

# THE THERMAL REGIME OF EGGS DURING LAYING AND INCUBATION IN GREATER SNOW GEESE<sup>1</sup>

CATHERINE POUSSART

*Département de biologie and Centre d'études nordiques, Université Laval, Québec, Qc, Canada, G1K 7P4*

JACQUES LAROCHELLE

*Département de biologie, Université Laval, Québec, Qc, Canada, G1K 7P4*

GILLES GAUTHIER<sup>2</sup>

*Département de biologie and Centre d'études nordiques, Université Laval, Québec, Qc, Canada, G1K 7P4*

**Abstract.** Dummy eggs were added to naturally incubated clutches of Greater Snow Geese (*Chen caerulescens atlantica*), an arctic-nesting species, in order to evaluate egg temperature during laying and incubation, and factors influencing egg cooling rate during female recesses. As laying progressed, both nest attentiveness by females and egg temperature progressively increased. Although the time spent at nest after laying the penultimate egg was relatively high (69% vs. 91% during incubation), mean egg temperature was still 5.7°C lower than during the early incubation period. This suggests that little embryonic development began before clutch completion. Thereafter, egg temperature averaged  $37.1 \pm 0.1^\circ\text{C}$  during periods where females were present, a value that decreased only slightly when incubation recesses are included (36.8°C). This is a high temperature in comparison to other arctic-nesting geese. A modest increase (1.7°C) in mean egg temperature was observed as incubation progressed, but egg temperature was not influenced by clutch size or by the laying date of the first egg. During recesses lasting  $24.7 \pm 1.3$  min on average, egg temperature dropped by  $2.8 \pm 0.3^\circ\text{C}$ , at an instantaneous rate of  $0.23 \pm 0.02^\circ\text{C hr}^{-1} \text{ } ^\circ\text{C}^{-1}$ . Cooling rates increased under windy conditions and decreased with high solar radiation, but were little affected by air temperature.

**Key words:** Arctic, *Chen caerulescens atlantica*, egg temperature, Greater Snow Goose, incubation, laying.

## INTRODUCTION

Development of the avian embryo is influenced by the thermal regime of eggs during laying and incubation. Some studies have shown that female Anatids spend progressively more time at their nest as laying proceeds and that nest attentiveness toward the end of the laying period can be high (Afton 1980, Kennamer et al. 1990). However, it is not clear whether the adoption of an incubation posture by females during laying results in egg temperatures sufficiently high to initiate development, as this behavior may not necessarily imply an effective heat transfer from the brood patch to the eggs.

In a cold environment like the Arctic, ambient temperatures are well below the optimal values for embryonic development (Webb 1987). This could influence the incubation temperature maintained during presence of a parent on the nest, as well as the temperature drop experi-

enced by the eggs during a parent's absence. In arctic-nesting geese, low incubation temperatures have been reported (32 to 34°C) in comparison to other waterfowl species (Afton and Paulus 1992), and the optimum temperature reported for the development of avian embryos (35 to 40°C; Webb 1987).

We have examined the thermal regime of eggs in Greater Snow Geese (*Chen caerulescens atlantica*) during their whole nesting period. Greater Snow Geese are large body-size geese (body mass about 2.8 kg) breeding in the Canadian High Arctic. Visual observations have shown that, like other species of geese, females spend some time at their nest during laying (Gauthier and Tardif 1991), although the extent of egg warming occurring during this period is unknown. In contrast, nest attentiveness during incubation is relatively low for a large body-size goose (Reed et al. 1995). The objectives of the present research were to (1) document the thermal regime of eggs during the laying period in relation to female attentiveness, (2) monitor egg temperature during incubation to verify whether

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<sup>2</sup> Corresponding author. E-mail: gilles.gauthier@bio.ulaval.ca

a low embryonic temperature is generalized in arctic-nesting geese, and (3) examine the effect of meteorological conditions on egg temperature and cooling rate during parental absence.

## METHODS

Field work was carried out during the summers of 1995–1998 on Bylot Island, Nunavut, Canada (73°N, 80°W). Data were collected at two nesting sites: a glacial valley characterized by wet polygon tundra and a low-elevation plateau 30 km south of the main study site (see Lepage et al. 1996). Geese nest colonially at each site and benefit from 24-hr daylight during the entire nesting period.

### EGG TEMPERATURES

Egg temperatures were measured with artificial eggs (hereafter called EGGS) added to goose nests. The EGGS were made of a hollow copper shell 1 mm thick to insure thermal uniformity. The shells, close in size and shape to a goose egg, were covered by a few millimeters of plaster to give the right texture and color to the surface. A thermistor in contact with the copper shell was read with an electronic data logger. In 1995, the logger was housed within the EGG. Afterwards, loggers were placed in a waterproof plastic tube outside the EGGS and fastened to a metal stake driven into the ground about 0.5 m from the nest. The sensor wire between the EGG and the data logger was reinforced with a fine metal wire and hidden in the soil litter. This wire somewhat restricted movements of the EGGS in the nests although they could still be turned, to a certain extent, along their long axis.

In 1995 and 1996, 11 and 12 EGGS, respectively, were added to goose nests during laying. In the first year, nine EGGS were lost to predators. As a result, the egg temperature over the complete incubation period was monitored in only 12 nests (2 in 1995 and 10 in 1996). In 1997 and 1998, 10 and 11 EGGS, respectively, were placed in clutches to follow the laying period only. All EGGS were accepted except by four females which rejected the EGG by rolling it outside their nest. Loggers stored the mean temperature recorded during a given interval every 0.67 to 1.6 min (3.2 min in a few cases) with an accuracy of 0.5°C.

### WEATHER PARAMETERS

An automated weather station at the main study site recorded air temperature (°C) and solar ra-

diation ( $W\ m^{-2}$ ) at 2 m above ground, and wind velocity ( $m\ sec^{-1}$ ) at a height of 2.5 m every min. Mean hourly values were saved by a data logger. Air temperature was measured with a shielded temperature probe, solar radiation with a pyranometer, and wind velocity with a propeller anemometer. In 1995, nests monitored were located about 2.5 km from the weather station, but from 1996 to 1998, they were 30 km farther south. The weather station was located in the same type of habitat that geese nested at both sites and thus should have recorded the general meteorological conditions experienced by nesting geese.

### DETERMINATION OF NEST ATTENTIVENESS BY THE FEMALES

Due to their low thermal inertia and high conductivity, EGGS had a rapid thermal response which facilitated the detection of the absences (recesses) of incubating females. Abrupt and sustained drops in temperature lasting 6 min or more were easy to recognize on graphs of EGG temperature vs. time and were assumed to represent absences of the female. The validity of this assumption was checked by visual observations of five nests with EGGS over a period of 54 hr during which the times of departure and return of incubating females to their nest were precisely recorded. Recess duration was defined as the period of time elapsed between the last recording of a constant incubation temperature and the first recording indicating a rewarming. Recess duration determined by EGG temperatures and visual observations did not differ significantly ( $22.85 \pm 0.81\ min$  vs.  $22.93 \pm 0.80\ min$ , two-tailed paired  $t_{38} = 0.2$ ,  $P > 0.8$ ).

Nest attentiveness of females during laying was calculated by summing all periods of time when EGG temperature was rising rapidly or was stable but high ( $\geq 10^{\circ}C$  above ambient air temperature). As nests were visited 2–7 times each during incubation and twice during laying, the corresponding periods of disturbance were excluded from all calculations.

### EGG COOLING RATES

The cooling and heating rates of EGGS were more rapid than those of living eggs. Their response was calibrated against freshly laid goose eggs collected in the field (see Appendix). This enabled us to calculate time constants based on an exponential model of temperature drop over

time. These time constants, which are defined as the time required for a temperature drop corresponding to 63.2% of the initial temperature gradient (33°C) were 25.5 min for EGGs and 61.5 min for eggs. These values were used to transform the EGG final temperature at the end of a recess into a value which would represent the final temperature reached by living goose eggs. Corrections were applied to 677 recesses longer than 15 min. We then calculated, for each recess, (1) the temperature drop during the entire duration of the recess, (2) the average cooling rate, which represents the linearized rate of temperature drop ( $^{\circ}\text{C min}^{-1}$ ), and (3) the instantaneous cooling rate which takes into account the thermal gradient between the egg and the air temperature during the recess ( $^{\circ}\text{C hr}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ). Temperature drop was defined as the difference between the constant incubation temperature before the recess and the minimum temperature during the recess. Data for air temperature used in the calculation of instantaneous cooling rates were recorded at the weather station and are the mean hourly temperatures closest to the midpoint of the recess. The first and last temperature recordings of each recess were not used in the calculation of cooling rates. This procedure avoided a possible bias due to the presence of the incubating female during an unknown fraction of the first and last sampling interval of a recess. We are aware that the corrected cooling rates do not account for the heat production of embryos which may modify egg cooling rates late in the incubation period (Turner 1990). However, our procedure should yield cooling rates and temperature drops close to those observed in living goose eggs during most of the incubation period. Corrected temperatures during recesses also were used to calculate the mean egg temperature during incubation with recesses included.

#### STATISTICAL ANALYSIS

Individual nests were used as the sampling unit in statistical analyses unless specified otherwise. Nest attentiveness and egg temperature were compared between laying and early incubation in the same nests with two-tailed paired *t*-tests. Nest attentiveness at the beginning of the incubation period was compared with mean values recorded during the rest of the incubation period for all nests with two-tailed *t*-tests. Among-nest variability in EGG temperature (over 3-hr peri-

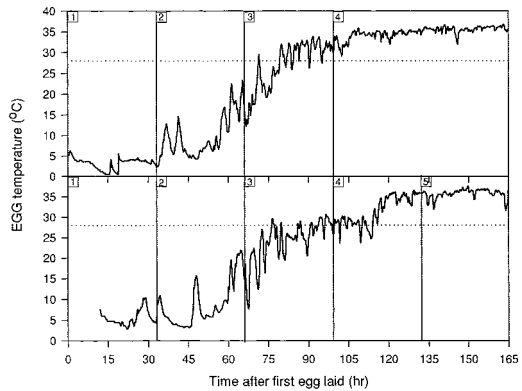


FIGURE 1. Mean artificial egg (EGG) temperature in Greater Snow Goose nests (top: clutch size 4,  $n = 3$ ; bottom: clutch size 5,  $n = 2$ ) during laying and early incubation. The vertical lines show the estimated time of laying of each egg assuming a constant laying interval of 33 hr. The number of eggs in the nests is shown in boxes. The stippled line is assumed to be the temperature threshold for embryonic development in birds (28°C).

ods) was investigated during incubation with a one-way ANOVA (model II). The effects of clutch size, laying date, and recess duration on mean egg temperature, temperature drops, and cooling rate during recesses were examined using linear regressions. Among-nest variability in temperature drop, average cooling rate, and instantaneous cooling rate during recesses also were investigated with one-way ANOVA (model II). The effect of weather conditions (air temperature, solar radiation, and wind velocity) and recess duration on average cooling rate was investigated with general linear models using individual recesses as the sampling unit (GLM; SAS Institute 1992). Only significant variables were retained in the final model. Analyses were performed using a significance level of 0.05, and results are presented as mean  $\pm$  SE.

#### RESULTS

##### EGG TEMPERATURE DURING LAYING

Many nests to which EGGs were added during laying were destroyed by predation. Hence, data from the laying period and the transition from laying to incubation are only available for seven nests. The most complete data came from five nests which received an EGG at the one-egg stage and in which three or four additional eggs were laid (Fig. 1). Visits every other day during this period allowed us to determine a mean lay-

TABLE 1. Mean ( $\pm$  SE) artificial egg temperature (including recesses) and nest attentiveness during laying and early incubation according to clutch size in Greater Snow Geese. Each laying stage corresponds to the number of eggs remaining to be laid in the nest and lasts 33 hr, the estimated laying interval. Stage 1 of incubation is the first 33 hr interval following estimated time of clutch completion.

	Clutch size	<i>n</i>	Laying stage				Incubation
			-4	-3	-2	-1	1
Temperature (°C)	5	2	5.3 $\pm$ 0.3	8.7 $\pm$ 1.2	22.6 $\pm$ 5.6	31.3 $\pm$ 4.3	35.8 $\pm$ 0.7
	4	4		3.7 $\pm$ 1.0	12.2 $\pm$ 3.0	29.3 $\pm$ 2.2	34.7 $\pm$ 1.0
	3	1			8.3	25.4	34.3
Attentiveness (%)	5	2	0.0 $\pm$ 0.0	17.9 $\pm$ 3.3	57.6 $\pm$ 17.0	70.9 $\pm$ 7.8	94.9 $\pm$ 1.9
	4	4		1.0 $\pm$ 1.0	35.1 $\pm$ 7.3	66.2 $\pm$ 5.9	93.2 $\pm$ 2.8
	3	1			20.1	77.3	93.0

ing interval of 33 hr, assuming a constant laying rate. Partial data also were available from two nests where two eggs were laid after the addition of the EGG. Assuming a laying interval of 33 hr for these nests as well (see also Schubert and Cooke 1993), we estimated that an egg was laid 30 min before our first visit.

All females showed a similar pattern as both EGG temperature ( $5.0 \pm 0.9^\circ\text{C}$ ,  $n = 7$ ) and nest attentiveness ( $3.8 \pm 3.6\%$ ) were very low at the one-egg stage but gradually increased as the laying period progressed (Fig. 1, Table 1). The lowest EGG temperature ( $0.01^\circ\text{C}$ ) was recorded at the one-egg stage. EGG temperature never dropped below freezing even though the minimum air temperature recorded during laying was  $-2.9^\circ\text{C}$  (mean air temperature:  $1.7^\circ\text{C}$ ). At the penultimate egg stage, nest attentiveness was relatively high ( $69.1 \pm 3.9\%$  on average) but still much lower than during the first 33 hr following laying of the last egg ( $93.6 \pm 1.6\%$ ; paired  $t_6 = 7.6$ ,  $P < 0.001$ ). Mean EGG tem-

perature at the penultimate egg stage ( $29.3 \pm 1.7^\circ\text{C}$ ) was still  $5.7^\circ\text{C}$  below the temperature recorded during early incubation (paired  $t_6 = 4.8$ ,  $P = 0.003$ , Table 1). EGG temperature during the first 33 hr following laying of the last egg averaged  $35.0 \pm 0.6^\circ\text{C}$  (including recesses), about  $1.5^\circ\text{C}$  lower than mean EGG temperature observed throughout the rest of the incubation period ( $t_{17} = 3.2$ ,  $P < 0.006$ ) even though nest attentiveness was similar ( $93.6 \pm 1.6$  vs.  $91.4 \pm 1.2\%$ , respectively;  $t_{17} = 1.2$ ,  $P > 0.2$ ).

EGG TEMPERATURE DURING INCUBATION

Egg temperature, expected to be accurately represented by the EGG temperature when females are sitting on their clutch, averaged  $37.1 \pm 0.1^\circ\text{C}$  ( $n = 12$  females with 2,787 to 12,519 individual recordings per female). When incubation recesses were included in the calculation, average temperature dropped to  $36.5 \pm 0.2^\circ\text{C}$  for EGGS, corresponding to  $36.8 \pm 0.1^\circ\text{C}$  for eggs after correction for the faster cooling rate of EGGS during recesses. The difference between the highest and lowest mean incubation temperatures among nests was less than  $1^\circ\text{C}$ . Variability in mean EGG temperature (including recesses) was significant among nests ( $F_{11,1662} = 41.8$ ,  $P < 0.001$ ) although the variation within nests explained 77% of the total variation.

Egg temperature (excluding recesses) increased with the progression of incubation from a low value of  $35.7^\circ\text{C}$  on the first day of incubation to a high of  $37.4^\circ\text{C}$  on the day of hatching (Fig. 2). A curvilinear relationship provided a better fit to the data than a linear one ( $r^2 = 0.97$ ,  $P < 0.001$ ) and suggested that the increase took place mostly during the first half of incubation, the temperature being relatively stable thereafter. Among-nest variability in temperature followed

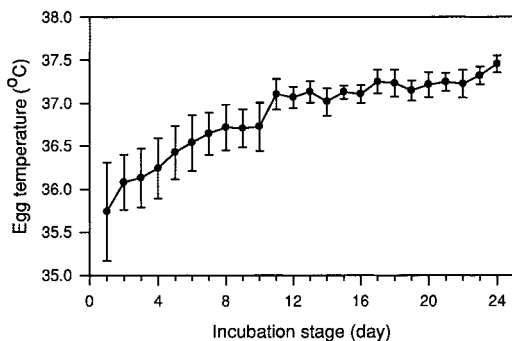


FIGURE 2. Time course of egg temperature (excluding recesses) during the incubation stage in Greater Snow Goose clutches. Circles (mean  $\pm$  SE) are daily average temperatures of 6 to 12 nests.

an inverse pattern from a high of 5.0% (coefficient of variation) on day one to <1.5% after day 12.

Clutch size of nests with EGGS averaged  $4.0 \pm 0.4$  eggs ( $n = 12$ , range: 2–7) and mean laying date was 15 June (range 10–19), which is close to the population average for these years. Mean egg temperature (excluding recesses) was not related to clutch size ( $r^2 = 0.09$ ,  $n = 12$ ,  $P > 0.3$ ) or laying date of the first egg ( $r^2 = 0.01$ ,  $n = 12$ ,  $P > 0.8$ ).

#### COOLING RATE AND TEMPERATURE DROP DURING INCUBATION RECESS

Females' recesses took place when air temperature was slightly higher ( $7.1 \pm 0.1^\circ\text{C}$ ) than the average over the whole incubation period ( $5.2 \pm 0.1^\circ\text{C}$ ). Egg temperature during recesses longer than 15 min dropped by only  $2.8 \pm 0.3^\circ\text{C}$  on average ( $n = 12$  females with 25 to 92 individual recesses by females; mean recess duration:  $24.7 \pm 1.3$  min), and was significantly related to the average recess duration across females ( $r^2 = 0.46$ ,  $n = 12$ ,  $P < 0.02$ ). Mean temperature drop during recesses differed among nests (range: 1.7–4.6°C;  $F_{11,665} = 35.5$ ,  $P < 0.001$ ) but variability was greater within (62%) than among nests. Average egg cooling rate was  $0.11 \pm 0.01^\circ\text{C min}^{-1}$ , corresponding to an instantaneous cooling rate of  $0.23 \pm 0.02^\circ\text{C hr}^{-1} \text{ } ^\circ\text{C}^{-1}$  ( $n = 12$ ). Cooling rates differed among nests (average,  $F_{11,665} = 19.4$ ,  $P < 0.001$ ; instantaneous,  $F_{11,665} = 19.3$ ,  $P < 0.001$ ) but again within nests fluctuations explained most (75%) of the variability. Instantaneous cooling rates nonetheless varied by more than a factor of two between nests with the lowest and highest average values (range: 0.16–0.38). Average egg cooling rate was neither influenced by clutch size ( $r^2 = 0.02$ ,  $n = 12$ ,  $P > 0.6$ ) nor by laying date ( $r^2 = 0.09$ ,  $n = 12$ ,  $P > 0.3$ ).

Eggs cooled at a slower rate under high solar radiation and low wind velocity (Table 2). For example, their average cooling rate under calm conditions became nil at  $600 \text{ W m}^{-2}$ , whereas at low irradiance it was increased by 65% under a  $6 \text{ m sec}^{-1}$  wind. Slight but significant interactions were found between wind velocity and air temperature, recess duration, and solar radiation. The first two interactions indicate that the wind-induced cooling of the eggs was dependent on the fall of the eggs-to-air thermal gradient at high ambient temperature over the recess period.

TABLE 2. The effect of weather parameters, recess duration, and their interactions on average cooling rates ( $^\circ\text{C min}^{-1}$ ) of Greater Snow Goose eggs. The significance of each variable and its coefficients are presented (general linear model;  $r^2 = 0.28$ ,  $n = 677$ ,  $P < 0.001$ ).

Variables <sup>a</sup>	Coefficients	P
Solar radiation ( $\text{W m}^{-2}$ )	-1.7E-4	<0.001
Wind velocity ( $\text{m sec}^{-1}$ )	0.012	<0.001
Wind velocity $\times$ Solar radiation	3.0E-5	<0.001
Wind velocity $\times$ Air temperature	-1.5E-3	<0.001
Wind velocity $\times$ Recess duration	-2.5E-4	<0.01

<sup>a</sup> Air temperature, recess duration, and other two-way interactions were not significant ( $P > 0.05$ ).

The interaction between wind and radiation implies that the solar influence was reduced by wind, becoming negligible when the wind speed reached  $6 \text{ m sec}^{-1}$ . Air temperature and recess duration alone had no effect on average cooling rate. Altogether, the model explained 28% of the variation in the cooling rate.

## DISCUSSION

### EFFECT OF USING ARTIFICIAL EGGS

Our results show that during incubation, eggs of an arctic-nesting species can be maintained at a high temperature ( $36.8^\circ\text{C}$ ) which is little affected by the frequent recesses of the incubating female. The accuracy of these conclusions is unlikely to be limited by the procedure used to predict the temperature of living goose eggs from that of artificial eggs (EGGS). The untransformed mean temperature of the EGGS would still lead to the same conclusions. However, because our EGGS were calibrated with freshly laid eggs, the mean temperature of developing eggs may differ slightly from the calculated ones because of the changes in the thermal properties of incubated eggs due to metabolic heat production, circulatory convection, and dehydration.

Because EGGS warmed up and cooled down more rapidly than living eggs, fluctuations in temperature of goose eggs during laying should be less pronounced than those observed in Figure 1. However, mean temperatures experienced by goose eggs before clutch completion should be roughly similar to those recorded by EGGS.

### LAYING PERIOD

Even though our sample size is small, female Greater Snow Geese attended their nest during

the laying period, and both the presence on the clutch and the egg temperature increased as clutch completion approached. A gradual increase in attentiveness or egg temperature during this period also was observed in Giant Canada Geese (*Branta canadensis maxima*; Cooper 1978), Lesser Snow Geese (*Chen caerulescens caerulescens*; Krechmar and Syroechkovsky 1978), and Emperor Geese (*Chen canagica*; Krechmar and Kondratiev 1982). However, our results indicate that temperatures putatively high enough to allow embryonic development in birds ( $\geq 28^{\circ}\text{C}$ ; White and Kinney 1974, Drent 1975, Haftorn 1988) were not reached until the very end of the laying period in Greater Snow Geese. Although temperature at the penultimate egg stage was at times high enough (up to  $35^{\circ}\text{C}$ ) to allow embryonic development, mean EGG temperature was still only  $29^{\circ}\text{C}$ , well below the one maintained during incubation. Embryonic development at such a low temperature would presumably be very slow. Thus, even though presence of the female on the eggs before clutch completion warms the eggs, only slight embryonic development may occur during this period. Transition to a constant high temperature occurred rapidly around laying of the last egg. Nest attentiveness during the subsequent 33-hr period was similar to the rest of the incubation period, and egg temperature was high and constant, although still about  $1.5^{\circ}\text{C}$  below the mean egg temperature during the whole incubation.

Although we did not measure embryonic activity, our results apparently do not support the conclusion of Cargill and Cooke (1981) that development occurs throughout the laying period in Snow Geese. These authors based their conclusion on the observed relationship between the laying and hatching sequences in Lesser Snow Goose clutches, although they did not give the time between hatching of the first and the last egg. Flint et al. (1994) measured egg temperature during laying in Brant (*Branta bernicla*) and reported that first laid eggs received up to 48 hr of incubation above  $28^{\circ}\text{C}$  before the last egg was laid. This is considerably higher than what we found in Greater Snow Geese as comparable figures are 18 hr and 35 hr of temperature above  $28^{\circ}\text{C}$  in clutches of 4 and 5, respectively (Fig. 1). However, the extent of embryonic development achieved by the end of the laying period and its variability within clutches were not determined in their study either. In

Mallards (*Anas platyrhynchos*), MacCluskie et al. (1997) found significant variations in metabolic rate of eggs according to the laying sequence which could explain some of the intra-clutch variation in development time.

It is not surprising that nest attentiveness remains low during most of the laying period. Laying females must feed extensively in order to acquire the energy necessary to complete egg formation and to sustain incubation (Gauthier and Tardif 1991, Choinière and Gauthier 1995). Brief visits to the nest during laying could be a reaction to the presence of predators, a response to freezing temperatures, or an attempt to verify that eggs are still in the nest.

#### INCUBATION TEMPERATURE

Incubation temperature recorded in this study ( $36.8^{\circ}\text{C}$ ) falls within the range of those reported in many other species of birds ( $35$  to  $40^{\circ}\text{C}$ ; Webb 1987), but is higher than the mean value reported for ducks and geese ( $35.6^{\circ}\text{C}$ ; Afton and Paulus 1992). Our value also is surprisingly high compared to those previously measured in White-Fronted Geese (*Anser albifrons frontalis*;  $33.9^{\circ}\text{C}$ ), Emperor Geese ( $31.8^{\circ}\text{C}$ ), and Lesser Snow Geese ( $32.9^{\circ}\text{C}$ ) by Russian workers (Krechmar and Syroechkovsky 1978, Krechmar and Kondratiev 1982, Krechmar 1986 in Afton and Paulus 1992). Consequently, our results do not support the hypothesis that arctic-nesting geese have low incubation temperatures. Although temperature recordings in the Russian studies also were obtained with thermistors placed in artificial eggs, it is not known whether these eggs, which were made of paraffin, were thermally uniform and calibrated against living eggs of the studied species. Differences could therefore come in part from divergent thermal properties of artificial eggs used. However, the thermal characteristics of nests may also vary between species.

A gradual rise in egg temperature as the incubation period progresses has been observed in many waterfowl species (Caldwell and Cornwell 1975, Wilson and Verbeek 1995). This increase has often been attributed to a reduction in egg cooling during parental absence due to a higher heat production by the growing embryo. However, our results also show this characteristic rising trend, even though temperature was recorded with artificial eggs and only periods when females were sitting on the clutch were consid-

ered. Rising temperature also could be a consequence of an increased heat transfer from the incubating parent, but this appears unlikely as brood patch temperature is thought to stay constant throughout the incubation period (from day 4 to 20 in the Northern Shoveler *Anas chrypeata*; Afton 1979). Alternatively, higher egg temperature during the second half of incubation may be a consequence of a warmer nest environment. This could be due to a larger total heat production by the growing embryos and/or by higher ground temperature which reduces heat losses by conduction. The latter factor, however, should be of little importance in our case because mean temperature at 2 cm below ground only rose 0.2°C during incubation at our weather station. Hence, the available data do not enable us to single out any factor explaining the rising egg temperature as incubation progresses.

Egg temperature was not related to laying date although many aspects of the reproductive behavior of Greater Snow Geese vary seasonally, such as growth (Lindholm et al. 1994, Lepage et al. 1998). Time is presumably a constraint for incubating females because early-hatched birds have higher success (Cooke et al. 1984, Sedinger and Flint 1991, Lepage et al. 2000). In Brant, Eichholz and Sedinger (1998) reported that late-nesting females had a shorter incubation period than early-nesting ones. However, egg temperature is apparently not a parameter that females can adjust to advance hatching.

#### EGG COOLING RATE

An average temperature drop of less than 3°C during recesses lasting 25 min indicates that Greater Snow Goose eggs are far from being exposed to temperatures which could endanger the embryos' development or survival. This drop is actually lower than those recorded in other naturally incubated eggs of waterfowl species nesting at lower latitudes. Drops of 5.4°C were reported in Mallard eggs (recess duration: 24 min; Caldwell and Cornwell 1975), 7.6°C in Northern Shoveler eggs (recess duration: 101 min; Afton 1979) and 4.2°C in Spectacled Eider (*Somateria fisheri*) eggs (recess duration: 37 min; Flint and Grand 1999). The small temperature drop during recesses and the ensuing high, constant temperature throughout incubation must contribute to the short incubation period of arctic-nesting geese, presumably an adaptation to the brief Arctic summer. Temperature drops

were nonetheless related to recess duration in Greater Snow Geese, which suggests that females taking longer recesses may delay hatching. Instantaneous cooling rate ( $0.23 \pm 0.02^\circ\text{C hr}^{-1} \text{ }^\circ\text{C}^{-1}$ ) was similar to that measured in naturally incubated and covered eggs of Canada Geese ( $0.26^\circ\text{C hr}^{-1} \text{ }^\circ\text{C}^{-1}$ ; Cooper 1978) and Northern Shovelers ( $0.22^\circ\text{C hr}^{-1} \text{ }^\circ\text{C}^{-1}$ ; Afton 1979). In a controlled experiment with Emperor, Cackling (*Branta canadensis minima*), and Brant Goose eggs, transferring eggs from an artificial environment at 38.7°C to a nest covered with down at an ambient temperature of 6.4°C yielded instantaneous cooling rates slightly higher than our value (0.25 to  $0.30^\circ\text{C hr}^{-1} \text{ }^\circ\text{C}^{-1}$ ). However, these eggs have a smaller mass than those of Greater Snow Geese by 14 to 36% (Thompson and Raveling 1988).

Cooling rates were mostly influenced by solar radiation and wind speed. If females are sensitive to egg temperature at their return to the nest and/or to the environmental cooling capacity as determined by wind and solar radiation, they should adjust their recess frequency and duration accordingly. Recesses should be longer and more frequent under sunny conditions as this promotes a warm microclimate within the nest, and also when wind speed is too low to penetrate down feathers or blow them away from the eggs in the absence of an incubating parent. However, the effect of wind is complex and dependent on other variables. As wind velocity was recorded nearly 30 km from the study area and at 2.5 m above ground, the wind experienced by the eggs also may have differed somewhat from the values used in our calculations.

Weather variables explained a small portion of the variation in cooling rates (28%), which implies that other factors also were important. Differences in the insulative properties of nests among individuals, because of variable amount of down and other nest material, may influence the thermal relationship of eggs with their environment (Thompson and Raveling 1988). Microtopography and soil properties such as humidity around nests also may affect the microclimate that eggs experience under various prevailing weather conditions. It is, however, surprising that the egg cooling rate was not correlated with clutch size. Frost and Siegfried (1977) found a clear negative relationship between the number of eggs in a nest and the rate at which they cooled under controlled conditions

in Moorhens (*Gallinula chloropus*). Our data suggest that, under natural conditions, the number of eggs may be less influential on the thermal properties of a nest than its structure and location.

In conclusion, our results indicate that the incubation temperature in Greater Snow Geese is considerably higher than that reported in other arctic-nesting goose species. A high egg temperature also was maintained during parental recesses, with little dependency on meteorological factors. However, egg temperature during the laying period generally remained below the level expected for embryonic development.

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## APPENDIX

Artificial eggs were built from material with thermal properties that differed from those of living eggs. It was therefore necessary to apply a correction factor to transform cooling rates of the artificial eggs during the absence of females into values which would more adequately reflect those of living eggs.

Three freshly laid goose eggs (mass of 111, 118, and 120 g) were fitted with a thermistor inserted near their center. Living and artificial eggs ( $n = 3$ ) were simultaneously exposed to six sessions of cooling and heating. All eggs were placed in an oven at 37°C until equilibrium was reached (4 hr) and were then transferred to a closed box which was put in an environment of about 4°C for another 4 hr. The operation was reversed for heating experiments. This allowed us to calculate time constants, which are defined as the time required for a temperature drop corresponding to 63.2% of the initial temperature gradient, 33°C (the difference between initial egg temperature and ambient temperature). Cooling experiments yielded mean ( $\pm$  SD) time constants of  $25.5 \pm 3.4$  min for artificial eggs and  $61.5 \pm 10.4$  min for living eggs.

These time constants were incorporated into an exponential model to transform the final temperature obtained with artificial eggs during each recess into the

value expected for a living egg. This corrected temperature was used to calculate (1) the difference in temperature between initial and final temperature (temperature drop), (2) the average egg cooling rates ( $^{\circ}\text{C min}^{-1}$ ), and (3) the instantaneous egg cooling rates ( $^{\circ}\text{C hr}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ) during female absences. The first and last temperature recordings by the artificial eggs were excluded from the calculation of cooling rates. The model was as follows:

$$T_f = T_i - \frac{\Delta T_e}{(1 - e^{-L/K_e}) / (1 - e^{-L/K_g})} \quad (1)$$

$$R_a = \frac{T_i^* - T_f^*}{L^*} \quad (2)$$

$$R_i = \frac{R_a \times 60}{\Delta T_{ga}^*} \quad (3)$$

where:

$K_e$  = Time constant of artificial eggs (min)

$K_g$  = Time constant of living goose eggs (min)

$L$  = Total recess duration (min)

$R_a$  = Average egg cooling rate ( $^{\circ}\text{C min}^{-1}$ )

$R_i$  = Instantaneous egg cooling rate ( $^{\circ}\text{C hr}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ )

$\Delta T_e$  = Difference between the initial and final temperature measured by artificial eggs during female absence ( $^{\circ}\text{C}$ )

$\Delta T_{ga}$  = Difference between mean goose egg and ambient temperature during a recess ( $^{\circ}\text{C}$ )

$T_f$  = Predicted final temperature of goose eggs during female recess ( $^{\circ}\text{C}$ )

$T_i$  = Initial (i.e., incubating) temperature of artificial eggs, considered to be equal to the temperature of goose eggs ( $^{\circ}\text{C}$ )

Variables with an asterisk (\*) in the equations exclude the initial and final recordings of temperature and time during a recess.