level, it is controlled by a genetically programmed reduction in the set point for body weight (or some component of it; Sherry et al. 1980). The *set point* for body weight is the mass below which physiological and behavioral reactions will intervene to maintain that weight.

There is a progressive decline in the rate of weight loss as incubation progresses in all subspecies of Canada Geese studied to date (Cooper 1978, Aldrich 1983, Bromley 1984). Some of this change in the rate of weight loss must result from decreased metabolic requirements associated with progressively lower body mass (Owen 1980), and decreased thermal stress associated with increasing ambient temperatures over the period of incubation (Aldrich 1983). However, behavioral changes concurrent with

the change in rate of weight loss suggest that increased reliance on direct food intake also contributes to the decline in the rate of weight loss (and presumed use of body reserves). Cooper (1978), Aldrich (1983), and Bromley (1984) all observed decreases in the attentiveness of incubating Canada Geese over the period of incubation. Aldrich (1983) also reported that the proportion of time females (both cackling and western subspecies) devoted to feeding while they were off their nests increased in late incubation.

Raveling (1979) and Bromley (1984) calculated the energy derived from food intake by subtracting the energy derived from body reserves from the estimated energy requirement for the entire incubation period. This method, however, only estimates the average contribution of food intake. If food intake increased as incubation progressed, then average values would overestimate the energy contribution from food intake in early incubation and underestimate it in late incubation.

Because incubating female geese retain undigested food until they leave the nest on their next incubation recess (Owen 1980), it may be possible to estimate the amount of food ingested on the previous incubation recess from the amount of undigested food remaining in the gut (by correcting for absorption through the gut wall). Energy available to the goose from that amount of food could then be estimated as well.

We estimated the contributions that body reserves and direct food intake made to the energy budget of Canada Geese nesting in southeastern Alberta. We calculated the average contribution of body reserves over most (21 days) of the incubation period, and estimated the average contribution of food by subtraction. We also calculated the energy that females derived

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from food ingested during a single incubation recess in the first and final weeks of incubation. Incubation rhythms of five females in late incubation were recorded in an effort to determine the number of recesses taken per day. This information allowed us to estimate daily food consumption at this stage of incubation (rather than average consumption over the entire incubation period).

METHODS

We searched for nests of wild Canada Geese on islands at Gleddie Lake (GL) and Rolling Hills Lake (RHL) near Brooks, Alberta (see Leblanc 1986 for a description of these areas), during the laying periods of 1985 and 1986. The interval between searches varied from 2 to 4 days. Eggs in each nest were marked individually and nest locations were recorded on maps. We measured the length and breadth of each egg to the nearest 0.1 mm with Vernier calipers. These measurements were used to identify parasitized nests and to estimate fresh egg and clutch weights of females that were collected subsequently.

Incubating females were collected from nests found during these nest searches. One group (early-incubation females) was collected at approximately day 3 of incubation and another group (late-incubation females) was collected at approximately day 24 of incubation. We collected only females that had initiated their clutches within 4 days of the peak of nest initiation. The first day of incubation was defined as the day the clutch was completed. This date was predicted based upon the number of eggs in the nest on the previous visit, mean clutch size, and observed laying rate (taken from Cooper 1978). Nests were not visited for several days before collection in order to minimize disturbance. The number of eggs laid in a given nest was used to refine the estimated stage of incubation for early-incubation females. The clutches of collected females were artificially incubated. Hatching date was used to refine estimated stage of incubation for late-incubation females. Goslings hatched from these eggs were reared at the Brooks Wildlife Centre until mid-July, and were then released by Alberta Fish and Wildlife.

Birds were collected in late afternoon and evening. As recesses are initiated predominately during late afternoon (Aldrich 1983), this collection time provided a representative sample of ingesta mass and minimized the extent of digestion at the time of collection.

Geese were sealed inside two plastic bags and placed in a freezer within 3 h of collection. They were later thawed and weighed to the nearest 1.0 g. Remiges and rectrices were removed, and the birds were skinned and dissected. The abdominal cavity was opened and

the gut (esophagus to cloaca inclusive) removed. Intestinal mesenteries were severed and the length of the small intestine was measured (Ankney 1977).

Ingesta from the esophagus and proventriculus, the small intestine, the caecae, and the large intestine and cloaca were gently expressed and weighed separately. The small intestine was severed immediately anterior and posterior to concentrations of ingesta to minimize the inclusion of endogenously derived material (mucous). Grasses from the esophagi of collected geese were identified according to Looman (1982).

The ventriculus was excised, weighed, opened, washed thoroughly, towel dried, and reweighed. The difference between the gross and net weights of the ventriculus was taken as the weight of the grit. Ventriculi never contained measurable amounts of ingesta.

Soft tissue was removed from each skeleton and recombined with the skin and digestive organs. This material (the bone-free carcass) was then sealed in an individually marked plastic bag and immediately refrozen. The bone-free carcasses were passed five times through a commercial meat grinder (Butcher Boy TCA 22, 1.5 hp) and the material was mixed thoroughly between grindings. Four replicate 30-g samples were removed from the resulting homogenate and immediately refrozen. Two of these samples were later weighed, oven dried (56°C) to constant weight, reweighed, and further homogenized with a mortar and pestle. We subjected 3-g samples of this homogenate to fat extraction (4 h—using petroleum ether in a Soxhlet apparatus). If these two replicates agreed within 1.5%, the mean of the fat content of these two replicates was used to calculate the carcass fat content. Otherwise, we analyzed two additional replicates, and the mean of the pair of replicates that agreed most closely was used (maximum difference was 1.8%).

The mass of remiges and rectrices and wet mass of all ingesta plus estimated grit weight were subtracted from the thawed goose weight to give analyzed carcass mass. Analyzed carcass mass was multiplied by proportional dry matter content (mean of two replicates) to calculate dry mass of the carcass. Total fat weight was calculated by multiplying dry mass of the carcass by fat content (mean proportion of two replicates) of samples subjected to fat extraction. Campbell and Leatherland's (1980) equations were used to calculate the protein content of carcasses. A water : nitrogen ratio of 18.1:1, and a protein : nitrogen ratio of 6.25:1 were used in these calculations. We did not attempt to measure carbohydrates (primarily glycogen) because their biomass is negligible in birds (Ricklefs 1974).

Standard metabolic rate (SMR) in kJ/day was calculated as $307.7 \times$ (mass in kg)$^{0.734}$ (Aschoff and Pohl 1970). We used the average of the early-incubation and late-incubation weights in this calculation. We followed the procedures of Raveling (1979) to esti-

mate the cost of incubation (1.25 × SMR), and to estimate the energy that females could derive from the catabolism of body reserves. The energy equivalent of fat was taken to be 37.7 kJ/g and that of protein, 18.0 kJ/g.

Ingesta were oven dried (56°C) to constant weight. Because the mean length of incubation bouts (Cooper 1978, Aldrich 1983) is considerably longer than the average passage rate of ingesta through geese (Ebbinge et al. 1975, Owen 1975, and others), we assumed that all ingesta within a goose's gut (with the possible exception of that in the caecae) had been collected on that female's last incubation recess before collection. Because incubating females do not defecate at their nests, we assumed that the guts of incubating females contained all of the food that had been ingested on the previous recess except for the portion that had been absorbed through the wall of the gut. It is conceivable that defecation may have occurred during collection. We believe, however, that this is unlikely because defecation was never observed during collection, and feces were found in cloacae of several females.

Dry weights of ingesta from the caecae and the large intestine and cloacae were multiplied by 1.67 to correct for absorption of dry matter that had presumably taken place. This correction factor corresponds to the 40% retention rate (digestibility) that Owen (1980) suggested for geese using new-growth grasses. It is the inverse of the undigested portion of ingested food: $(1.0 - 0.4)^{-1} = 1.67$. We did not correct the weight of ingesta from the small intestine for absorption. While some absorption undoubtedly occurred, we believe that the effect of this absorption was minimal and it may have been offset to some extent by the inclusion of some endogenously derived material (mucous) with ingesta. Dry weight of ingesta gathered on a single recess was calculated as the sum of the dry weights of ingesta from the small intestine, the esophagus and proventriculus, and the corrected (for absorption) dry weights of ingesta in the caecae and the large intestine and cloaca. We used the total energy content of very young prairie grasses (17.9 kJ/g; Coupland 1973) and the retention rate (0.40) suggested by Owen (1980) to estimate the energy that the geese could obtain from ingesta.

Egg measurements were used to calculate volume indices according to the formula: volume index = length × breadth² (Leblanc 1986). These indices were used to calculate fresh egg weights: egg weight (g) = (0.537 × volume index) + 8.797 (Leblanc 1986). The calculated fresh weights of all eggs in a clutch were summed to provide estimates of fresh clutch mass. All clutches in which eggs were added at a rate of >1 egg/day or in which eggs of markedly different size or shape were found were considered parasitized and were excluded from analyses.

Incubation rhythms were monitored with super-

eight movie cameras that exposed 1 frame/min. The cameras were housed in adapted ammunition boxes that were placed on the ground and concealed in natural vegetation 2–5 m from nests. Aldrich and Raveling (1983) reported that, in a population of Canada Geese that they studied, inexperienced breeders laid clutches of 4 eggs, while experienced breeders produced clutches of 5 or more eggs. In addition, lower body reserves of inexperienced breeders relative to experienced breeders caused reduced nest attentiveness among inexperienced breeders during the final week of incubation (Aldrich and Raveling 1983). We monitored incubation rhythms at two nests that contained 4 eggs and at three nests that contained 5 or more eggs in order to contrast the behavior of presumed (based on clutch size) experienced and inexperienced breeders.

We attempted to observe with a 20× spotting scope the behavior of females during incubation recesses. We observed several females concurrently as long as they were on their nests and then focused exclusively on the first female that left her nest. We recorded 21 h of observations and observed 12 recesses. Unfortunately, dense cattails and undulating topography prevented, in most instances, constant observation of females throughout the entire recess. We have only four uninterrupted observations of females from the time they left their nests until they returned.

Statistical methods.—All statistical procedures were performed with the SPSSx statistical package. A probability level of 0.05 was used to evaluate statistical tests. One-tailed tests were used whenever consistent results from previous studies allowed us to predict the direction of potential differences. Means (x̄) are reported ± standard deviations (SD).

RESULTS

Carcass composition.—The mean wet body mass of females declined by 17% between early and late incubation (Table 1). Most of the weight loss (71%) was the result of a marked decrease in fat content. Fat content declined by 87% during this period. Protein content also declined (Table 1), but the change (6%) was minimal relative to that of fat.

Clutch size and weight.—The clutches of three early-incubation females and two late-incubation females appeared to have been parasitized and were excluded. All but one of the apparently unparasitized nests contained >4 eggs. Although some parasitism may have gone undetected (if host and parasite eggs were of similar size and shape), these clutch sizes suggest that nearly all females collected from these nests were experienced breeders (Aldrich and Rav-

TABLE 1.   Body mass and composition ($\bar{x} \pm$ SD) of incubating female Canada Geese at two stages of incubation.

| | Incubation stage | | | | |
	Early (n = 13 or 14)[a]	Late (n = 12)	Difference (%)	t[b]	P
Body mass (g)	3,817.5 ± 229.0	3,186.1 ± 196.0	631.4 (17)	7.4	<0.001
Fat content (g)	510.7 ± 127.3	65.6 ± 31.6	445.1 (87)	12.6	<0.001
Protein content (g)	761.9 ± 49.1	714.0 ± 47.8	47.0 (6)	2.4	0.024

[a] We excluded body- and protein-mass values of one specimen because of considerable blood loss. We used the fat-mass value.
[b] Pooled t-test, one-tailed probability.

eling 1983). The calculated fresh weights of clutches from the early-incubation sample (n = 11, $\bar{x}$ = 984.9 ± 165.8 g) and the late-incubation sample (n = 10, $\bar{x}$ = 1,026.0 ± 111.2 g) were similar (t = 0.7, two-tailed, P = 0.509). Hence, differences in carcass composition of females in the two groups were presumably not the result of differences in either experience or the extent of body reserve use for clutch formation (based on calculated fresh clutch weights).

Ingesta weight.—The guts of most early-incubation females contained very little or no food. Half contained <2 g of ingesta, and only one contained >8 g (Fig. 1). This contrasts with the situation among late-incubation females, all of which had some food in the gut. Ingesta weights from late-incubation females varied considerably, and ranged between <4 and >22 g (Fig. 1). Incubating Canada Geese had significantly (Mann-Whitney U = 151.5, P = 0.0002) more ingesta in their guts during late incubation (n = 12; median = 10.3 g dry weight) than they did during early incubation (n = 14; median = 1.9 g dry weight).

Six of the collected females had some ingesta in their esophagi. Esophageal contents were composed entirely of upland grasses. Sedge leaves or seeds were absent. By far the most prevalent species was Sandberg's blue grass (*Poa sandbergii*). Traces of northern wheatgrass (*Agropyron dasystachum*) and blue grama grass (*Bouteloua gracilis*) were also identified.

Incubation rhythms and recess behavior.—The mean length of incubation recesses taken in the final week of incubation was similar for females that incubated clutches of ≥4 eggs, but there was no overlap in the number of recesses taken by these groups (Table 2). Females that incubated clutches of ≥5 eggs (presumably experienced breeders) took, at most, 2 recesses/day. The two females that were incubating clutches

of 4 eggs (presumably first-time breeders) took at least 3 recesses/day.

Two females with clutches of ≥5 eggs that were observed for one entire recess on days 18 and 24 of incubation spent 20 of 33 min (61%) and 14 of 16 min (88%) feeding. One female with a clutch of 6 eggs was observed for 2 complete recesses: on day 15 of incubation, 12 of 19 min (63%) were spent feeding; and on day 20, 13 of 20 min (65%) were spent feeding.

The female that was observed during 2 complete recesses was collected ca. 95 min after she completed the second recess. This goose was observed on her nest for 66 min before she took the recess (total recess length = 20 min) and throughout the 95 min that separated the end of her recess from her collection. The dry weight of all ingesta in this goose's gut was 20.2 g. The location of the ingesta (1.9 g dry weight in the esophagus and the remainder in the anterior and middle portions of the small intestine) confirmed that all of this ingesta was collected during the observed recess. This rate of grazing (20.2 g in 13.0 min) is equivalent to 93.2 g dry weight per hour.

Energy from body reserves and food intake.—Energy from fat catabolism supplied most (83%) of the energy requirements of incubating females (Table 3). Energy derived from protein catabolism during incubation was minimal (4%). Based on the difference between the energy available from the catabolism of body reserves (between day 3 and day 24 of incubation) and the total energy requirement for that period, females presumed to have breeding experience should have obtained an average of 13% (100% − 87%; Table 3) of their energy requirement from food over that period.

The median contribution of exogenous energy derived from feeding during a single recess taken early in incubation was 1.3% (Table
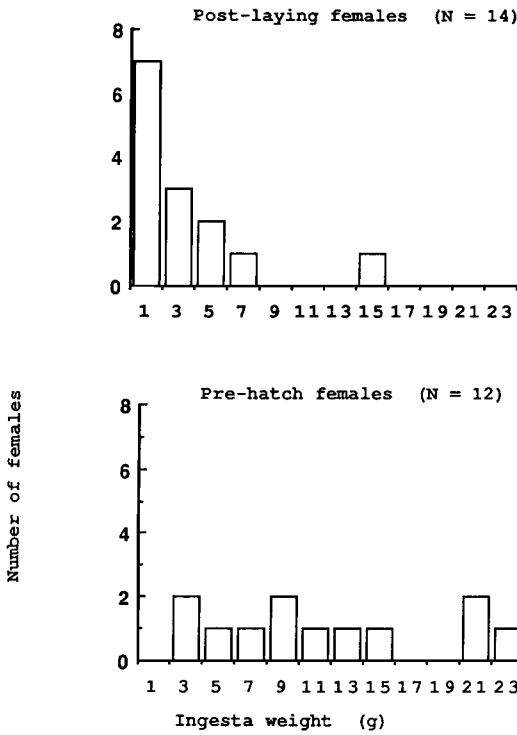
Post-laying females   (N = 14)

Pre-hatch females   (N = 12)

Ingesta weight   (g)

Fig. 1. Frequency distribution of dry mass of ingesta from the guts of female Canada Geese collected during early and late incubation.

TABLE 3. Energy required (kJ/day) by incubating female Canada Geese and its availability from various sources.

Source	Incubation period	Energy required[a]	Energy provided	% of total required
Body reserves				
Body fat	Days 3–24	965.1	798.9[b]	82.8
Protein			40.2[c]	4.2
Total			839.1[d]	87.0
Ingesta/recess[e]				
Minimum	Day 3	1,023.3	0.0	0.0
Median			13.0	1.3
Maximum			107.6	10.5
Minimum	Day 24	900.6	18.0	2.0
Median			64.5	7.2
Maximum			168.3	18.7

[a] Based on the equation of Aschoff and Pohl (1970): SMR (kJ/day) = $307.7 \times$ (mass in kg)$^{0.734}$ and Raveling's (1979) cost of incubation (1.25 × SMR).

[b] Based on the total decline in fat (g) between days 3 and 24 divided by 21 and multiplied by the energy equivalent for fat: (445.1 g/21 days) × 37.7 kJ/g = 798.9 kJ/day.

[c] Based on the total decline in protein (g) between days 3 and 24 divided by 21 and multiplied by the energy equivalent for protein: (47.0 g/21 days) × 18.0 kJ/g = 40.2 kJ/day.

[d] The sum of energy provided by endogenous fat and protein.

[e] Based on corrected (for absorption) ingesta weights, the energy content of spring grass (17.9 kJ/g), and the retention rate (digestibility) of that grass by geese (0.40; Owen 1980).

3). The median energy contribution attributable to food consumed on a single recess during the final week of incubation (7.2%; Table 3) was 5.5 times as great as during early incubation, but was still considerably less than the calculated average requirement for exogenous energy (100% − 87% = 13%; Table 3).

One or two recesses/day seemed to be typical of experienced breeders (Table 2). The median experienced female derived 1.3–2.6% and 7.2–14.4% (depending on the number of recesses/day) of its energy requirement from food in early and late incubation, respectively. Assuming that the change in the amount of food collected per recess occurred at a constant rate, then a female that took a single recess/day and consumed the median amount of food/recess

TABLE 2. Incubation behavior during the final week of incubation of experienced or inexperienced[a] breeders.

Clutch size[a]	Nest no.	Days observed (n)	Recess/day $\bar{x}$ (range)	Recess length[b] $\bar{x} \pm$ SD (n)	Attentiveness[c] $\bar{x}$ (range)
≥5 eggs	1	2	1.0 (1–1)	27.5 ± 2.1 (2)	98.1 (98.0–98.2)
	2	3	1.7 (1–2)	26.4 ± 14.0(5)	96.9 (94.4–99.1)
	3	1	1.0 (—)	22.0 ± — (1)	98.5 (—)
4 eggs	1	2	7.0 (4–10)	14.3 ± 7.8 (14)	93.0 (91.5–94.5)
	2	3	3.3 (3–4)	28.6 ± 18.0(10)	93.4 (90.2–96.7)

[a] The first 3 females were presumed to be experienced breeders (second-time or later) and the second 2, inexperienced breeders (first-time).

[b] In minutes.

[c] The percentage of the 24-h period that females were thought to be on their nests. We assumed that females left their nests only during the diurnal period because we could not monitor incubation behavior after dark.

MURPHY AND BOAG

would have acquired 4.3% [(1.3 + 7.2)/2] of her energy requirement from food between day 3 and day 24 of incubation. A female on 2 recesses/day who consumed the median amount of food/recess would have acquired 8.5% [(2.6 + 14.4)/2] of her energy requirement from food over that period.

Three or four recesses/day was typical of inexperienced breeders (Table 2). Assuming that inexperienced breeders obtained the median amount of food/recess that was observed among females presumed to be experienced breeders, then inexperienced breeders would have derived 3.9–5.2% of their energy requirement from food in early incubation and 21.6–28.8% of their energy requirement from food during late incubation. Inexperienced females, however, attempt to maximize exogenous energy acquisition (Aldrich and Raveling 1983), and it may be more reasonable to assume that they consumed the maximum amount that was recorded in experienced breeders. If the latter assumption is correct, inexperienced females would have derived 31.5–42.0% (3 to 4 times 10.5; Table 3) and 56.1 to 74.8% (3 to 4 times 18.7; Table 3) of their energy requirement from food during early and late incubation.

DISCUSSION

Ingesta weight.—The increase in dry weights of ingesta we recorded is similar to a phenomenon in incubating Snow Geese (*Chen c. caerulescens*; Ankney 1977) and substantiates suggestions that Canada Geese also increase their reliance on food intake as incubation progresses (Aldrich 1983, Bromley 1984).

A weak inverse relationship between ingesta mass and fat content of early incubation females ($n = 14$; Spearman rank correlation coefficient = -0.438, $P = 0.059$) suggests that variation in ingesta weight was a function of the relative demand for exogenous energy (inversely related to fat reserves) and the female's willingness to feed rather than the female's ability to obtain food. If variation in ingesta weight reflected a female's ability to consume food, then we would have predicted a direct relationship between fat content and ingesta weight (assuming that a female's ability to consume food was reflected in higher fat content). Such was not the case.

The presence of 15.0 g of ingesta in one early incubation female and the ability of a late-incubation female to collect 20.2 g dry weight of food in only 13 min of feeding also suggest that food was available (in at least some locations) both early and late in the incubation period. Because incubating females sometimes fly to areas away from their insular nesting territories to feed (Ewaschuk 1970), all females should have had access to exploitable food sources.

Low ingesta weights, particularly early in incubation, presumably reflect a decision not to feed rather than difficulty in obtaining food. Nevertheless, of the four recesses we observed in their entirety, all contained at least 12 min of feeding (from 61 to 88% of total time off the nest). Although we observed no recesses without feeding, Cooper (1978) and Aldrich (1983) each recorded recesses that contained little or no feeding. The fact that we observed no recesses of this kind may reflect the timing of our observations, a potential bias in our methods, and the small number of recesses observed. All recesses we observed in their entirety were recorded in the last half of the incubation period when females seemed to rely more heavily on food intake. Moreover, we observed several females until one left the nest and then followed the recess behavior of that female. Conceivably, our observations may have been biased towards females that left the nest more frequently than the rest of the population. Because recess frequency and feeding activity both are related inversely to body reserves (Aldrich 1983), our observations may have been biased toward females inclined to spend a higher than average proportion of their recess time feeding.

Energy from body reserves and food intake.—The use of body reserves during incubation has now been investigated in four subspecies of Canada Geese (*B. c. minima, B. c. occidentalis, B. c. moffitti,* and *B. c. maxima*). Females of *B. c. moffitti* derived more (87%) of their incubation energy requirement from body reserves than smaller subspecies (*minima* and *occidentalis*; Table 4). This is consistent with observations that larger geese derive more of their incubation energy requirement from body reserves than smaller geese (Thompson and Raveling 1987). Contrary to this relationship, however, incubating *B. c. moffitti* also derived more of their energy requirement from body reserves than larger *B. c. maxima* (71.5%).

Food supplies an increasing proportion of the total energy requirement as incubation pro-

TABLE 4.   Calculated proportion of energy required during incubation that is supplied from body reserves in various subspecies of Canada Geese (*Branta canadensis*).

Subspecies	Post-laying body weight	% energy from body reserves	Source
minima	1,390	48.0	Raveling 1979
occidentalis	3,206	66.1	Bromley 1984
moffitti	3,792	87.0	This study
maxima	4,162	71.5[a]	Mainguy & Thomas 1985

[a] Our calculation based on data from Mainguy and Thomas (1985: tables 2, 7).

gresses (Table 3). Some of the observed difference may result from the fact that our late-incubation specimens were collected on approximately day 24 of incubation whereas *B. c. maxima* females were collected on day 26 (early-incubation females were collected on approximately day 3 of incubation in both studies). This difference could not explain very much of the difference between *B. c. moffitti* and *B. c. maxima*. Even if all *B. c. moffitti* females had taken 2 recesses/day and consumed the maximum amount of food recorded on each of days 25 and 26 of incubation, their body reserves would have supplied an average of 85% ([(2 days × 63%) + (21 days × 87%)]/23 days) of their total energy requirement over the 23-day period.

B. c. maxima retained more than twice as much fat on day 26 of incubation (166 ± 18 g; Mainguy and Thomas 1985) as *B. c. moffitti* an average of 24 days after incubation began (66 ± 32 g; Table 1). The availability of body reserves does not appear to explain the difference in the proportion of the incubation energy requirement met by reserves. Differences in the abilities of geese to repel predators may explain differences in the use of body reserves by different groups of geese during incubation (Thompson and Raveling 1987). We were, however, unable to identify any predator-related difference that might account for greater use of body reserves by *B. c. moffitti* than by *B. c. maxima*.

Inexperienced females retain smaller energy reserves after laying than experienced females (Aldrich and Raveling 1983). Differences in the breeding experience of the females collected in the two studies or in the experience of early and late incubation samples in one or both of the studies may explain the greater apparent use of body reserves by *B. c. moffitti*.

Experienced female *B. c. moffitti* derive an average of 87% of their energy requirement from body reserves between day 3 and day 24 of incubation (based on changes in body composition). Presumably they derive 13% of their energy requirement from exogenous food sources during that period. However, the average energy supplied by food intake consumed on a single recess at day 3 and at day 24 was only 4.3% [(1.3 + 7.2)/2; Table 3]. Thus, an experienced female would derive only 8.6% (4.3% × 2) of its energy requirement from food even if it took 2 recesses/day. Uric acid produced by incubating Turkey (*Meleagris gallopavo*) hens was re-used by caecal microorganisms that potentially supply the hens with metabolizable substrates (Zadworny 1985). If this occurs in incubating geese, it may explain the difference between the calculated demand for exogenous energy (based on changes in body composition) and energy provided by direct food intake (based on ingesta weights). The uncorrected absorption of dry matter from the small intestine may also account for some of this apparent discrepancy.

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