INCUBATION BEHAVIOR AND BODY MASS OF FEMALE GREATER SNOW GEESE[1]

AUSTIN REED

*Canadian Wildlife Service, 1141 Route de l'Eglise, Ste-Foy,
Québec, G1V 4H5, Canada*

R. JOHN HUGHES AND GILLES GAUTHIER

*Départment de Biologie and Centre d'Etudes Nordiques, Université Laval,
Ste-Foy, Québec, G1K 7P4, Canada*

Abstract. Nest attentiveness and behavior of incubating female Greater Snow Geese (*Anser caerulescens atlanticus*) was monitored on Bylot Island, NWT in 1990–1991. Females incubated about 94% of the time through much of the incubation period but nest attentiveness declined to 91% at approximately 6 days before hatch then rose to close to 100% in the last 1–4 days. Females took recesses throughout the 24 day incubation period, but frequency increased in the third week of incubation then decreased markedly in the last 1–4 days. During the latter half of the incubation period, individual females took an average of 5–7 recesses/day during which they remained close to the nest, and most devoted more than 90% of the time to feeding vigorously on sprouting graminoids. Mean recess duration was constant at about 15–16 min, except for the last 1–4 days when it increased to >30 min. Females captured during late incubation had relatively high body mass ($\bar{x} = 2,158$ g) which represented a loss of only 17% in mass during incubation and showed that body reserves had not been depleted. Retaining some body reserves through to hatch may increase survival of females and may enhance their capability of caring for the young during brood rearing. In comparison with other large geese, Greater Snow Geese showed a low rate of nest attentiveness and took frequent recesses during which they fed intensively; they relied more heavily on food obtained in the breeding area (as opposed to reserves laid down during migration) and lost a smaller proportion of their initial mass during incubation. This strategy appears to be imposed by the lengthy migration to the high Arctic, which reduces the amount of stored reserves available for the demands of nesting.

Key words: Anser caerulescens atlanticus; *Arctic; body condition; Bylot Island; Greater Snow Goose; incubation behavior.*

INTRODUCTION

Most geese of the Northern Hemisphere breed in the Arctic. The constraints imposed by this choice of breeding area include the requirement to undertake lengthy flights from southerly staging and wintering areas, a short summer season in which to carry out nesting and brood rearing, and the relatively low biomass of arctic graminoid plants which constitute the summer diet (Owen 1980, Afton and Paulus 1992, Manseau and Gauthier 1993). Egg laying occurs before new growth of vegetation has begun and when food availability is low, making a large demand on the nutrient reserves of the female just before she begins incubation. Only females incubate and the requirement to maintain a sufficiently warm nest environment for embryonic development and to provide protection against egg predators

limits opportunities to feed (Thompson and Raveling 1987). The stressful nature of this period was evident in studies of Lesser Snow Geese (*Anser caerulescens caerulescens*) breeding on the west coast of Hudson Bay where females lost more than 30% of initial body mass during incubation (Ankney and MacInnes 1978) and some individuals actually starved just before hatch (Harvey 1971).

In all species of geese studied to date, incubating females spend more than 90% of their time on the nest and lose a substantial proportion of their initial body mass (Owen 1980, Thompson and Raveling 1987) but there are important interspecific differences in incubation behavior and rates of body mass loss. Thompson and Raveling (1987) attributed these differences mainly to body size: smaller species such as Brant (*Branta bernicla*) incubate about 93% of the day, the remaining time being spent in several short recesses during which they feed intensively

(Thompson and Raveling 1987, Madsen et al. 1989). In contrast, larger species such as Giant and Western Canada Geese (*B. canadensis maxima* and *B.c. moffitti*) (Cooper 1978, Aldrich and Raveling 1983, Murphy and Boag 1989) and Emperor Geese (*Anser canagica*) (Thompson and Raveling 1987) spend more time on the nest (97–99%) and take fewer but longer recesses during which less than half of the time is devoted to feeding. Thus, larger species generally have low food intake during incubation, rely almost entirely on body reserves accumulated earlier on spring staging areas (Ankney and MacInnes 1978, Thomas 1983) and tend to lose a larger proportion of their body mass during incubation than do smaller species (Thompson and Raveling 1987). Many large geese (e.g., larger races of Canada Geese) migrate shorter distances and nest further south in comparison to small geese (small races of Canada Geese, Brant). A lower mass-specific metabolic rate and the ability to store large nutrient reserves allow large geese to adopt a strategy maximizing reliance on stored reserves and a high rate of nest attentiveness (Afton and Paulus 1992).

One of the largest subspecies, the Greater Snow Goose (*Anser caerulescens atlanticus*), does not fit the pattern described by Thompson and Raveling (1987). This large goose migrates long distances and nests at very high latitudes (Gauthier et al. 1992) and initiates incubation with only moderate body reserves (Choinière and Gauthier, in press). When weighing female Greater Snow Geese captured in late incubation during an earlier study (Hughes et al. 1994a), we found a mean body mass higher than expected based on studies of other large geese. We therefore undertook this study to (1) further document body mass loss by incubating females and (2) examine whether behavioral patterns could explain the maintenance of a relatively high body mass through incubation in this unique stock of large geese breeding in the high Arctic.

STUDY AREA AND METHODS

The study area was a glacial valley near the western extremity of the southwest plain of Bylot Island (73°N, 80°W), Northwest Territories. The southwest plain is the most important nesting location for Greater Snow Geese, accommodating approximately 15% of the breeding population (Reed and Chagnon 1987, Reed et al. 1992); our study site supported one of the highest nesting concentrations on that plain. Most geese, including those observed in 1991 and those weighed in 1990–1991, nested on low ridges separating wet polygon depressions in a generally flat, lowland plain. The dry ridges supported willow (*Salix arctica*) and a variety of forbs and graminoids whereas the depressions were dominated by the graminoids *Dupontia fisheri, Carex aquatilis* var. *stans,* and *Eriophorum* spp. (Hughes et al. 1994b, Gauthier et al. 1995). Predators of Snow Goose eggs included, in approximate order of importance, Arctic Foxes (*Alopex lagopus*), Parasitic Jaegers (*Stercorarius parasiticus*), Long-tailed Jaegers (*S. longicaudus*), Glaucous Gulls (*Larus hyperboreus*) and Common Ravens (*Corvus corax*); only Arctic Foxes were a potential threat to adult geese. There was daylight over the entire 24-hr period during incubation.

Geese were captured (1989–91) on the nest, during the last nine days of the approximately 24-day incubation period (Gauthier and Reed, unpubl. data), with a modified bow net trap triggered at a distance from a blind (*n* = 11 females in 1989, 19 in 1990, 15 in 1991). In 1992 a sample of 12 females was shot on the nest to determine the mass of ingesta. Geese were weighed with a spring balance to the nearest 50 g.

The main body of our data on incubation behavior comes from observations made from a blind overlooking an expanse of lowland polygon depressions occupied by several dozen nesting pairs in 1991. We recorded incubation behavior for 24-hr periods at four dates during incubation: 16–17, 22–23, 26–28 June and 1–3 July 1991 (peak of hatch was 9 July). During each of the first two dates, we covered an uninterrupted 24-hr session using a combination of visual observation and time-lapse (1 image min^{-1}) video recording (8 mm Canon E57). The two remaining dates were each covered by two 12-hr sessions (12:00–24:00, 24:00–12:00, EST) over a 48-hr period, using only visual observations. During visual observations, we kept nests (*n* = 8 for the first two dates, *n* = 13 for the last two dates) under continual surveillance, recording times of departure and return of incubating females to the nearest minute. For females on recess we recorded their approximate distance from the nest at a randomly selected point in time during the recess; this yielded 4–28 records/female for estimating individual mean distances. We determined the proportion of time spent feeding during recesses on the last two dates by recording the instantaneous behavior of females every 10 sec for the entire recess (up to 1,260 sec) or for

periods distributed randomly within the recess (80–300 sec, mostly 250 sec). We also recorded pecking rates (time for 25 pecks) which were converted to pecks/min. Mean rates for individual females during all but the first date were determined using 3–13 (mostly 10) records per female per recess.

We compared nest attentiveness, recess duration and recess frequency among the four observation dates and among times of day (four periods: 00:00–06:00, 06:00–12:00, 12:00–18:00, 18:00–24:00). Nest attentiveness was determined as the percentage of total time spent on the nest by day/period. For recess duration and frequency, only complete (both start and end recorded) recesses were retained and each was assigned to one of the four periods based on its midpoint in time. Incubation bout length was not compared because many incubation bouts extended beyond the beginning or end of the observation sessions. Thus, the duration of some of the longest bouts could not be determined. For comparisons between dates, we restricted our analysis to data recorded between 07:00 and 19:30 (data were incomplete for other time periods, mainly for the first two dates). Similarly, for comparisons between times of day, we restricted our analysis to the last two dates. Analyses were conducted using two-way analysis of variance (ANOVA) with females considered as a factor to control for between-female differences in incubation behavior. Multiple a posteriori comparisons were conducted using Tukey's Honestly Significant Difference test. Pecking rates at different dates were compared using Kruskall-Wallis analysis of variance because of heterogenous variances among dates.

In 1990, additional observations (6 hr on 6 July and 18 hr on 7–8 July) were conducted on 12 incubating females during the last 1–4 days before hatch, a phase of the incubation period not covered by the 1991 observations.

We used linear regression to examine the relationship between body mass and the number of days before hatch during the last nine days of incubation. Only the body masses of females with known hatch date ($n = 36$) were used.

RESULTS

INCUBATION BEHAVIOR

Because of equipment limitations or poor lighting, video recording yielded only five records of recess duration and none of incubation bouts.

Thus, visual observations provided most of the data.

Mean nest attentiveness among the females observed in 1991 averaged 93.0% across both the four observation dates (07:00 and 19:30) and the four time periods (dates 3 and 4). Between 07:00 and 19:30, individual females ($n = 13$) incubated for 88 to 98% of the time. Mean nest attentiveness was constant during the first three dates, ranging from 93.8 to 94.3%, but declined to 91.0% on 1–3 July ($F = 4.46$, 3, 25 df, $P = 0.012$) (Fig. 1). The approximate mean number of days into incubation for the females under observation at these four dates were two ($n = 7$ females with known hatch date), nine ($n = 8$), 13 ($n = 10$), and 18 ($n = 10$) respectively. Nest attentiveness varied among times of day during the last two observation dates ($F = 4.14$, 3, 84 df, $P = 0.009$) (Fig. 2). Females were less attentive (90.6%) between 12:00 and 18:00 than earlier in the day (94.3–94.7%).

Recess duration was constant seasonally ($F = 1.39$, 3, 109 df, $P = 0.250$) (Fig. 1). Although the test among times of day suggested a temporal difference in recess duration ($F = 2.96$, 3, 137 df, $P = 0.035$), the subsequent multiple comparison did not reveal any among-period differences ($P \geq 0.05$) (Fig. 2). Overall mean recess duration was approximately 15–16 min across both the four dates and four times of day.

Recess frequency increased seasonally ($F = 6.58$, 3, 23 df, $P = 0.002$) (Fig. 1). Although recesses occurred at all times of day, they were more frequent later in the day, particularly between 12:00 and 18:00 ($F = 3.83$, 3, 84 df, $P = 0.013$) (Fig. 2). Based on the most complete records, after 26 June, individual females took two to eight recesses per day, with a mean ($\pm$SE) of 5.3 ($\pm$0.5) on 26–28 June and 6.9 ($\pm$0.3) on 1–3 July.

Mean duration of complete incubation bouts recorded between 07:00 and 19:30 for all dates was just under 3 hr ($\bar{x} = 173.0$ min, SE = 8.1, $n = 68$). Some incubation bouts were, however, in progress at the start and termination of each observation session, preventing determination of their duration; a few were known to exceed the maximum observed duration of 8.8 hr including two >10 and >12 hr respectively on 26 June.

The additional observations of 12 females in 1990 (6–8 July) were unique in two respects: firstly they were conducted later in incubation than those of 1991 (after $\geq$20 days of incubation versus a mean of $\leq$18 days) and secondly, they re-
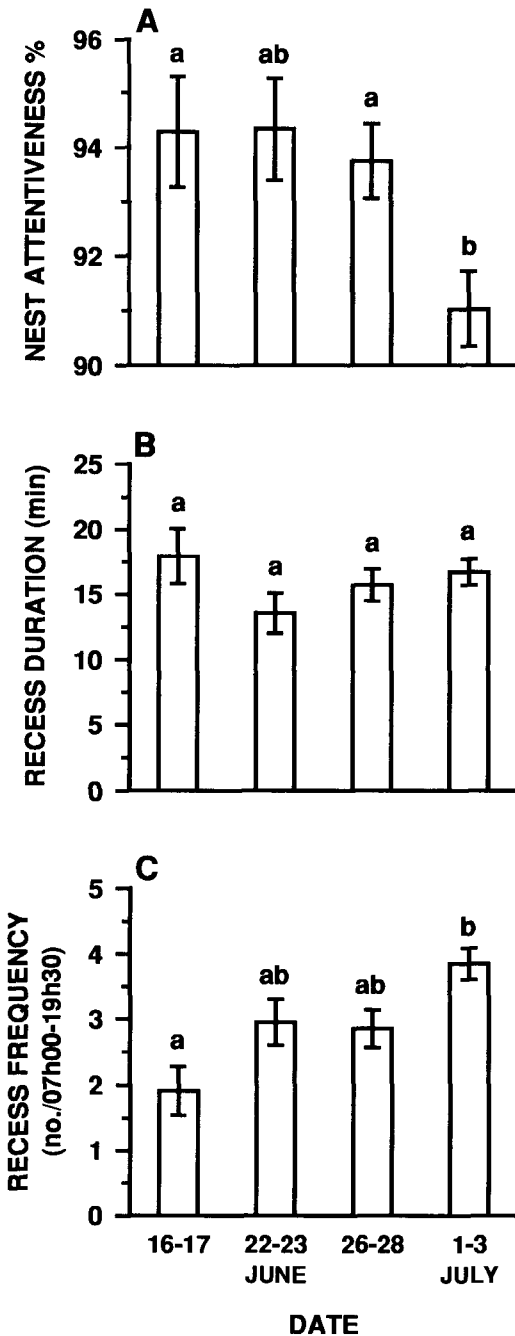
FIGURE 1. Nest attentiveness (A), recess duration (B), and recess frequency (C) of Greater Snow Geese in relation to date, Bylot Island 1991. Vertical bars represent standard errors. Sample sizes (females) are the following: 16–17 June ($n = 7$), 22–23 June ($n = 8$), 26–28 June ($n = 13$), and 1–3 July ($n = 13$). Columns with different letters are significantly different ($P < 0.05$), Tukey's HSD.

vealed a higher mean rate of nest attentiveness (98.8% versus 93.0% in 1991) which was the result of nine females taking no recesses during 24 hr of observation and the three others taking a total of six long recesses ($\bar{x} = 34.3$ min, SE = 9.0).

BEHAVIOR DURING INCUBATION RECESSES

While off the nest, females devoted most of their time to feeding. On 26 June, the mean proportion of time spent feeding by seven females was 88% (range 63–96%). The female which fed the least was not accompanied by her mate. For seven females monitored between 1–3 July, mean feeding time was 81% (range 33–100%). On both dates, most females (5 and 4 respectively) spent >90% of the time feeding. The remainder of the time was mainly devoted to alert behavior.

Most feeding occurred in polygon depressions where females grazed vigorously on emerging shoots of graminoids. Mean ($\pm$SE) pecking rates (pecks/min) were 133 (± 11) on 22–23 June ($n = 6$ females), 131 (± 1) on 26–28 June ($n = 6$), and increased to 153 (± 8) on 1–3 July ($n = 9$) (Kruskall-Wallis, $P = 0.052$). One exceptionally low rate observed on July 3 (60 pecks/min) was excluded. Occasionally females fed on willow catkins, pecking at a lower rate of 64 (± 18) pecks/min ($n = 3$). Casual observations in 1990 showed that some females also fed on the flowers of *Oxytropis maydelliana*, a leguminous plant common in the study area.

During recesses females usually remained close to their nests. More than 90% of all records ($n = 183$) were within 20 m of the nest (range 1–80 m), although casual observations indicated a few cases of distances >100 m. The mean distance from the nest (26 June–3 July, $n = 13$ females) was 13.7 m (SE = 1.4).

BODY MASS OF INCUBATING FEMALES

From 2 to 8 July 1991, 15 incubating females were captured on the nest and weighed, including seven whose incubation behavior had been monitored. Body mass was also available for 30 females caught in 1989–1990. Mean mass did not differ between years ($F = 0.449$, 2, 42 df, $P = 0.641$) and the pooled mean was 2,158 g (SE = 31, $n = 45$). Females whose hatch dates were not known exactly were assumed to be in the latter stage of incubation because all birds were captured within the same period in each year and
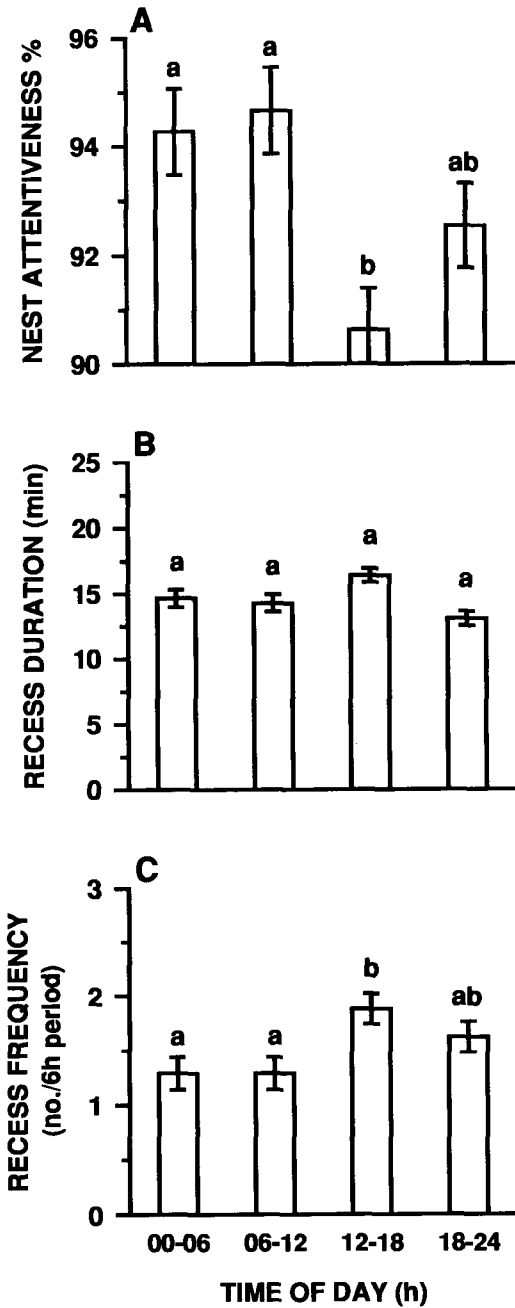
FIGURE 2.   Nest attentiveness (A), recess duration (B), and recess frequency (C) of Greater Snow Geese in relation to time of day, Bylot Island 1991. Vertical bars represent standard errors. Sample sizes (females) are the following: 00:00–06:00 ($n = 12$), 06:00–12:00 ($n = 12$), 12:00–18:00 ($n = 13$), and 18:00–24:00 ($n = 13$). Columns with different letters are significantly different ($P < 0.05$), Tukey's HSD.
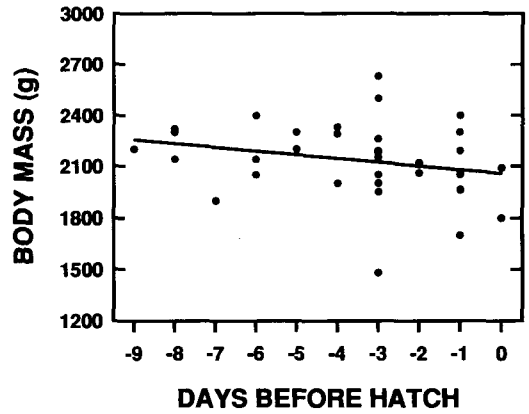

FIGURE 3.   Relationship between body mass and the number of days before hatch, during the last nine days of incubation, for incubating Greater Snow Geese at Bylot Island 1989–1991: Y = 2257-22X, $r^2 = 0.06$, $P = 0.146$, $n = 36$.

hatching at Bylot Island is highly synchronous (G. Gauthier and A. Reed, unpubl. data). Body mass of females with known hatch date was not correlated with the number of days (0–9) remaining before hatch (Fig. 3). Because geese were captured after returning from a forced recess (while the trap was being set), their body masses included the weight of any recently consumed food. We could not directly correct for that possible bias because they were released alive. However, for 12 incubating females collected during late incubation (0–7 days before peak hatch date) in 1992, the mean mass ($\pm$SE) of ingesta in the esophagus and proventriculus was 7.5 g (±2.7), in the gizzard 21.7 (±4.4), and in the intestine 55.1 (±9.1). The total amount of ingesta in the esophagus, proventriculus and gizzard was ≤36 g in 10 females and 52 and 62 g in the two others. The mean body mass of the 12 females was 2,144 g (SE = 51).

DISCUSSION

With no periods of darkness, female Greater Snow Geese on Bylot Island adopted a regular pattern alternating incubation bouts with recesses over the full 24-hr cycle. The average duration of recesses (15–16 min) is shorter than the overall mean (19 min) calculated for five species of geese by Afton and Paulus (1992). Short recesses are advantageous by reducing the probability of egg loss to predators (Inglis 1977, Thompson and Raveling 1987, Spaans et al. 1993) and by re-

ducing heat loss from the eggs (Afton and Paulus 1992). The lack of variability in recess duration of Greater Snow Geese over the season (except for the last 1–4 days of incubation—see below) or throughout the 24 hr cycle suggests that ambient temperatures had little influence on recess length. The number of recesses per day did, however, increase seasonally (Fig. 1), and because recess duration remained stable, total recess time per day increased through all but the last few days of incubation. An increase in total recess time (or decrease in nest attentiveness) as incubation progressed was observed for Canada Geese (Aldrich and Raveling 1983) and for Brant (Spaans et al. 1993), but not for Emperor Geese (Thompson and Raveling 1987); for Canada Geese, the increasing time off nest was attributed to deteriorating body condition and the need to increase time spent feeding, whereas Emperor Geese were thought to be maintaining adequate body condition to be able to remain highly attentive.

During the last 1–4 days of incubation nest attentiveness increased substantially, although the infrequent recesses were longer. Increased attentiveness in the last few days of incubation has been reported for Emperor Geese (Thompson and Raveling 1987) and for Giant Canada Geese (Cooper 1978), and is probably the result of increasing communication between the embryos and the female. The females that take recesses during this period may be those in poorest condition and therefore in greatest need of food. Regardless of their condition, once off the nest they may remain away longer because eggs advanced in incubation cool less quickly (Afton and Paulus 1992).

Females on recess, by remaining close to the nest and devoting most of their time to feeding with a rapid peck rate, were probably minimizing energy expenditure and maximizing food intake. Toward the end of most recesses the females had swollen necks, indicating that the esophagus was full. Appreciable quantities of food (≥ 80 g, on average) were found in the digestive tract of breeding females collected during incubation at the same study site in 1989–1990 (Gauthier 1993) and in 1992 (this study). Most of the food consumed by females during incubation was newly sprouting graminoid foliage and willow catkins which have a high nutritive value (Gauthier 1993). Thus, females completely filled their

esophagi 5–7 times a day and by retaining that high quality food in the digestive system for extended periods (usually ≥ 3 hr) were enhancing nutrient assimilation (Owen 1980, Prop and Vulink 1992). In Barnacle Geese (*Branta leucopsis*) feeding on graminoids, prolonging food retention beyond the approximately 2 hr normal retention time to 3–4 hr, substantially increased organic matter digestibility (Prop and Vulink 1992).

On average, females devoted 93% of their time to incubating eggs. In addition to ensuring proper embryonic development, such constancy undoubtedly served to protect the eggs from predators (Thompson and Raveling 1987). On several occasions, the regular pattern of nest attentiveness appeared to have been adjusted in response to predatory activity. Females on recess almost invariably returned immediately to the nest when Parasitic Jaegers, Common Ravens or Arctic Foxes approached. All female geese remained on the nest while foxes were in the colony and none took recesses for at least 1 hr after departure of the foxes. Although body mass of the seven females whose behavior had been monitored was not correlated with their rate of nest attentiveness, nor with the duration of their recesses, the lightest of them (1,800 g) had the largest clutch (7 eggs), the longest average recess duration (21 min), and the lowest percentage of time spent on the nest (88%). This suggests that she began incubation with a low level of body reserves and was adjusting her schedule to increase the intake of nutrients. Despite the relatively low levels of her nutrient reserves and her reduced attentiveness to the nest, she was successful in hatching her eggs. The two lightest geese weighed in 1989 (1,480 and 1,700 g) also hatched their eggs and the lightest of them was known to have survived at least four months as she was observed staging 3,000 km to the south in October. From a sample of several hundred nests over six full seasons of observation in this colony, no deaths of incubating females from exhaustion or starvation have been recorded (G. Gauthier and A. Reed, unpubl. data) which contrasts with the situation reported for Lesser Snow Geese in western Hudson Bay (Harvey 1971, Ankney and MacInnes 1978).

The females we weighed in late incubation, because they were captured after a forced recess, may have contained a larger-than-average quantity of recently ingested food. That bias in mass

is probably not greater than the maximum values of ingesta found in the anterior portion of the digestive tract of females collected while incubating (i.e., 52 and 62 g in two of 12 females). The mean body mass of 2,158 g (SE = 31, n = 45, 1989-91) in late incubation, even after accounting for about 50–60 g of newly ingested food, indicates that nutrient reserves had not been entirely depleted; from laboratory studies (Boismenu et al. 1992), it is known that a fasting Greater Snow Goose weighing 2,100 g has sufficient reserves to survive >12 days on average.

The mean body mass of females during early incubation (day 3) in the same population in 1989–1990 was 2,480 g (SE = 55, n = 11) (Choinière and Gauthier, in press). Assuming that body mass is lost at a more rapid rate during the first few days of incubation than later on, we estimate a total mass loss over the full incubation period of 430 g or 17% (Table 1). Mass loss must occur mainly in early incubation because we detected no relationship between body mass and the number of days pre-hatch during the last nine days of incubation (though there was a slightly negative slope). The approximate period of 9–4 days before hatch appears to be characterized by lower nest attentiveness and an increased frequency of recesses which may allow geese to maintain their body condition, perhaps in preparation for the very last days of incubation when nest attentiveness approaches 100%.

Our results indicate a pattern rather different from that described for closely related Lesser Snow Geese in Hudson Bay. Female Lesser Snow Geese fed only 65% of their time away from the nest and fed with pecking rates <100 pecks/min (Harwood 1977). They left the nest infrequently during incubation and lost, on average, >30% of their body mass with many females starving at the nest during late incubation (Ankney and MacInnes 1978). Almost all of the reserves used to sustain females through incubation came from stores remaining after relatively short migrations from spring staging areas in southern Manitoba and the James Bay/Hudson Bay lowlands (Ankney and MacInnes 1978, Alisauskas and Ankney 1992). Thus, despite their smaller size, Lesser Snow Geese initiated incubation with similar body mass to Greater Snow Geese, but by relying almost entirely on stored reserves they lost mass more rapidly and terminated incubation in poorer condition (Table 1).

TABLE 1. Nest attentiveness, feeding activity, and loss of body mass of Greater Snow Geese and other northern geese during incubation.

Species/subspecies	Mass (g) at start of incubation	% Time incubating	Minutes feeding/day	% Mass loss
Western Canada Goose	4,300	97.5	14	27
Greater Snow Goose[1]	2,590[2]	93.0	83[3]	17
Lesser Snow Goose[4]	2,530	97.1	n.a.	32
Emperor Goose	2,230	99.5	1	21
Cackling Canada Goose	1,387	93.6	71	21
Black Brant	1,140	89.6	95	11

Data from Thompson and Raveling (1987), except for [1] Greater Snow Goose (this study), and [4] Lesser Snow Goose (Ankney and MacInnes 1978).

[2] Adjusted to day one of incubation from value of 2,480 g on day three, published by Choinière and Gauthier (in press), assuming a daily rate of body mass loss during the first three days twice that occurring over the rest of the incubation period.

[3] Average of 26–28 June (73 min) and 1–3 July (93 min).

Nest attentiveness, feeding intensity, and body mass loss of Greater Snow Geese is compared with that of other northern nesting geese in Table 1. Thompson and Raveling (1987), in comparing Western Canada Geese, Emperor Geese, Cackling Canada Geese (*Branta canadensis minima*) and Brant, suggested that the larger species devoted more time to incubation, less to feeding, and lost proportionately more body mass than the smaller species. Using the Emperor Goose as an example, they argued that the medium and large sized species, by remaining on the nest almost continuously, were ensuring maximal protection of the nest against both mammalian and avian predators. This is possible because larger species have more reserves and expend less energy per unit of mass. As a corollary of this, larger species generally take <3 recesses per day (large races of Canada Geese [Cooper 1978, Aldrich and Raveling 1983], Emperor Geese [Thompson and Raveling 1987], White-fronted Geese *Anser albifrons* [Stroud 1982], Pink-footed Geese *A. brachyrhynchus* [Inglis 1977]) whereas the diminutive Brant takes 6–14 recesses per day (Thompson, cited in Thompson and Raveling 1987, Madsen et al. 1989, Spaans et al. 1993).

The geese we studied did not fit the pattern between body size and nest attentiveness suggested by Thompson and Raveling (1987). Despite their large body size, Greater Snow Geese took frequent recesses, devoted considerable time to feeding, and lost a relatively small proportion of their body mass, resembling in those respects

much smaller species such as Brant and Cackling Canada Geese. Greater Snow Geese must use a large proportion of the nutrient reserves accumulated on the spring staging area in southern Quebec during the 2,500–3,000 km flight to the high Arctic (Gauthier et al. 1992), and must rely on food obtained on the breeding grounds to meet nutrient demands during pre-laying and laying (Gauthier and Tardif 1991, Gauthier 1993). With smaller imported nutrient reserves to draw on during incubation, relative to other large geese, they must continue feeding regularly through incubation. This requirement is apparently met by alternating short recesses, the duration of which probably represents the time required to fill the esophagus, with incubation bouts long enough to maximize assimilation of nutrients. In the high Arctic this pattern is unhampered by periods of darkness. By feeding close to their nests during recesses, they are capable of defending their nests against predators, and by feeding intensively maintain a level of body condition which ensures their own survival through incubation. By starting the brood-rearing period in good condition, they may also enhance survival of their goslings in the days following hatch.

ACKNOWLEDGMENTS

LITERATURE CITED

AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care, p. 62–108. *In* B.D.J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], Ecology and management of breeding waterfowl. Univ. of Minnesota Press, Minneapolis.

ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behavior of Canada Geese. Auk 100:670–679.

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. Spring habitat use and diets of midcontinent adult Lesser Snow Geese. J. Wildl. Manage. 56:43–54.

ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

BOISMENU, C., G. GAUTHIER, AND J. LAROCHELLE. 1992. Physiology of prolonged fasting in greater snow geese *Chen caerulescens atlantica*. Auk 109:511–521.

CHOINIÈRE, L., AND G. GAUTHIER. In press. Energetics of reproduction in female and male Greater Snow Geese. Oecologia.

COOPER, J. A. 1978. The history and breeding biology of the Canada Goose of Marshy Point, Manitoba. Wildl. Monogr. 61.

GAUTHIER, G. 1993. Feeding ecology of nesting Greater Snow Geese. J. Wildl. Manage. 57:216–223.

GAUTHIER, G., J.-F. GIROUX, AND J. BÉDARD. 1992. Dynamics of fat and protein reserves during winter and spring migration in Greater Snow Geese. Can. J. Zool. 70:2077–2087.

GAUTHIER, G., R. J. HUGHES, A. REED, J. BEAULIEU, AND L. ROCHEFORT. 1995. Effect of grazing by Greater Snow Geese on the production of graminoids at an arctic site. J. Ecol. 83:653–664.

GAUTHIER, G., AND J. TARDIF. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. Condor 93:701–711.

HARWOOD, J. 1977. Summer feeding ecology of Lesser Snow Geese. J. Wildl. Manage. 41:48–55.

HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. Can. J. Zool. 49:223–234.

HUGHES, R. J., A. REED, AND G. GAUTHIER. 1994a. Space and habitat use by Greater Snow Goose broods on Bylot Island, Northwest Territories. J. Wildl. Manage. 58:536–545.

HUGHES, R. J., G. GAUTHIER, AND A. REED. 1994b. Summer habitat use and behaviour of Greater Snow Geese *Anser caerulescens*. Wildfowl 45:49–64.

INGLIS, I. R. 1977. The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. Behav.25:747–764.

MADSEN, J., T. BREGNBALLE, AND F. MEHLUM. 1989. Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. Polar Research 7:1–21.

MANSEAU, M., AND G. GAUTHIER. 1993. Interactions between Greater Snow Geese and their rearing habitat. Ecology 74:2045–2055.

MURPHY, A. J., AND D. A. BOAG. 1989. Body reserve and food use by incubating Canada geese. Auk 106:439–446.

OWEN, M. 1980. Wild geese of the world. Batsford Ltd., London.

PROP, J., AND T. VULINK. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6:180–189.

REED, A., AND P. CHAGNON. 1987. Greater snow geese on Bylot Island, Northwest Territories, 1983. J. Wildl. Manage. 51:128–131.

REED, A., H. BOYD, P. CHAGNON, AND J. HAWKINGS.

1992. The numbers and distribution of Greater Snow Geese on Bylot Island and near Jungersen Bay, Baffin Island, in 1988 and 1983. Arctic 45: 115–119.

SPAANS, B., M. STOCK, A. ST. JOSEPH, H. H. BERGMANN, AND B. S. EBBINGE. 1993. Breeding biology of Dark-bellied Brent Geese in Taimyr in 1990 in the absence of arctic foxes and under favourable weather conditions. Polar Research 12: 117–130.

STROUD, D. A. 1982. Observations on the incubation and post-hatching behaviour of the Greenland White-fronted Goose. Wildfowl 33:63–72.

THOMAS, V. D. 1983. Spring migration: the prelude to goose reproduction and a review of its implications, p. 73–81. In H. Boyd [ed.], First Western Hemisphere Waterfowl and Waterbirds Symposium. IWRB and Canadian Wildlife Service, Ottawa.

THOMPSON, S. C., AND D. G. RAVELING. 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. Auk 104:707–716.