

FEMALE FEEDING AND MALE VIGILANCE DURING NESTING IN GREATER SNOW GEESE¹

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Abstract. We studied the duration of the pre-laying period, female feeding activity, male vigilance, and the potential for parent-offspring conflicts in high-Arctic nesting Greater Snow Geese (*Chen caerulescens atlantica*). The pre-laying period is unusually long for a goose species nesting at high latitudes (73° N). Geese arrived at Bylot Island around 27 May but the peak initiation of egg-laying was around 12–14 June. During pre-laying, paired females fed for 75% and were alert for 6% of the 24-hr day, whereas males fed for 44% and were alert for 33% of the day. In one year that laying geese were observed, females fed less than during pre-laying and time spent at the nest increased. Time budget was not related to time of day or number of days before egg-laying. Although male vigilance apparently enabled females to devote more time to feeding, male alert behavior was poorly synchronized with female feeding. Pair copulations were recorded frequently (0.23/hr) and 2 extra-pair copulations were observed. Males were involved more often than females in aggressive interactions (2.55 vs. 0.36 aggressions bird⁻¹ hr⁻¹) and often attacked neighboring pairs. The proportion of pairs with yearlings was low (6.3%) and parents frequently attacked their young (1.53 bird⁻¹ hr⁻¹). However, presence of yearlings did not influence time budget of pairs. The long pre-laying delay and the intense feeding activity of females suggest that, in addition to energy reserves accumulated during the spring migration, food intake on the nesting ground may also be an important source of energy for laying Greater Snow Geese.

Key words: Greater Snow Goose; *Chen caerulescens atlantica*; time budget; nesting behavior; social interaction.

INTRODUCTION

Seasonal monogamy is the dominant mating system in birds (Oring 1982). In altricial species, monogamy has been imposed largely by the need for two parents to care for the offspring (Wittenberger and Tilson 1980). In precocial birds, monogamy also prevails even though parents are freed from the need to feed their young. In these species, monogamy is apparently imposed by the need for male vigilance to defend the nesting female from harassment by conspecific males, thereby ensuring undisturbed feeding for her during laying, a period of high energy demand (Mineau and Cooke 1979; Patterson 1982; McKinney et al. 1983; Martin et al. 1985; Gauthier 1987, 1988).

Arctic-nesting geese are unique among precocial birds because (1) they maintain long-term pair bonds that often last the lifetime of individuals (Cooke et al. 1981, Owen et al. 1988) and (2) they seem to feed very little during the laying period (Newton 1977, Ankney and MacInnes 1978). Long-term pair bonds in geese are

associated with prolonged parental care for the offspring, usually up to one year (Prevett and MacInnes 1980, Black and Owen 1989). In Lesser Snow Geese (*Chen caerulescens caerulescens*), family break-ups occur mostly upon arrival on the breeding grounds and adults chase yearlings away (Prevett and MacInnes 1980). Family break-ups thus occur when the pair's next breeding effort is well under way, which may lead to parent-offspring conflicts (sensu Trivers 1972, Lazarus and Inglis 1986, Turcotte and Bédard 1989).

The absence of feeding opportunities during laying requires that Arctic-nesting geese use energy reserves accumulated during spring migration to sustain their breeding effort (Ryder 1970, Newton 1977, Ankney and MacInnes 1978, Ebbinge et al. 1982, Thomas 1983). In Lesser Snow Geese and Ross Geese (*Chen rossii*), birds initiate nesting within a few days of arrival on the breeding ground at a time when plant growth has not yet started (Raveling 1978). This early nesting is imposed by the short summers of the central Canadian Arctic.

The Greater Snow Goose (*Chen caerulescens atlantica*) is the northernmost breeding species of geese in North America, nesting throughout the eastern Canadian Arctic Archipelago and

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Northwest Greenland (Bellrose 1980). Previous observations suggested that this species had an unusually long delay between arrival on the nesting ground and nest initiation (Lemieux 1959, Gauthier, unpubl. obs.). This was surprising because nesting Greater Snow Geese, like Lesser Snow Geese and Ross Geese, are constrained by short Arctic summers. A long pre-laying delay should force geese to feed in order to maintain energy reserves accumulated in spring (Gauthier et al. 1984).

In this study, our main objectives were (1) to establish the duration of the pre-laying period in Greater Snow Geese, (2) to evaluate whether pre-laying and laying females rely on feeding to supplement their energy budget, and (3) to determine whether vigilance is mostly assumed by males and to what extent females benefit from it. This was achieved by documenting the nesting phenology and conducting detailed observations on time budget of individual birds. A secondary objective was to examine whether the presence of yearlings interfered with the current breeding effort of nesting pairs.

METHODS

STUDY POPULATION AND STUDY AREA

Greater Snow Geese winter along the mid-Atlantic coast of the United States and stage along the St. Lawrence River of southern Québec in spring and fall (Gauthier et al. 1988). They breed in discrete colonies scattered in the Canadian high-Arctic from central Baffin Island (67° N) to north Ellesmere Island (82° N). The largest single breeding colony is located on the south plain of Bylot Island and where 13,400 nesting pairs were censused in 1988 (16% of the total population; Reed and Chagnon 1987, Reed et al., in prep.). The spring migration is fairly synchronous and most of the population leaves the St. Lawrence River directly for the Arctic nesting grounds within 2–3 days around 20 May.

Our study area was located in a glacial valley on southwest Bylot Island (73° N, 80° W). The valley is about 12 km long with an opening to the sea. In 1990, a minimum of 1,200 pairs nested in the valley based on visual counts made from high-ground during incubation. The study area is characterized by polygon tundra (Tarnocai and Zoltai 1988). Sunken polygons form numerous small, shallow ponds of irregular shape that dominate lowlands. Shallower ponds develop into wet sedge meadows where *Carex*

aquatilis var. *stans*, *Dupontia fisheri*, *Eriophorum scheuchzeri* and *E. angustifolium* dominate. Polygon rims are raised by 0.5 m or less and, being drier, are preferred by geese as nesting sites. When geese arrive in late May, they concentrate in the few snow-free areas on hill slopes bordering the valley. However, geese rapidly start to use the lowlands as snowmelt progresses quickly, aided by 24-hr sunlight. Behavioral observations were conducted both on the slopes and in the lowlands.

BREEDING PHENOLOGY

In 1988, we were present on the island from 5–14 June whereas in 1989 and 1990 we were present from 25 May until mid-August. Arrival dates of geese at the colony are known only for the two latter years. Arriving geese were identified by their large group size (from 10 to several hundred birds), the typical flight formation of migrating geese and their high altitude.

In all years, nest searches were conducted during the laying period. Dates of egg-laying (defined as the day when the first egg was laid) were estimated as follows: assuming that the most recent egg was laid on the day that the nest was found, we subtracted one day for each additional egg in the nest. Laying interval is unknown in Greater Snow Geese but it is of 1.2 day in Lesser Snow Geese (Findlay and Cooke 1982) and 1.5 day in Ross Geese (Ryder 1967). Thus, for nests found later than at the 3-egg stage, an additional day was subtracted to account for a "skip" in the laying sequence. Pre-laying was defined as the period between the arrival of geese and the peak of egg-laying for the population. Laying was defined as the period between the peak of egg-laying and the start of incubation.

BEHAVIORAL OBSERVATIONS

Behavioral observations were conducted throughout the 24-hr daylight cycle, usually in 4-hr blocks, using focal animal sampling (Altmann 1974). Geese did not use specific roosting site at "night" and could be kept under observation at all time. Geese were observed using 15–60× spotting scopes from portable blinds set on high vantage points located in different parts of the study area. Individual pairs were randomly selected by scanning the study area and choosing the first pair encountered. The area scanned could range from a few hundred meters to more than 1 km depending on the light conditions and the vantage point chosen.

Both pair members were followed simultaneously by two different observers (except in 1988 when they were observed consecutively) during 15-min observation periods. Two types of samplings were conducted. First, instantaneous behavior was noted every 10 sec at the sound of an electronic metronome (interval sampling). Behavioral categories were as follows: feeding (head below horizontal, either grazing, grubbing or searching for food), alert (head up, standing still on land or in water), walking (head up, moving on land), resting (head tucked in feathers, either standing or sitting), preening (all comfort movements), swimming, flying, nest attendance (either building the nest or sitting on it) and social interactions. Second, all copulations and aggressive interactions observed during each 15-min session were recorded and analyzed separately.

Sexes were identified before the start of observations by visually comparing abdomen profile or pair members when both were in alert. We assumed that the one with the more rounded abdomen was the female because of (1) presence of the developing follicles and, (2) larger abdominal fat depots in pre-laying and laying females than in males (Choinière and Gauthier, unpubl. data). Sexing in this manner proved 100% accurate when tested against birds wearing individually marked neck-collars (marking done by Maisonneuve 1988; $n = 3$) and with behavior of both pair members during copulations ($n = 9$) and triumph ceremony ($n = 5$) (Raveling 1970). Females could be identified as early as 10 days prior to egg-laying.

Presence of yearlings (<1 year old; recognized by their gray plumage) with pairs selected for observations was noted. Families were identified by cohesion shown during movements following Turcotte and Bédard (1989). In 1988, observations were made during the laying period and we were able to conduct daily counts of the number of pairs and the proportion of those with yearlings over a fixed portion of the study area. This technique could not be applied in 1989 and 1990 because, compared to 1988, geese were distributed differently during pre-laying.

STATISTICAL ANALYSES

Individual birds (or pairs) were used as the sampling unit in all statistical analyses. Because of the large number of pairs nesting in the valley, of frequent movements by geese during pre-laying, and our use of several observation sites, we believe that the probability of choosing the same

pair more than once was small. We used the Wilcoxon (for comparisons between paired males and females), Mann-Whitney (MW) *U*-test and Kruskal-Wallis (KW) analysis of variance to test for differences in behavior because several behaviors showed a U-shaped frequency distribution (Gauthier et al. 1988). To analyze the effect of time of day, we pooled data in 12 2-hr blocks from 0:00 hr to 24:00 hr.

RESULTS

NESTING PHENOLOGY AND DISTRIBUTION OF GEESE

In 1988, snow melted very early and geese arrived and settled on their nesting territory prior to arrival on 5 June. At that time, snow cover over the nesting area was estimated at less than 20%. Snow melted later in both 1989 and 1990 than in 1988 with about 85% of the nesting area still snow-covered on 5 June. A small number of geese (up to 200) were already present upon our arrival (25 May). We observed the major arrival of goose flocks (several hundreds) on 27 May in both years (Table 1).

Shortly after their arrival, goose flocks tended to break into individual pairs. During the pre-laying period, goose pairs clustered around snow-free patches or around thawing ponds. During egg-laying, geese dispersed on nesting territories where they were more evenly spaced (inter-nest distance in dense areas ranged from 30–200 m).

Nesting phenology was similar in the three years of the study although start of egg-laying was slightly earlier in 1988 (Table 1), the year of early snow-melt. Nesting was highly synchronous as 65% to 73% of the nests were initiated within a four-day period in all years. In 1988, we observed laying geese from 7–12 June, just after the peak of egg-laying (Table 1). In contrast, we observed mostly pre-laying geese in 1989 and 1990 because observations were only conducted from 1–12 June and 6–12 June, respectively, which was before the peak in egg-laying. However, the exact nesting stage of individual pairs was unknown.

TIME BUDGET

A total of 79 hours of behavioral observation evenly split between sexes was obtained on 158 different pairs. Time budget data did not differ between 1989 and 1990 in both sexes for any behavior (MW, $P > 0.05$; $n = 84$ and 48 respectively) except swimming which was significantly higher in 1990 ($P < 0.01$). However, because swimming was a minor behavior (less than

TABLE 1. Nesting phenology of Greater Snow Geese on Bylot Island during 1988–1990 (n = number of nests found).

	1988	1989	1990
Peak of arrival by geese	—	27 May (1–2 June) ^a	27 May
First egg laid	5 June	7 June	6 June
Peak ^b of egg-laying	8 June ($n = 24$)	11 June ($n = 52$)	14 June ($n = 164$)

^a A smaller number of arriving flocks of geese were observed on those dates.

^b Mode of the egg-laying frequency distribution.

1% in both years and sexes), we pooled data for both years. Data from 1988 were not pooled because, unlike 1989 and 1990, they were collected only on laying geese. When comparing data from 1988 with those of 1989–1990, it is tempting to explain any difference by an effect of nesting stage (laying vs. pre-laying). However, this interpretation must be made with caution because we cannot control for a year effect in the comparison.

Male and female time budgets were very different. Pre-laying females spent more than 75% of the day feeding compared to less than 44% in males, a highly significant difference (Table 2). Conversely, pre-laying females spent about 6% of their time in alert compared to more than 32% in males, also a highly significant difference (Ta-

ble 2). In both sexes, only 8% of the day was spent resting and 6% walking. All other behaviors combined accounted for less than 7% of the total time budget. Time budgets were very similar in 1989–1990 (pre-laying) compared to 1988 (laying). Both sexes devoted slightly more time to other behaviors in 1989–1990 compared to 1988 (Table 2). The time spent by females attending the nest in 1988 (13%) was taken at the expense of feeding which decreased by 11% compared to females in 1989–1990, a significant difference (Table 2).

Time budget of both sexes showed very little variation according to time of day during pre-laying (Fig. 1). Among the four dominant behaviors (feeding, alert, resting and walking), only walking varied significantly according to time of

TABLE 2. Daily time budget (%) of male and female Greater Snow Geese at Bylot Island in 1989 and 1990 (pre-laying period; $n = 132$ for each sex) and 1988 (laying period; $n = 26$ for each sex). Mean (SE). Statistical tests are Mann-Whitney (1989–1990 vs. 1988) and Wilcoxon (male vs. female).

Behaviors	Year	Male		Female
Feeding	1989–1990	43.9 (2.6)	***	75.5 (2.7)
	1988	NS		*
Alert	1989–1990	39.9 (5.1)	**	64.5 (6.2)
	1988	32.6 (2.2)	***	6.3 (0.7)
Walking	1989–1990	NS		NS
	1988	32.1 (4.6)	***	6.3 (1.3)
Resting	1989–1990	9.0 (0.8)	***	5.3 (0.6)
	1988	5.9 (1.6)	NS	6.3 (1.5)
Nest attendance	1989–1990	7.7 (2.2)	NS	8.2 (2.1)
	1988	NS		NS
Others	1989–1990	10.3 (4.8)	NS	4.6 (3.1)
	1988	0.0	—	0.0
Others	1989–1990	—	—	—
	1988	0.0	—	12.9 (6.2)
Others	1989–1990	6.7 (0.9)	***	4.8 (1.2)
	1988	*		**
		11.8 (3.1)	NS	5.4 (1.1)

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

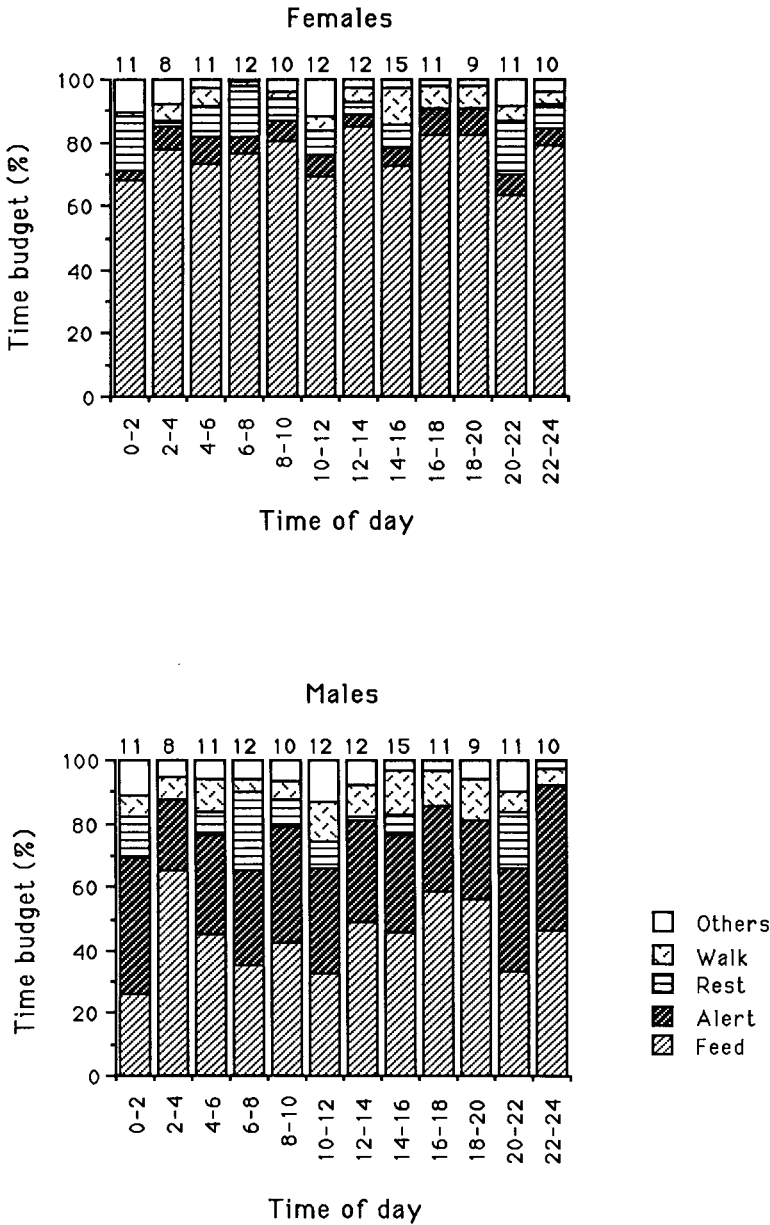


FIGURE 1. Activity budget of pre-laying Greater Snow Geese at Bylot Island according to the time of day. Data are grouped in 2-hr blocks. Sample sizes are shown above bars.

day (KW; $H = 20.1$, $P = 0.04$, and $H = 21.3$, $P = 0.03$ in males and females, respectively). Both sexes walked more often during the afternoon. In males, feeding also tended to be higher in early morning and late afternoon, (KW, $H = 16.0$, P

$= 0.13$; Fig. 1). Sample sizes were too small to perform a similar analysis in laying birds.

To examine the effect of date on time budget of pre-laying geese, we standardized for the start in laying by subtracting, for each pair observed,

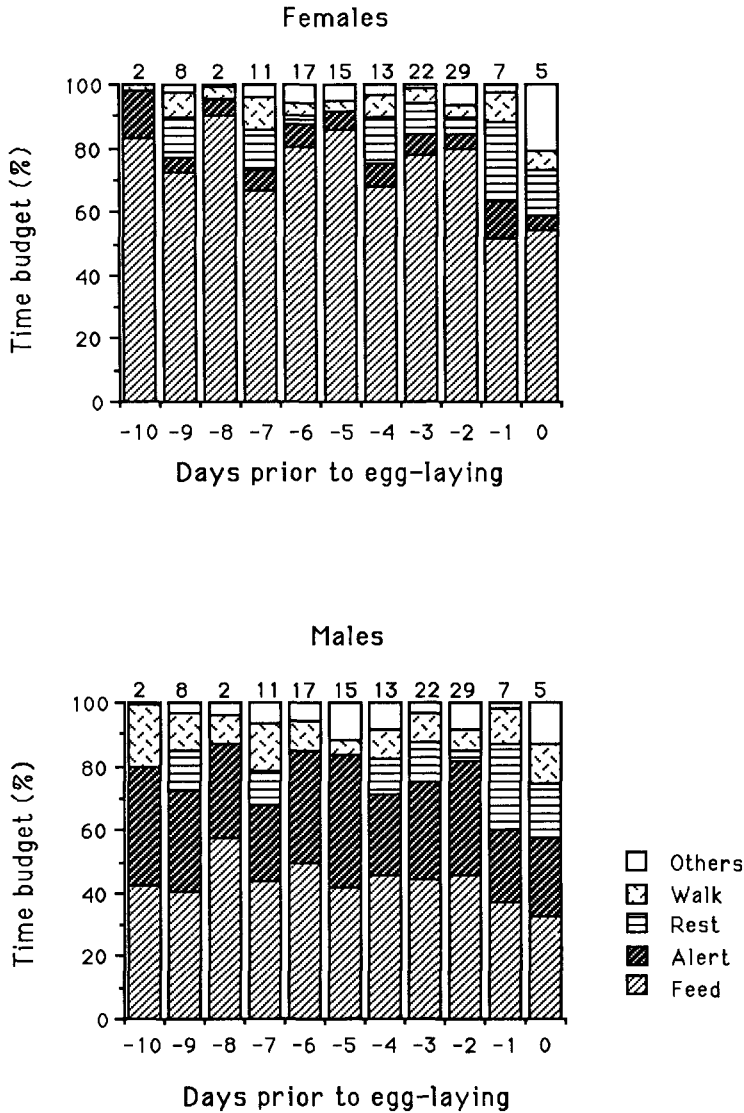


FIGURE 2. Activity budget of pre-laying Greater Snow Geese at Bylot Island according to the stage of the nesting cycle (day 0 = peak of egg-laying for the population). Sample sizes are shown above bars.

the date of observation from the date of peak egg-laying (day 0 in Fig. 2). In both sexes, none of the dominant behaviors varied significantly over a 10-day period before egg-laying (KW, all comparisons $P > 0.05$; Fig. 2).

We compared time budget of pairs with yearlings to those without yearlings. We did not find any differences in both sexes (MW, $P > 0.05$ for all comparisons; $n = 11$ and 121 respectively).

We correlated the behavior of pre-laying male and female snow geese that were observed si-

multaneously to determine if, within pairs, males were more alert when females were actively feeding. Female feeding was more correlated with male alert behavior than with male feeding, but correlations, though significant, were weak (Table 3). Alert behavior of male increased with female feeding but variability in male alertness also increased enormously (Fig. 3). At high level of female feeding, a high proportion of males devoted their time to other behaviors than alert. Male resting was also associated with female

feeding through an inverse relationship (Table 3). Resting and walking were the two behaviors most highly correlated between sexes (Table 3).

SOCIAL INTERACTIONS BETWEEN ADULTS

Frequency of aggressive interactions within pairs was very low (0.15 ± 0.10 [SE] aggression pair⁻¹ hr⁻¹). Intensity of aggression was also low and consisted only of displacements. Aggressive interactions between pairs were much more frequent and more intense, often involving overt attacks, chases or fights. Males were involved significantly more often in aggressive interactions with other pairs than were females (2.55 ± 0.60 vs. 0.36 ± 0.17 aggressions bird⁻¹ hr⁻¹; Wilcoxon, $Z = 4.18$, $P < 0.001$, $n = 132$ for each sex) during pre-laying. Frequency of aggressive interactions in 1988 (laying period; 1.38 ± 0.96 aggressions bird⁻¹ hr⁻¹ in males and 0.44 ± 0.33 in females) did not differ significantly from 1989–1990 (pre-laying period; MW, $P > 0.05$ in both sexes) even though pairs tended to be more dispersed at that time (see above).

Seven pair copulations and one extra-pair copulation were observed in 1989–1990, and three pair copulations were observed in 1988. Frequency of pair copulations in 1989–1990 (pre-laying; 0.21 ± 0.08 copulations bird⁻¹ hr⁻¹) did not differ significantly from 1988 (laying; 0.23 ± 0.13 copulations bird⁻¹ hr⁻¹, MW, $Z = 0.79$, $P = 0.43$). Copulations were observed at all times of day with no morning or evening peaks. The extra-pair copulation occurred after a female followed her mate in an aggressive charge toward a neighboring pair. In the ensuing commotion, the attacked male took the opportunity to grab and mount the female of the attacking male. Another extra-pair copulation was witnessed during pre-laying when a paired male attempted to

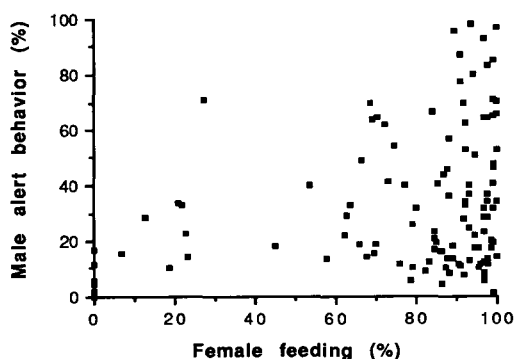


FIGURE 3. Relationship between the percentage of time spent in alert by males and the percentage of time spent feeding by females within the same pair in pre-laying Greater Snow Geese at Bylot Island during simultaneous 15-min observation periods.

mount a recently shot bird used to attract other geese.

SOCIAL INTERACTIONS WITH YEARLINGS

The proportion of pairs with yearlings was low during the pre-laying and laying periods (Table 4). This was not due to general breeding failures in any of the three years of the study because proportion of pairs with juveniles in the previous fall was high in all years (Table 4). A comparison of our data with those collected by Tardif (1990) on the same population in the St. Lawrence estuary showed that the proportion of pairs with yearlings dropped markedly between the spring staging halt (April and May) and the breeding staging ground (early June) in 1988. However, mean brood size on the breeding ground (1.62 ± 0.18 , $n = 13$) did not differ from mean brood size in the St. Lawrence estuary (1.95 ± 0.16 , $n = 40$; MW, $Z = 0.85$, $P = 0.39$; data from Tardif 1990).

TABLE 3. Spearman rank correlation of the percentage of time devoted to four behaviors by males and females within the same pairs in pre-laying Greater Snow Geese during 15-min simultaneous observation periods ($n = 120$).

	Male			
	Feeding	Alert	Resting	Walking
Female				
Feeding	0.255**	0.342***	-0.440***	-0.182
Alert	-0.102	-0.019	0.074	0.158
Resting	-0.378***	-0.365***	0.785***	-0.308***
Walking	0.087	-0.007	-0.242*	0.747***

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

TABLE 4. Proportion of Greater Snow Geese pairs with yearlings on the spring staging ground and on the breeding ground during the pre-laying (1989 and 1990) and laying (1988) periods, and proportion of pairs with juveniles during the previous fall.

Year	Previous fall ^a	Spring staging ^b	Breeding ground
1988	66.4%	22.8% (n = 215)	4.8% (n = 70)
1989	60.4%	—	6.4% (n = 140)
1990	65.4%	—	8.3% (n = 48)

^a Estimated by Austin Reed from counts of brood size and percentage of juveniles along the St. Lawrence river in fall.

^b Data from Tardif (1990).

The frequency of aggressive interactions by adults toward their yearlings was fairly high (1.31 ± 0.98 and 1.75 ± 1.38 aggressions bird⁻¹ hr⁻¹ in males and females, respectively; frequency calculated only for pairs with yearlings). Yearlings were often attacked when they approached within a few meters from their parents.

DISCUSSION

TIME BUDGET OF MALES AND FEMALES

The time devoted to feeding by pre-laying female Greater Snow Geese (75.5% or more than 18 hr/day) was extremely high. Few, if any, other goose or waterfowl species show such intense daily feeding activity except Greenland White-fronted Geese (*Anser albifrons flavirostris*), also a High Arctic-nesting species which feeds 68% of the day during pre-laying (Fox and Madsen 1981). During spring staging, Greater Snow Geese feed about 50% of the day (both sexes combined; Gauthier et al. 1988). This suggests that maximizing energy intake is of paramount importance to pre-laying females. The considerable amount of time spent feeding may partly compensate for low food availability and quality when new growth has not yet started.

Two other unusual features of the Greater Snow Goose's time budget are the low level of resting (8% or less than 2 hr/day) and the absence of an influence of time of day on their activity. During spring migration, Greater Snow Geese spend up to 40% of the day resting and this behavior shows a pronounced circadian rhythm: resting occur mostly at night whereas feeding activity peak in early morning and late afternoon (Gauthier et al. 1988). Presence of the sun during the whole 24-hr cycle at Bylot Island apparently suppressed

their circadian activity rhythm completely and reduced resting activity to a very low level. Brood-rearing Greater Snow Geese also had no circadian rhythm under similar light conditions although resting was more frequent (15%; Giroux et al. 1986). This contrasted with pre-laying Greenland White-fronted Geese which roosted between 1:00 hr and 5:00 hr under 24-hr sunlight conditions (Fox and Madsen 1981). These authors suggested that it was a consequence of colder temperature between 1:00 hr and 5:00 hr. Although this is also true on Bylot Island, it did not affect geese activity. An activity rhythm based on other periodicity than 24-hr may have operated.

Male Greater Snow Geese spent considerably more time in alert behavior during pre-laying than females. Pre-laying male Pink-footed Geese (*Anser brachyrhynchus*) also spent about 25% of their time in alert (Inglis 1977). Alert males presumably watched for the presence of predators such as Arctic foxes (*Alopex lagopus*) and for attacks or harassments by other males. We witnessed an unsuccessful attack by fox on three pairs, and two extra-pair copulations attempts (see also Inglis 1977, Mineau and Cooke 1979). Extra-pair copulations can be dangerous for females as evidenced by the persistent harassment suffered by experimentally widowed nesting female Lesser Snow Geese (Mineau and Cooke 1979, Martin et al. 1985), all of which eventually failed to produce any young. Another important benefit of male vigilance for females is that it relieves females from the need to be vigilant themselves and enables them to increase their feeding time (Ashcroft 1976, Patterson 1982, Gauthier 1987). In addition to assuming the major role in vigilance, males also perform most of the active defense against conspecifics as they were involved seven times more often than females in aggressive interactions with neighboring pairs.

During nesting, pairs are often dispersed and may not always benefit from group vigilance (Lazarus 1978, Inglis and Lazarus 1981). We therefore expected males to synchronize their activity with females and to be more vigilant when females are most vulnerable such as when they are feeding. However, male vigilance was only loosely correlated with female feeding intensity. Presence of neighboring pairs with whom vigilance could be shared may explain the low level of alertness shown by some males accompanying

actively feeding females (Fig. 3). Alternatively, body condition of the male may influence vigilance, forcing those with few energy reserves to feed more at the expense of vigilance.

Resting and walking were two behaviors highly synchronized between pair members. Typically, both pair members rested simultaneously and chose elevated sites from which the surrounding terrain could be easily scanned during short awakening periods. Synchrony in walking behavior presumably showed the cohesion of the pair and the need for the male to be in close proximity to the female to protect her from conspecifics (Anderson 1984).

PARENT-OFFSPRING CONFLICT

Few studies have documented the process of family break-ups in geese. Prevet and MacInnes (1980) found that most Lesser Snow Goose families arrive intact on breeding grounds and that break-ups take place shortly after. In contrast, Black and Owen (1989) reported a gradual family break-up starting in late winter and accelerating on the spring staging ground in Barnacle Geese (*Branta leucopsis*). Our results suggest that, in Greater Snow Geese, most family break-ups occur during the short period (3–6 days) of the 3,000-km northward migration between the St. Lawrence and Bylot Island. Family break-up is probably a sudden event within families because family size did not change between the St. Lawrence and the Arctic whereas proportion of pairs with yearlings decreased by a factor of 4. We do not know where the yearlings went because groups of yearlings were not observed on Bylot Island before the incubation stage. Although there is a considerable decrease in the proportion of pairs with yearlings between fall and spring (Table 4), it is probably caused by mortality rather than by family break-ups because yearlings without parents are rare throughout spring staging (Turcotte 1987, Tardif 1990).

Turcotte and Bédard (1989) showed the existence of parent-offspring conflicts over feeding opportunities in Greater Snow Goose families during spring staging. The frequency of aggression by parents towards yearlings was higher on the breeding ground than on the St. Lawrence spring staging (1.53 vs. 0.51 aggressions $\text{bird}^{-1} \text{hr}^{-1}$; in spring, mean calculated from Turcotte and Bédard [1989] for the range of brood sizes observed at Bylot Island, 1 to 3). In spring, aggressions by adults toward yearlings are mostly

contests over feeding opportunities (Turcotte and Bédard 1989). On Bylot Island, attacks by parents were probably attempts to chase yearlings rather than contests over food because parents were often not feeding before or after attacks toward yearlings. Black and Owen (1989) also reported an increase in aggressions by parent Barnacle Geese toward yearlings during family break-ups in spring. We did not detect any effect of this conflict on time budget of pre-laying pairs still with yearlings.

GREATER SNOW GOOSE REPRODUCTIVE STRATEGY

In Lesser Snow Geese and Ross Geese, females typically start laying within 3–5 days of arrival on the breeding ground and they feed very little (Cooch 1958; Ryder 1967, 1970; Ankney and MacInnes 1978). Raveling (1978) suggested that copulations and rapid follicular development take place on the final staging area in Arctic-nesting geese. These are assumed to be adaptations to the short Arctic summer enabling geese to initiate nesting as early as possible.

Our results suggest that Greater Snow Geese adopt a different reproductive strategy than these species. They show a prolonged delay between arrival on the nesting ground and start of egg-laying (16–18 days), and they feed and copulate extensively during that period. The long pre-laying delays that we observed in 1989 and 1990 were not unusual because even in a very early year (1988), start of egg-laying was advanced by only three days (see also Lemieux 1959). The high frequency of copulations reported here contrasts with the St. Lawrence estuary, the last staging before the Arctic, where Tardif (1990; unpubl. data) never observed a single copulation during more than 100 hr of behavioral observations.

We suggest that the long pre-laying delay of Greater Snow Geese at Bylot Island and their intense feeding activity enable females to replenish their energy reserves depleted during a long and costly migration from the St. Lawrence estuary. Other Arctic-nesting geese with a long spring migration have also been reported to feed intensively after their arrival on the nesting ground (Pink-footed Geese, Inglis 1977; White-fronted Geese, Fox and Madsen 1981; Brant [*Branta bernicla*], Ankney 1984; Dusky Canada Geese [*B. canadensis occidentalis*], Bromley 1984). Thus, in addition to energy reserves ac-

cumulated during the spring migration, food intake on the nesting ground may also be an important source of energy for laying females in these species. We are currently testing this hypothesis in Greater Snow Geese.

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