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BODY TEMPERATURE AND RESTING BEHAVIOR OF GREATER SNOW GOOSE GOSLINGS IN THE HIGH ARCTIC[1]

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Abstract. We examined the control of body temperature during active and resting behaviors in chicks of a large precocial bird, the Greater Snow Goose (*Chen caerulescens atlantica*), growing in a cold Arctic environment. Imprinted goslings from 4 to 31 days old maintained their mean (± SD) body core temperature within a narrow range around 40.6 ± 0.2°C (range: 38.7–42.2°C), independently of changes in their thermal environment. Average body temperature increased <0.4°C between 4 and 31 days of age. Hypothermia, potentially an energy-saving mechanism, was not used by active goslings. The potential for heat loss to the environment influenced the length of resting bouts in wild goslings. As environmental temperature increased, wild goslings remained sitting alone for longer periods, whereas when it decreased, brooding behavior was prolonged. The time spent huddling increased with the number of goslings involved. Body temperature during huddling bouts measured in imprinted chicks was significantly lower than during periods of activity, showing a rapid decrease averaging 0.8°C at the onset of huddling, followed by a slow recovery before activity was resumed. Thus, huddling behavior was not used as a rewarming mechanism. Greater Snow Goose goslings appear to prioritize metabolic activity by maintaining a high body temperature, despite the high energy costs that may be involved. Social thermoregulation is used to reduce the energy costs entailed by the strict maintenance of homeothermy.

Key words: Arctic, body temperature, Chen caerulescens atlantica, *Greater Snow Goose, huddling, hypothermia, social thermoregulation.*

INTRODUCTION

Neonate birds hatching in the Arctic have a short season to complete their growth and fledge in time for the autumn migration. Any factor delaying their development thus increases the risk of not attaining adequate size or accumulating sufficient body reserves for the migration (Lesage and Gauthier 1997). To maximize growth rate, chicks must allocate as much energy as possible to biosynthesis of tissues. This could be facilitated by reducing energy allocated to thermoregulation through morphological, physiological, and behavioral adjustments (Lustick 1984, Ricklefs 1989).

In a cold environment, lowering body core temperature (T_b) reduces the body-to-environment thermal gradient in endotherms, and thus usually leads to a diminution of the energy allocated to temperature regulation. Accordingly, most neonate birds maintain a T_b lower than the adult T_b even within the thermoneutral zone (Myhre et al. 1975, Beasley 1986, Vongraven et al. 1989). Some chicks may let their T_b drop further and enter hypothermia when unable to compensate for heat loss by metabolic production. T_b as low as 26°C without impaired motor activity has been reported in some hypothermic precocial chicks (Myhre and Steen 1979, Eppley 1984). Although hypothermia is an effective energy-saving mechanism, it also entails some costs because it reduces biochemical activity and hence growth rate (Ricklefs 1989).

The energy costs associated with the maintenance of a body temperature favorable to rapid growth also can be reduced by the use of brooding and huddling behaviors. In altricial birds, young nestlings rely largely on parental heat to thermoregulate (Webb and King 1983). Precocial chicks must leave the nest soon after hatch to forage but they also may be brooded by their parents. For instance, goslings are regularly brooded during the first two weeks following hatch (Warhurst and Bookhout 1983, Sedinger and Raveling 1990). Some precocial chicks di-

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rectly depend upon parental heat to remain homeothermic, being active until T_b falls below a critical temperature after which they return to their parents for rewarming. This critical T_b is approximately 30°C in sandpipers, *Calidris* sp. (Chappell 1980) and 35°C in Willow Grouse, *Lagopus lagopus* (Myhre and Steen 1979). Huddling together is another social behavior used by precocial chicks (Blix and Steen 1979, Ankney 1980, Beasley 1986) to reduce heat loss. Although huddling and brooding decrease energy expenditure in cold environments, they also entail some costs as they reduce the time available for foraging.

This study focuses on the control of body temperature and the resting behaviors of young in a large precocial bird nesting in the Arctic, the Greater Snow Goose (*Chen caerulescens atlantica*). Our aims were to determine whether (1) T_b varies with age and environmental temperature in goslings, (2) goslings rely on hypothermia under cold conditions, and (3) huddling is used as a rewarming mechanism, and how it is influenced by the potential for heat exchange with the environment.

METHODS

The study was conducted at the Bylot Island Greater Snow Goose colony, Nunavut (73°08′N, 80°00′W) Canada, during the summer of 1993. On 1–3 July (3 July was the colony median hatching date), 16 newly-hatched goslings were removed from nests, 1 bird (2 in few cases) per nest. As goslings leave the nest within 24 hr after hatching, they were assigned ages 0 or 1 day according to their mobility and the dryness of their down. These goslings were imprinted on humans and raised in semi-captivity in the field, as described in Fortin (1995). At the end of the experiment, goslings (then 30–31 days old) were sexed by cloacal inspection.

T_b was measured using VHF radio transmitters (Holohil Systems Ltd., Ottawa, Canada, model BD-2GTI, 22 × 8 × 5 mm, <2 g) implanted in the abdominal cavity of eight imprinted goslings when they were 3 days old (body mass ca. 100 g). One gosling accidentally died at 13 days of age, and its transmitter was subsequently re-implanted in a wild gosling. When captured, this gosling weighed 416 g and was consequently considered 11 days old, 2–3 days younger than the other goslings. Prior to implantation, the relationships between transmitter temperature and pulse interval was determined ($r^2 > 0.99$, SE of estimate <0.2°C for all transmitters). Following this calibration, T_b was determined by timing 15 pulse-intervals with a stopwatch.

Growth of the captive birds was monitored to insure that transmitter implantation did not affect their development. Goslings were weighed and the head, culmen, and tarsus were measured to the nearest 0.1 mm daily for the first week and every other day thereafter. Head, culmen, and tarsus length were then combined into a principal component analysis, and the first principal component (PC1) was used as an index of body size (Lindholm et al. 1994). The growth curves of goslings with and without implanted transmitters were similar, and at 30 days mean (± SD) gosling mass with implants was 1,507 ± 174 g ($n = 6$), whereas chicks without implants weighed 1,545 ± 246 g ($n = 5$, two-tailed t-test, $t_{10} = -0.30$, $P = 0.77$). Similarly, there was no significant difference in PC1 between goslings with implants (2.9 ± 0.4) and those without (3.0 ± 0.5, $t_{10} = -0.65$, $P = 0.53$).

Behavioral observations of imprinted goslings were conducted within a 25-m² pen made of chicken wire (4 cm mesh size) located in a representative brood-rearing habitat. During experiments, goslings were free to feed on natural plants, and water was provided in a tray. Individuals were introduced into the pen four at a time to reproduce a typical brood size. Within each brood of four goslings, two had implanted thermally-sensitive transmitters.

Because goslings are active throughout the 24-hr daylight period in the summer, behavioral observations of imprinted birds were conducted daily during the warmest and coldest periods of the day (i.e., between 10:00–14:00 and 22:00–02:00), from 5 July to 1 August 1993. The time at which resting behavior started and ended and the number of goslings involved (1–4), were recorded for each individual. T_b was measured approximately every 5 min when goslings were active, and approximately every 3 min during huddling bouts. A huddling bout was defined as a period during which two or more goslings sat on the ground and remained in close contact for at least 1 min.

We also observed the behavior of wild goslings in two areas of 3–5 ha used by broods. Observation of wild goslings started on 15 July 1993, 12 days after the median hatching date.

Therefore, most of the goslings were probably 7 days or older by the start of the observations. As for captive goslings, behavioral observations were conducted from 10:00–14:00 and from 22:00–02:00. Observations were made by a single observer using a 15–60× spotting scope from a portable blind set on an elevated vantage point. To insure that wild broods were exposed to meteorological conditions comparable to the conditions recorded at the nearby weather station, only broods localized in relatively flat areas were considered. The observer preferentially chose broods initiating a resting bout. The behaviors of all members of the focal broods (n = 65) were recorded continuously until the geese were out of view or until the end of the 4-hr observation period.

The behavioral categories considered were: huddling, brooding (goslings brooded under female's wing, or simply huddled against the female), standing (which included walking and feeding), sitting alone, swimming, and other. The number of goslings involved in huddling and brooding behaviors was recorded. When in a resting posture (i.e., sitting alone, huddling, or brooding), goslings normally had their feet under their belly. When older, they also often had their head pointing backward between the wings, with the distal part of the beak covered by down. Wild goslings were assigned to one of four groups by comparing their height to that of their parents. Individuals included in age class 1 had their head reaching the ventral surface of adults, in age class 2 their head was reaching the middle of the adult body, in age class 3 their head was reaching the middle of the adult neck, and in age class 4 their head was reaching the bill of adults. Then, to assign an actual age to those classes, we calculated the difference between the dates during which each height category was most often observed and the median hatching date of the colony. We estimated that age class 1 included goslings younger than 13 days (but probably older than 7 days, see above), age class 2 included 13–17-day-old goslings, age class 3 included 18–25-day-old goslings, and age class 4 included goslings older than 25 days.

Wind speed, radiation intensity, air and ground temperatures were automatically recorded each second by a Campbell Scientific CR-10 datalogger, and average values were saved at intervals of 10 sec for wind speed and radiation, and 5 min for temperatures. Wind speed (m sec^{-1}) was recorded using a hot wire anemometer (model 441S, Kurz Instruments Inc., Monterey, California) placed at the gosling's height, about 10–25 cm above ground depending on age. Global radiation (W m^{-2}) was determined using a pyranometer (LI-200SA Pyranometer Sensor, LI-COR). Air temperature was measured 40 cm above ground using a shielded thermistor probe, and soil temperature was recorded 1 cm under the ground surface using a thermistor probe. All measurements were taken in the center of the pen used for observation of imprinted goslings, which was 50–400 m from the sites where wild broods were observed.

DATA ANALYSIS

Standard operative temperature (T_{ES}, in °C) was used to describe the thermal environment of goslings. T_{ES} combines the complex effects of several abiotic (such as wind, air temperature, and solar radiation) and morphological (such as size, shape, coat color, and insulation) factors on heat loss into a unique temperature index (Bakken 1992). To estimate the T_{ES} of goslings in the field, we used equations derived from laboratory experiments using heated taxidermic mounts. These equations use air and ground temperature, wind speed, and radiation intensity to predict T_{ES} of goslings of various ages (for further details see Fortin 1995 and Fortin et al. 2000).

The effect of body mass and T_{ES} on T_b of imprinted goslings while alone, thus not involved in huddling, was analyzed with ANCOVAs using individual goslings as a random factor. Body mass was preferred to age in all analyses with imprinted goslings because it should be more closely related to the heat generating capacity of individuals. T_{ES} was calculated assuming that goslings were in a standing posture, and by using the environmental parameters measured each time T_b was recorded. Differences in T_b between sexes or period of day were compared with two-way ANOVAs using individual goslings as a random factor and sex or period of day as fixed factors.

To determine whether imprinted goslings used huddling as a rewarming mechanism, T_b at the beginning, during, and at the end of a huddling bout, and T_b of active goslings before and after huddling were compared using a two-way ANOVA for repeated measurements including individual goslings as a random factor. T_b values

during huddling were averages of seven or more measurements for each individual, whereas T_b at the beginning and the end of huddling had to be recorded within 1 min of the onset or termination of the huddling bout, respectively, to be considered. Such restrictions increased reliability but also resulted in missing values within some huddling bouts. Therefore, as a post-hoc approach, we compared T_b of goslings alone with T_b at the beginning, during, and at the end of huddling in three separate pairwise ANOVAs. The sample size of each pairwise comparison was consequently increased compared to the global ANOVA analysis. However, because performing three independent analyses increased the risk of type I error, we applied the Bonferroni correction (Miller 1981) by fixing the significance level at 0.016.

To further investigate factors related to the pattern of change in T_b during huddling bouts, we performed stepwise multiple regressions to determine whether body mass, starting T_b, T_{ES}, and the number of huddled goslings could explain variations in the difference between T_b of active goslings and the minimal T_b recorded during huddling, and in the time required to reach it. Because trends were similar among individuals, and no individual effects were detected in the previous analyses (ANOVA, goslings factor: $P > 0.6$), data from all goslings were pooled for this analysis.

Due to both the large number of families using the study area and their large home range (Hughes et al. 1994), the probability of observing the same brood twice was low, and thus all broods were considered as independent in our analyses. However, because the behavior of broodmates was not independent, we performed our analyses using the average time spent in each behavior by all goslings within a brood. Stepwise multiple regression analyses were used to determine whether T_{ES}, age, or the number of goslings huddled influenced the length of resting bouts. T_{ES} were calculated assuming a sitting posture as reference and using the mean environmental parameters recorded during each resting bout.

Averages are presented ± SD, with n indicating the total number of observations and N the number of individuals. Unless indicated otherwise, the level of significance was fixed at $P < 0.05$.

RESULTS

BODY TEMPERATURE DURING GROWTH

Between 4 and 31 days of age, solitary goslings maintained an average T_b of 40.6 ± 0.2°C (N = 9 goslings) in the field. The lowest and highest T_b value recorded were 38.7 and 42.2°C, respectively (n = 1,287 recordings). T_b of male goslings (N = 3) was on average 0.12°C warmer ($F_{1,1181} = 16.1$, $P < 0.001$) than females (N = 5). Nonetheless, because this difference was very slight, data from both sexes were not discriminated in subsequent analyses. T_b generally increased with age ($F_{1,1269} = 19.6$, $P < 0.001$; interaction mass × gosling, $F_{8,1269} = 8.13$, $P < 0.001$). Seven of the nine goslings experienced a slight (average $\beta = 0.40$°C kg^{-1}) but significant ($P < 0.003$) increase in T_b with age and one showed a significant negative trend (Fig. 1). The two individuals that did not show the positive trend were not studied for the entire growing season. One of the two goslings was followed from 3–13 days of age and the other from 13–27 days of age.

The cold meteorological conditions that prevailed during our T_b measurements were typical of those observed at Bylot Island during growth of Greater Snow Goose goslings. Mean air temperature was 7.7 ± 4.5°C and mean T_{ES}, which also takes into account the effects of wind and radiation, was 11.8 ± 11.5°C. Therefore, goslings were generally exposed to temperatures below their lower critical temperature, which remains at approximately 15°C between 2 and 40 days of age (Ratté 1998). Despite large fluctuations in ambient conditions, T_b was not related to T_{ES} ($F_{1,1036} = 0.29$, $P = 0.59$; interaction T_{ES} × gosling, $F_{8,1036} = 3.98$, $P < 0.001$). T_b was positively related to T_{ES} in one gosling, negatively so in another one (both, $P < 0.05$), and no significant relationship was found in the seven others. Moreover, there was no difference in goslings' T_b between daytime and nighttime ($F_{1,1277} = 0.02$, $P > 0.9$), although nighttime air temperature and T_{ES} were respectively 7.8 and 16.8°C colder than during daytime.

These results suggest that goslings could regulate their T_b within a narrow range of values, independently of ambient temperature, and did not use hypothermia.

RESTING BEHAVIORS

The resting behaviors of wild goslings were usually highly synchronized among broodmates, al-

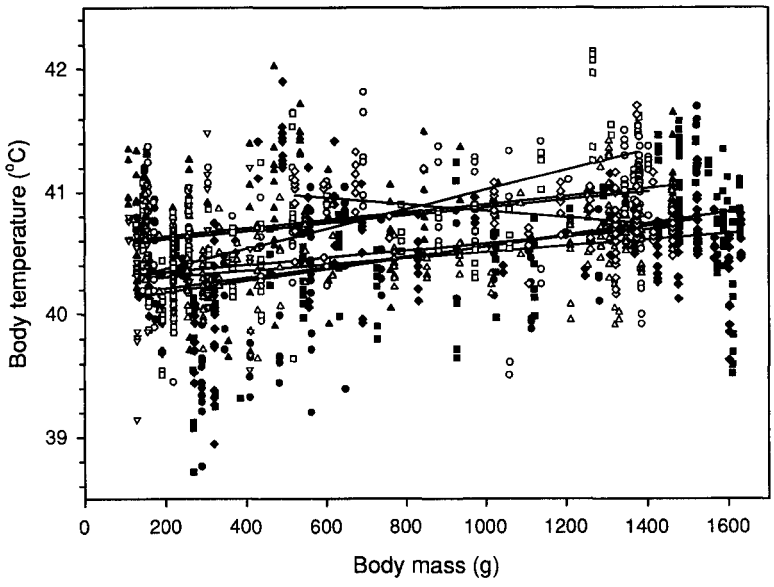

FIGURE 1. The effect of body mass on body core temperature of nine imprinted Greater Snow Goose goslings during non-huddling behaviors throughout the growing period. Each individual is represented by a different symbol. Regression lines are significant ($P < 0.05$) for all individual goslings but one (line not shown in this case).

though individuals sometimes shifted from huddling to brooding or sitting alone, and some goslings occasionally indulged in alternate activities while others remained at rest. The average length of a resting bout for the entire brood was 84 ± 50 min ($n = 65$ families) and could include more than one type of resting behavior. Broods rarely entered into another resting period within the 4-hr observation period. It thus appears that a 4-hr period was in most cases insufficient for goslings to complete an entire activity cycle, from one resting bout to another.

Brooding periods lasted about 1 hr on average, but their length varied considerably (Table 1). These variations were partly explained by changes in T_{ES} because goslings were brooded for longer periods as T_{ES} decreased. The duration of huddling bouts averaged 43 min, and increased with the number of birds involved. Huddling bouts involved on average 3.7 ± 1.4 goslings (range: 2–7). T_{ES} did not influence the duration of huddling bouts. However, under warm T_{ES}, the occurrence of huddling was reduced, and goslings rested alone for longer periods. Under these circumstances, resting bouts became less distinct and less synchronized among brood members. These results suggest that goslings are sensitive to environmental conditions and use brooding and/or huddling for social thermoregulation. The duration of resting behaviors did not vary significantly during the growing season, and thus with goslings' age (Table 1).

TABLE 1. Duration of individual bouts of various resting behaviors in wild Greater Snow Goose goslings. The effect of T_{ES}, number of goslings involved, and age on duration was determined by a stepwise multiple regression analysis.

Behavior	Mean ± SD (min)	n	Range (min)	Independent variables[a]	Slope	R^2	n[b]	P
Brooding	59 ± 40	28	10–150	T_{ES}	−3.09	0.27	23	< 0.01
Huddling	43 ± 48	38	1–176	Number of goslings	14.1	0.15	30	< 0.05
Sitting alone	12 ± 14	43	1–53	T_{ES}	0.47	0.26	30	< 0.001

[a] Only significant variables ($P < 0.05$) are reported.
[b] n is lower in the regression models because of missing values for some independent variables.

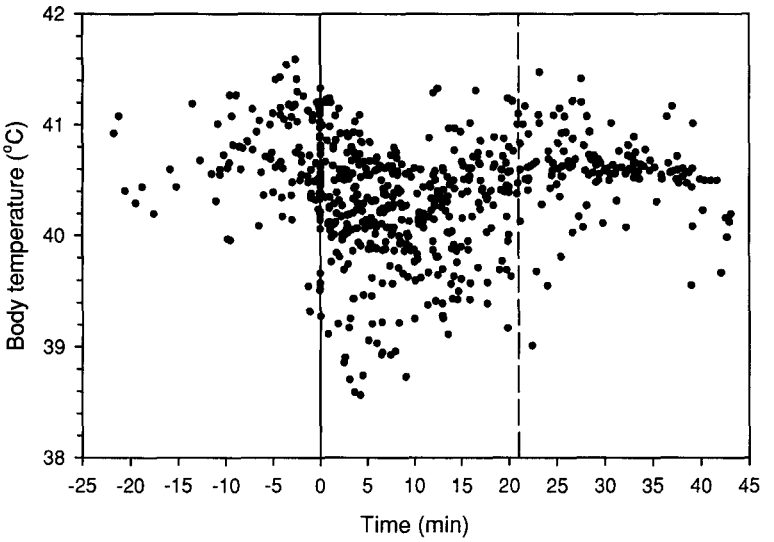

FIGURE 2. Time course of body temperature during huddling bouts (n = 45) of nine Greater Snow Goose goslings between 4 to 27 days of age. Time 0 corresponds to the onset of the huddling behavior and the vertical dashed line represents the average offset time.

To test the hypothesis that huddling was used as a rewarming mechanism, we examined variations in T_b of imprinted goslings during spontaneous huddling episodes in the field. T_b of active goslings in the minutes before and after a huddling bout, and at the beginning, during, and at the end of a huddling period differed ($F_{3,8}$ = 4.73, $P < 0.01$). During huddling, T_b was on average 0.3 ± 0.5°C (Fig. 2) lower than during activity, a result contrary to the rewarming hypothesis. During the course of huddling bouts, the change in T_b followed the same pattern in 89% of the 52 bouts considered (i.e., those that had a minimum of seven T_b values per individual recorded at regular intervals along the resting period). Following the onset of huddling, T_b dropped rapidly before increasing slowly until the end of the huddling bout. T_b fell from 40.6 ± 0.5°C (n = 41, N = 9) when active to a minimal value of 39.8 ± 0.5°C (n = 46) during huddling, a mean difference of 0.8 ± 0.4°C (n = 41, range = 0.2 to 1.6°C). Minimum T_b was reached 7.4 ± 4.4 min after the onset of huddling bouts, which lasted 21 ± 9 min on average (n = 46). The magnitude of the change in T_b during huddling was larger for heavier goslings and when T_b had a higher starting value (R^2 = 0.18, $P < 0.001$, n = 45), but was not influenced by T_{ES} ($P > 0.8$). The minimal T_b was also reached faster in heavier goslings and in warmer environments (R^2 = 0.23, $P < 0.01$, n = 46), but it was not influenced by the number of goslings involved ($P > 0.5$). Our results therefore indicate that huddling was not used by goslings as a rewarming mechanism.

DISCUSSION

Age-dependent changes in T_b have been reported in several avian species (Modrey and Nichelmann 1992) including domestic (Poczopko 1968) and wild goslings (Lesser Snow Goose *Chen caerulescens caerulescens,* Beasley 1986). An increase of T_b with mass (and hence age) also was observed in Greater Snow Goose goslings between 4 and 31 days. However, the increase was slight because 4-day-old goslings already maintained a T_b (Fig. 1) close to that of 40.7°C maintained by adults over a similar range of environmental temperatures (Thibault 1994). The age at which chicks reach adult T_b varies among species (Myhre and Steen 1979, Booth 1984, Eppley 1984). For instance, Myhre and Steen (1979) reported that 4-day-old Greylag Goose goslings (*Anser anser*) had already reached adult T_b.

Greater Snow Goose goslings as young as 4 days old appeared to be accomplished homeotherms even though they have to grow in a cold and highly variable thermal environment. Indeed, T_b was maintained within a narrow range

and was independent of T_{ES}. No signs of hypothermia were actually observed. Hypothermia during cold exposure can have two advantages in neonate birds: it may reduce the energy allocated to thermoregulation and thus save energy that could be later allocated to biosynthesis, and it may allow the animal to forage under adverse conditions for longer periods of time (Eppley 1984). However, lowering T_b will temporarily reduce growth rate by decreasing metabolic activity (Ricklefs 1989). Greater Snow Goose goslings thus appear to maximize their metabolic capacity through the maintenance of a high T_b. According to Myhre and Steen (1979), chicks of large body-size species do not commonly reduce T_b by more than 1–2°C. The results obtained by Beasley (1986) in the Lesser Snow Goose, and by Poczopko (1968) in the domestic goose, as well as our own findings, support this conclusion.

The rewarming hypothesis predicts that chicks' T_b will be minimal at the onset of huddling or brooding periods, after which T_b should increase. The absence of hypothermia in active goslings and the decrease in T_b during huddling strongly suggest that this resting behavior is not used as a rewarming mechanism. The basic thermal advantage of huddling in the cold comes from a reduction of the surface area exposed to the environment. Thus, if goslings were to maintain their metabolic rate during huddling, T_b would be expected to increase, not to fall as observed.

Two hypotheses can explain the reduction of T_b occurring in huddled goslings. First, it may result from an energy-saving decrease of the metabolic rate, and the magnitude of this decrease could be easily calculated from the average body cooling rate (ca. 0.1°C min^{-1}) and specific heat (3.48 J $°C^{-1}$ g^{-1}). For goslings of small (100 g) and large (1,500 g) body mass, the T_b decrease would require reductions in heat production of about 0.58 and 8.7 W, respectively. Because the thermoneutral resting metabolic rates of these goslings (when alone) would be respectively about 2 and 10 W (Ratté 1998), the observed cooling rate would thus require reductions in metabolic rate by corresponding factors of 3 and 8. These factors could be even higher considering that the temperature sensed by the transmitter lags behind tissue temperature and that huddling should decrease heat loss to the environment. Because drops in resting metabolic rate of such a magnitude are unexpected in fast-growing animals, it appears unlikely that the temperature drop observed during huddling results solely or even mainly from decreased metabolic rate. This hypothesis is further supported by the small daily energy saving (less than 0.3%) that would result from an average T_b decrease of only 0.3°C over a mean T_b-to-T_{ES} gradient of about 30°C, considering that goslings spent less than 30% of their time in huddling behavior.

However, an alternative hypothesis could also explain this result. An increase in peripheral vasodilation (and thus an increase in surface temperature and potential heat loss) while keeping the metabolic rate constant would also result in a decrease of the body core temperature. For example, assuming that the volume fractions of the thermal core and envelope in a gosling body are 90% and 10%, respectively, a 0.8°C drop in the core could be explained by an increase of about 7°C in the envelope. Cold-induced vasodilation of the peripheral tissues is periodically required in birds as in other homeotherms (Ostnes and Bech 1998). Huddling in a cold environment may then reduce the thermoregulatory cost associated with the episodes of extensive peripheral vasodilation required in a growing animal.

Huddling was the only social thermoregulation process available to our captive goslings and, between 4 and 31 days of age, they were able to maintain homeothermy despite the absence of brooding parents. We therefore suggest that, as for huddling behavior, parental brooding does not usually constitute a rewarming mechanism in wild goslings, but rather an energy-saving mechanism also aimed at minimizing the cost of cold-induced vasodilation. However, our study cannot reject the possibility that huddling and brooding serve as rewarming behaviors after a long exposure to cold water or for goslings younger than 4 days old.

Frequent resting periods have been observed in several species of chicks (Myhre and Steen 1979, Chappell 1980, Visser and Ricklefs 1993) including goslings (Sedinger and Raveling 1988, Sedinger et al. 1995). In small precocial birds (such as shorebirds), the cycling of resting and active periods may be imposed by the difficulty in maintaining homeothermy: once the T_b of active chicks decreases to a certain level, they stop foraging and return to their parents for rewarming (Myhre and Steen 1979, Chappell 1980).

However, our findings ruled out this hypothesis as an explanation for the activity cycles in goslings. Sedinger and Raveling (1988) found that at the end of feeding bouts, goslings had their esophagus distended by food, which limited further ingestion. They suggested that the length of foraging and non-foraging periods were related to the rate of ingestion and digestion of food, respectively. Although the digestive-constraint hypothesis could explain the activity cycle in Greater Snow Goose goslings, our results indicate that the length of resting bouts may also be influenced by the energy expended towards thermoregulation.

To maximize growth rate, individuals should seek a balance between the decrease in energy expenditure provided by huddling or brooding behaviors due to a reduction of the costs of homeothermy and activity, and the reduction in energy intake associated with rest. Accordingly, goslings could benefit from adjusting their resting behavior with respect to the prevailing T_{ES}. Several studies have shown that harsh weather conditions increase the length of brooding periods in precocial chicks (Zwickel 1967, Theberge and West 1973, Boggs et al. 1977). Our results also indicate that some variation in the duration and type of resting behavior used was related to the potential heat transfer between goslings and their environment. Brooding behavior lasted longer when T_{ES} was cold, and the duration of huddling increased with the number of goslings involved, i.e. as this behavior gained in efficiency. By sitting alone, resting goslings were likely to experience a higher rate of heat loss than those huddled or brooded, and this behavior lasted for a shorter period at low T_{ES}. This suggests that the type of resting behavior adopted by goslings was aimed at obtaining favorable thermal conditions, and hence at minimizing energy allocated towards thermoregulation.

The general absence of body thermolability in goslings demonstrates that they can maintain homeothermy over a wide range of T_{ES}, and thus do not need to be rewarmed by contact with parents and/or with siblings. The use of strict homeothermy suggests that maximization of the growth capacity is a priority in this species, despite the potentially high maintenance costs involved. Social thermoregulation may then be used to minimize the energy costs entailed by the maintenance of a high tissue temperature in a cold environment.

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