

NEST MORPHOLOGY AND BODY SIZE OF ROSS' GEESE AND LESSER SNOW GEESE

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ABSTRACT.—Arctic-nesting geese build large, insulated nests to protect developing embryos from cold ambient temperatures. Ross' Geese (*Chen rossii*) are about two-thirds the mass of Lesser Snow Geese (*C. caerulescens caerulescens*), have higher mass-specific metabolic rate, and maintain lower nest attentiveness, yet they hatch goslings with more functionally mature gizzards and more protein for their size than do Lesser Snow Geese. We compared nest size (a reflection of nest insulation) in four distinct habitats in a mixed breeding colony of Ross' Geese and Lesser Snow Geese at Karrak Lake, Northwest Territories, Canada. After adjusting measurements for nest-specific egg size and clutch size, we found that overall nest morphology differed between species and among habitats. Nest size increased progressively among heath, rock, mixed, and moss habitats. When nesting materials were not limiting, nests were smaller in habitats that provided cover from wind and precipitation than in habitats that did not provide cover. Ross' Geese constructed relatively larger, more insulated nests than did Lesser Snow Geese, which may hasten embryonic development, minimize energy expenditure during incubation, and minimize embryonic cooling during recesses. We suggest that relative differences in nest morphology reflect greater selection for Ross' Geese to improve nest insulation because of their smaller size (adults and embryos), higher mass-specific metabolic rate, and lower incubation constancy. Received 13 May 1996, accepted 18 March 1997.

IN BIRDS, HEAT IS SUPPLIED to developing embryos primarily by body warmth of the brooding parent (Afton and Paulus 1992). Heat loss from developing embryos and metabolic costs to parents can be minimized by increasing nest insulation. Nest insulation affects growth rates of nestlings (Winkler 1993), and probably affects embryonic growth as well, particularly in precocial species. Nest morphology and insulative properties of nests probably are influenced by body size, metabolic rates, incubation constancy, ambient thermal conditions, availability of nesting materials, and risk of predation (Møller 1984). Mass-specific metabolic rate and heat-transfer rate generally increase with declining body mass (Brody 1945, Lasiewski and Dawson 1967, Templeton 1970, Hill and Wyse 1989). Consequently, smaller species must assimilate nutrients at greater rates than larger species to maintain high metabolic rates. In addition, smaller species have less capacity to store endogenous nutrients than do larger

species. Thus, body size is of profound consequence to incubating parents, which must fast during incubation unless they are fed by mates or auxiliaries (von Haartman 1958, Skutch 1962, Afton and Paulus 1992). If endogenous nutrients are not sufficient to meet energy requirements during incubation sessions, parents may recess from incubation in order to feed, thereby decreasing incubation constancy and exposing nests to predators and heat loss. Afton and Paulus (1992) reported that incubation constancy is positively related to body mass among all species of waterfowl (Anatidae), particularly among geese and swans.

Within species, nest-building behavior may be adapted to maximize efficiency of nest insulation in response to cumulative embryonic metabolic rates, which are products of clutch size and embryo body size. Because of the relationship between surface area and volume, small eggs and clutches have greater rates of heat transfer than larger eggs and clutches, all else being equal. These factors are particularly important under the windy conditions that pre-

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vail in arctic latitudes (Thompson and Raveling 1988).

Nest morphology and insulation may be influenced further by local variation in temperature, wind, and availability of nesting materials. Comparative studies of hummingbirds (*Oreotrochilus* spp.; Pearson 1953, Corley Smith 1969), Village Weavers (*Ploceus cucullatus*; Collias and Collias 1971), and Helmeted Honeyeaters (*Lichenostomus melanops*; Franklin 1995) demonstrate that birds nesting in cold areas construct better insulated nests than those nesting under warmer conditions. Ryder (1964, 1967, 1972) found that nests of Ross' Geese (*Chen rossii*) were larger in habitats that did not provide shelter from wind than those in habitats that provided shelter. Experimental studies of egg cooling rates in three other species of arctic-nesting geese (*Chen canagica*, *Branta bernicla nigricans*, *Branta canadensis minima*) indicate that, across species, nest insulation and incubation constancy are inversely related (Thompson and Raveling 1988). Finally, intraspecific and interspecific competition for high-quality nest sites and nest materials also may influence nest morphology and insulation.

We measured nests of Ross' Geese and Lesser Snow Geese (*Chen caerulescens caerulescens*) in a mixed breeding colony in arctic Canada. We assumed that nest morphometrics are directly related to nest insulation according to the heat-flow equation:

$$dH = k \cdot dT \cdot (dx)^{-1}, \quad (1)$$

where H represents heat flow, k represents thermal conductivity, T represents temperature, and x represents thickness of insulating material (Serway 1990). We predicted that nest size would vary inversely with body size and incubation constancy and would vary positively with mass-specific metabolic rate. We also predicted that nest size should be greater in habitats that are more exposed to wind and precipitation, when adequate nest materials are available (Ryder 1964, 1967, 1972).

METHODS

We measured nests of Ross' Geese and Lesser Snow Geese at Karrak Lake, Northwest Territories, Canada (67°15'N, 100°15'W) between 19 June and 15 July 1994. Karrak Lake is located on the west tributary of the Simpson River in the central Canadian Arctic, south of the Queen Maud Gulf (Ryder 1972).

The area is characterized by tundra meadows and exposed Precambrian bedrock. Shallow lakes and streams are numerous. Karrak Lake contains the largest colony of Ross' Geese in North America (Kerbes 1994) and has nearly equal numbers of Lesser Snow Geese (Slattery and Alisauskas 1992, 1993). In 1993, about 364,000 Ross' and Lesser Snow geese nested at Karrak Lake (Slattery et al. 1994).

We examined nests on the largest island near the center of the lake. We arbitrarily selected 19 circular plots (20-m radius) every 100 m along a transect where Ross' and Lesser Snow geese nested together. We then selected every Ross' ($n = 54$) and Lesser Snow goose ($n = 51$) nest in the plots. Species, clutch size, egg length, and egg breadth were recorded for all nests. Embryo age was estimated (Weller 1956) to calculate clutch initiation date, assuming for both species a laying rate of 1.3 days per egg and an incubation period of 23 days (Ryder 1967, Ankney and MacInnes 1978). Nests were considered successful if at least one egg hatched. Nest habitat was classified as heath, rock, moss, or mixed according to dominant features of the immediate nest habitat (see Ryder 1967, 1972; McLandress 1983). Nests in heath habitats were built directly into patches of Labrador tea (*Ledum decumbens*), white heather (*Cassiope tetragona*), dwarf birch (*Betula glandulosa*), or willow (*Salix* spp.). Nests in rock habitat were built on either gravel or bedrock substrate and composed of gravel, soil, or twigs of dwarf birch and willow. Nests in moss habitats were composed of both living and dead *Sphagnum* species as well as nonliving heath fragments and birch or willow branches. Nests in mixed habitat possessed any combination of characters found in heath, rock, and moss habitats.

We measured (± 1 cm) outer diameter, wall thickness, circumference, rim height, bowl depth, and inner diameter of each nest during initial nest visits (Appendices 1 and 2). After the eggs hatched, nests were weighed on a portable electronic scale (± 1 g). Masses of 10 Lesser Snow Goose nests were estimated using stepwise multiple regression (PROC REG; SAS 1990) because nest markers were lost between initial and final nest visits. Best fit was obtained with separate equations for each habitat:

$$\begin{aligned} \text{mass}_{\text{heath}} = & -599.1 + 4.9(\text{circumference}) \\ & + 14.4(\text{outer diameter}) \\ (r^2 = 0.74, P < 0.0001); \end{aligned} \quad (2)$$

$$\begin{aligned} \text{mass}_{\text{rock}} = & -2073 + 170.8(\text{wall thickness}) \\ (r^2 = 0.76, P < 0.0046); \end{aligned} \quad \text{and} \quad (3)$$

$$\begin{aligned} \text{mass}_{\text{mixed}} = & -782.1 + 29.5(\text{outer diameter}) \\ (r^2 = 0.33, P < 0.0001). \end{aligned} \quad (4)$$

Total clutch volume was calculated for each nest

from length (± 0.1 mm) and breadth (± 0.1 mm) of each egg in a nest following Hoyt (1979; $K_v = 0.51$).

To estimate the relative difference in overall nest morphology between species and to account for variation due to differences in egg size and clutch size, we divided nest measurements by the square root of the total clutch volume for each nest, except for nest mass, which was divided by clutch volume. Using analysis of covariance (ANCOVA) with clutch volume as a covariate, or using residual nest measurements corrected for clutch volume, would be inappropriate because of significant heterogeneity in clutch volume between species ($F = 45.26$, $df = 1$ and 88 , $P < 0.0001$, $r^2 = 0.34$); i.e. significant interspecific colinearity was present among predictor variables in the model. We subsequently determined that the square root of clutch volume rather than clutch volume or the cube root of clutch volume is the appropriate denominator for linear measurements. Using clutch volume and the cube root of clutch volume as the denominator did not remove the species effect on inner diameter ($P < 0.05$), whereas dividing by the square root of clutch volume rendered species effects insignificant, as would be expected if nest inner diameters matched the body form of each species.

We used multivariate analysis of variance (MANOVA) to test whether nest measurements differed among species and habitats (PROC GLM; SAS 1990). We used a split-plot design to account for variance due to plot effect, which potentially contains components of both sampling error and natural variation due to density and nonrandom distributions of geese. In the full model, species and habitat were fixed effects, whereas plot was a random effect. F -values reported from MANOVA were determined using Wilks' lambda. Beginning with the largest-order interaction, nonsignificant effects were iteratively removed from the model until we obtained the most parsimonious model containing only significant effects. Following a significant MANOVA, we used analysis of variance (ANOVA) to test whether individual nest measurements differed among significant effects. We compared least squares means among habitat types with t -tests (PDIF option; SAS 1990). We did not find any Ross' Goose nests in rock habitats; consequently, only heath, moss, and mixed habitat nests were included in models comparing species and habitats. We subsequently compared the four habitats in a separate model for Lesser Snow Geese. In this model, we did not divide nest measurements by the square root of clutch volume but rather included the square root of clutch volume as a covariate because clutch volume and habitat were not related ($F = 0.96$, $df = 7$ and 40 , $P = 0.47$). We used ANOVA to test whether first-egg date differed between species, and among habitats and plots. We used ANCOVA to compare mean clutch size between species and among plots, with initiation date included as a covariate. We used categorical data analyses

(PROC CATMOD; SAS 1990) to test whether nest success varied between species and among habitat types.

RESULTS

The average date that first eggs were laid was 3 June, and this did not differ between species or among habitats and plots (all P s > 0.12). Clutch size was inversely related to first-egg date ($F = 1.44$, $df = 1$ and 101 , $P = 0.0001$) but did not differ between species or vary in relation to plot, species-by-initiation date, or plot-by-species-by-initiation date (all P s > 0.23). Mean nest success was $92.6 \pm$ SE of 2.8% and did not differ between species ($\chi^2 = 0.06$, $n = 87$, $P = 0.805$) or among habitats ($\chi^2 = 0.02$, $n = 87$, $P = 0.992$).

Variation between species and among habitats.—The overall nest morphology corrected for clutch volume differed between species (MANOVA, $F = 3.90$, $df = 7$ and 78 , $P = 0.001$) and among habitats ($F = 5.87$, $df = 14$ and 156 , $P = 0.0001$). Plot effects, and species-by-habitat and plot-by-species-by-habitat interactions were not significant (all P s > 0.10). The outer diameter, wall thickness, circumference, and rim height of Ross' Goose nests were relatively larger than those of Lesser Snow Goose nests (Table 1). Nest-bowl depth and nest inner diameter did not differ between species, probably because they are a function of female body size, egg size, and clutch size (all of which were accounted for by the correction factor). Despite differences in relative size of nests, nest mass did not differ between species, perhaps because nests were not dried, and small amounts of soil, pebbles, and old nest fragments could not be separated from nests. Outer diameter, wall thickness, circumference, rim height, and nest mass increased progressively across heath, mixed, and moss habitats, i.e. from more protected to less protected habitats. Bowl depth and inner diameter did not differ among habitats (Table 2).

Variation among habitats in Lesser Snow Geese.—The overall nest morphology of Lesser Snow Geese differed among habitats (MANCOVA, $F = 3.97$, $df = 21$ and 118 , $P = 0.0001$) but was unrelated to clutch volume ($F = 1.02$, $df = 7$ and 40 , $P = 0.43$). Outer diameter, wall thickness, circumference, rim height, and nest mass generally increased among heath, rock, mixed, and moss habitats, i.e. from more pro-

TABLE 1. Least-squares means ($\bar{x} \pm SE$) of nest dimensions and nest mass adjusted for clutch volume for Ross' Geese and Lesser Snow Geese nesting at Karrak Lake, 1994.

Measurement ^a	Ross' Goose (<i>n</i> = 54)	Lesser Snow Goose (<i>n</i> = 36)	<i>P</i> ^b
Outer diameter	0.0925 ± 0.0024	0.0838 ± 0.0031	0.031
Wall thickness	0.0347 ± 0.0012	0.0302 ± 0.0016	0.028
Circumference	0.0310 ± 0.0086	0.0265 ± 0.0110	0.002
Rim height	0.0127 ± 0.0006	0.0105 ± 0.0008	0.032
Bowl depth	0.0129 ± 0.0003	0.0120 ± 0.0004	0.072
Inner diameter	0.0287 ± 0.0005	0.0281 ± 0.0006	0.501
Nest mass	0.0030 ± 0.0002	0.0025 ± 0.0003	0.200

^a Measurements divided by the square root of clutch volume except for nest mass, which was divided by clutch volume.

^b ANOVA for species effect (*df* = 1 and 84 for each test).

tected to less protected habitats (Table 3). Nest bowls were shallowest in rock habitats and differed from those in heath, mixed, and moss habitats. As expected, the inner diameter of Lesser Snow Goose nests did not differ among habitats.

DISCUSSION

Thompson and Raveling (1987) suggested that predation interacts with body size in determining incubation constancy in geese, which in turn may be related to nest insulation. In areas with high rates of predation, the use of feathers in nests for insulation (Møller 1984) may be counteracted by selection for inconspicuous nests if feathers are not cryptic. We believe that concealment of eggs and nests of Ross' Geese and Lesser Snow Geese at Karrak Lake is not influenced by strong selective forces of predation. Ross' and Lesser Snow geese are non-cryptic, colonial, and nest in extremely dense numbers. Our claim is further supported by high nesting success (Slattery and Alisauskas 1992, 1993).

Like most waterfowl, Ross' and Lesser Snow geese line their nests with considerable amounts of down and cover their eggs before recessing from incubation. Down provides excellent insulation, and the amount of down in a nest may vary between species and among habitats. We did not quantify the amount of down or the specific composition of materials in each nest, but down may be particularly important for geese nesting in habitats where nesting materials are scarce. Different types of nesting materials (e.g. heath and moss) may differ in their insulative properties. Although we did not identify nest materials specifically, nest materials are related to the distribution of materials in a given habitat type, i.e. Ross' and Lesser Snow geese do not use different materials within a habitat (pers. obs.). Consequently, inclusion of the habitat effect in our analyses should account for variation in the insulative properties of different nest materials.

Nest morphology and habitat variation.—Ryder (1964, 1967, 1972) found that Ross' Goose nests were largest in moss habitats, intermediate in mixed habitats, and smallest in rock habitats.

TABLE 2. Least-squares means ($\bar{x} \pm SE$) of nest dimensions and nest mass adjusted for clutch volume for Ross' Goose and Lesser Snow Goose nests combined by habitat at Karrak Lake, 1994.

Measurement ^a	Nesting habitat			<i>P</i> ^b
	Heath (<i>n</i> = 18)	Mixed (<i>n</i> = 43)	Moss (<i>n</i> = 29)	
Outer diameter	0.0664 ± 0.0041 ^A	0.0948 ± 0.0025 ^B	0.1032 ± 0.0034 ^B	0.0001
Wall thickness	0.0218 ± 0.0021 ^A	0.0356 ± 0.0013 ^B	0.0399 ± 0.0017 ^B	0.0001
Circumference	0.2252 ± 0.0145 ^A	0.3006 ± 0.0092 ^B	0.3376 ± 0.0121 ^C	0.0001
Rim height	0.0086 ± 0.0011 ^A	0.0130 ± 0.0007 ^B	0.0133 ± 0.0009 ^B	0.001
Bowl depth	0.0121 ± 0.0005	0.0124 ± 0.0003	0.0127 ± 0.0004	0.727
Inner diameter	0.0287 ± 0.0008	0.0276 ± 0.0005	0.0289 ± 0.0007	0.274
Nest mass	0.0019 ± 0.0004 ^A	0.0025 ± 0.0002 ^A	0.0038 ± 0.0004 ^B	0.002

^a Measurements divided by the square root of clutch volume except for nest mass, which was divided by clutch volume.

^b ANOVA for habitat effect (*df* = 2 and 84 for each test). Within rows, values with different superscripts are significantly different (*P* < 0.05) based on *t*-tests following a significant effect of habitat.

TABLE 3. Least-squares means ($\bar{x} \pm SE$) of nest dimensions and nest mass for Lesser Snow Goose nests by habitat at Karrak Lake, 1994.

Measurement ^a	Nesting habitat				P ^a
	Heath (n = 7)	Rock (n = 15)	Mixed (n = 20)	Moss (n = 9)	
Outer diameter	38.7 \pm 2.9 ^A	49.7 \pm 2.0 ^B	58.5 \pm 1.7 ^C	60.8 \pm 2.6 ^C	0.0001
Wall thickness	12.1 \pm 1.5 ^A	17.5 \pm 1.0 ^B	21.6 \pm 0.9 ^C	23.1 \pm 1.3 ^C	0.0001
Circumference	121.0 \pm 11.2 ^A	164.3 \pm 7.6 ^B	177.2 \pm 6.6 ^B	201.2 \pm 9.8 ^C	0.0001
Rim height	4.7 \pm 1.0 ^A	5.7 \pm 0.7 ^{A,B}	7.3 \pm 0.6 ^B	7.8 \pm 0.9 ^B	0.043
Bowl depth	7.4 \pm 0.4 ^A	6.2 \pm 0.3 ^B	7.6 \pm 0.3 ^A	7.7 \pm 0.4 ^A	0.003
Inner diameter	18.1 \pm 0.7	18.0 \pm 0.5	17.6 \pm 0.4	17.6 \pm 0.6	0.827
Nest mass	563.7 \pm 177.0 ^A	910.7 \pm 120.9 ^A	921.7 \pm 104.7 ^A	1,379 \pm 156.1 ^B	0.011

^a ANOVA for habitat effect (df = 3 and 47 for each test). Within rows, values with different superscripts are significantly different ($P < 0.05$) based on *t*-tests following a significant effect of habitat.

He suggested that these differences resulted from differences in availability of nest material and exposure to weather. Our data for Ross' and Lesser Snow geese clearly are consistent with Ryder's observations. We also concur with his interpretation of the adaptive significance of variation in nest size among habitats. Nest materials are abundant in heath, mixed, and moss habitats (Ryder 1967, pers. obs.), but rock habitats typically possess little nesting material other than small twigs and gravel. Nests built in heath typically are sheltered by low (1 to 6 cm) vegetation that could decrease convective heat loss from nests. Nests built in mixed habitats often are constructed of vegetation or in rocks that may provide sheltering effects. Nests built in open moss appear to be the least sheltered. Although nests in rock typically occur in unvegetated sites where exposure is greatest, we suspect that placement of nests within crevices or in the lee of large rocks can dramatically decrease exposure and convective heat loss.

The outer nest dimensions, including outer diameter, wall thickness, circumference, and rim height, provide the best estimates of the size of the nest wall. These measurements should be a direct reflection of nest insulation according to the heat-flow equation. These measurements differed significantly among habitats and generally increased across heath, rock, mixed, and moss habitats. Inner nest measurements also should influence nest insulation, but should conform more closely to female body shape, egg size, and clutch size than to habitat. Inner diameter did not differ among habitats. Bowl depth did not vary among habitats except in rock, where it was smallest; the impenetrability of rock and gravel substrates probably explains this finding.

Competition.—Competition for high-quality nest sites and nest materials may influence nest-site selection such that access to the best sites varies among geese at both the macrohabitat and microhabitat levels. This, in turn, may influence nest size and nest success. In rock and other habitats where nest materials are limited, all available nest materials are incorporated into nests (Afton unpubl. data). Moreover, we have observed geese fighting (within and between species) over nest materials during the prelaying and early laying periods. In light of exponential population growth and habitat degradation at Karrak Lake and elsewhere (Slattery et al. 1994, Batt 1997), some geese may be nesting in poorer habitat with the net effect that global nest success may have declined from previous years when nest densities were lower.

Macrohabitat and microhabitat selection.—Macrohabitat selection probably is a function of habitat availability during nest initiation and exposure to weather caused by habitat topography. Ryder (1967, 1972) found that Ross' Goose nest densities were highest in mixed and heath habitats and lowest in the more exposed rock and moss habitats. McLandress (1983) demonstrated that Lesser Snow Geese show a marked preference for rock habitats. This may be because rock habitats are usually the first to clear of snow and dry out each spring, and Lesser Snow Geese typically initiate nesting earlier than Ross' Geese at Karrak Lake (Slattery and Alisauskas 1993). We found no Ross' Goose nests in rock habitats or on the uppermost parts of eskers, although Lesser Snow Geese were commonly found nesting in such locations. We argue that Ross' Geese do not occupy such habitats because of their smaller

body size, higher mass-specific metabolic rate, lower incubation constancy, and smaller egg and clutch size. Furthermore, Ross' Geese probably incur energetic advantages by initiating nests a few days after snow has cleared from the more sheltered heath and mixed habitats. Because of their larger body size, Lesser Snow Geese probably are better able to tolerate conditions in the more exposed rock habitats. Consequently, they tend to nest in rock habitats out of proportion to its availability.

Microhabitat nest-site selection probably occurs after geese have set up territories. Within a territory, there is considerable variation among possible nest sites, and females sometimes exhibit nest-building behavior in several locations within the territory prior to laying the first egg (Afton unpubl. data). A small dwarf birch, patch of Labrador tea, or pile of small boulders, less than a meter in diameter, may yield a nest site that provides excellent protection from wind, whereas an adjacent area of bare ground may offer little protection from the wind. Small-scale factors such as proximity to adjacent territory holders may influence nest-site selection further.

Nest morphology and variation between species.—Ross' Geese are about two-thirds the mass of Lesser Snow Geese and exhibit a mass-specific basal metabolic rate that is $1.18 \text{ kcal} \cdot \text{day}^{-1} \cdot \text{g}^{-1}$ higher than that of Lesser Snow Geese (Aschoff and Pohl 1970, Alisauskas and Ankney 1992). Female Ross' and Lesser Snow Geese exhibit high incubation constancy throughout the 23-day incubation period and rely heavily upon endogenous nutrients for both egg laying and incubation (Ryder 1967, 1970, Ankney and MacInnes 1978, Afton and Paulus 1992, Alisauskas and Ankney 1992). However, Ross' Geese have slightly lower incubation constancy than Lesser Snow Geese (Krechmar and Syroechkovsky 1978, Afton and Paulus 1992, LeSchack et al. 1998) and spend more time foraging during incubation (Afton unpubl. data). When corrected for clutch volume (which is a function of body size, egg size, and clutch size), nests of Ross' Geese are larger than nests of Lesser Snow Geese. These results probably reflect greater selection for efficient nest insulation by Ross' Geese because of their smaller body size (adults and embryos), greater mass-specific metabolic rate, and

lower incubation constancy relative to Lesser Snow Geese.

By constructing relatively larger and probably better-insulated nests, female Ross' Geese can minimize energy expenditure during incubation and embryonic cooling during recesses. Slattery and Alisauskas (1995) found that neonate Ross' Geese hatch with more functionally mature gizzards and more protein for their size than did Lesser Snow Geese. In addition, Ross' Goose broods disperse farther from nesting areas than do Lesser Snow Goose broods (Slattery 1994). Moreover, Ross' Goose goslings fledge two weeks earlier than Lesser Snow Goose goslings (Owen 1980). The relatively larger size and greater insulation of Ross' Goose nests probably buffer developing embryos against fluctuations in ambient temperatures, hasten embryonic development, and ultimately promote a greater propensity for activity during the brood-rearing period (Slattery and Alisauskas 1995).

In light of the physiological differences between Ross' Geese and Lesser Snow Geese, we suggest that overall fitness consequences are associated with nest construction and selection of nesting habitat in arctic-nesting geese. We hope that this paper will inspire more comprehensive studies of fitness consequences resulting from nest morphology and site selection. Experiments involving manipulation of nest materials (particularly down) coupled with measurements of incubation temperatures and hatchling body condition would be particularly informative.

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APPENDIX 1. Nest dimensions (cm) and nest mass (g) for Ross' Goose nests by habitat at Karrak Lake, 1994. Values are $\bar{x} \pm SE$, with range in parentheses.

Measurement	Heath (n = 11)	Mixed (n = 23)	Moss (n = 20)
Outer diameter	37.6 ± 2.8 (27-52)	51.6 ± 1.0 (36-59)	55.4 ± 1.4 (43-66)
Wall thickness	12.7 ± 1.4 (7-19)	19.7 ± 0.5 (13-24)	21.7 ± 0.8 (16-28)
Circumference	133.4 ± 9.5 (94-180)	171.5 ± 4.3 (120-222)	179.8 ± 4.1 (146-206)
Rim height	5.2 ± 0.6 (1-8)	7.6 ± 0.4 (4-10)	7.2 ± 0.4 (3-10)
Bowl depth	6.5 ± 0.2 (6-8)	7.0 ± 0.2 (6-10)	6.7 ± 0.2 (5-8)
Inner diameter	15.2 ± 0.4 (13-18)	14.7 ± 0.3 (12-19)	15.1 ± 0.4 (12-18)
Nest mass	585.0 ± 92.3 (218-1,050)	755.1 ± 66.3 (262-1,642)	935.9 ± 100.3 (295-1,790)

APPENDIX 2. Nest dimensions (cm) and nest mass (g) for Lesser Snow Goose nests by habitat at Karrak Lake, 1994. Values are $\bar{x} \pm SE$, with range in parentheses.

Measurement	Heath ($n = 7$)	Rock ($n = 15$)	Mixed ($n = 20$)	Moss ($n = 9$)
Outer diameter	38.7 \pm 2.3 (30-47)	49.7 \pm 1.6 (41-64)	58.5 \pm 1.9 (40-75)	60.8 \pm 2.9 (48-70)
Wall thickness	12.1 \pm 1.4 (9-20)	17.5 \pm 0.7 (13-21)	21.6 \pm 1.0 (10-28)	23.1 \pm 1.4 (15-28)
Circumference	121.0 \pm 10.0 (62-136)	164.3 \pm 5.5 (130-200)	177.2 \pm 8.0 (111-221)	201.2 \pm 9.3 (151-238)
Rim height	4.7 \pm 1.1 (2-9)	5.7 \pm 0.6 (3-10)	7.3 \pm 0.3 (3-14)	7.8 \pm 0.7 (5-11)
Bowl depth	7.4 \pm 0.4 (6-9)	6.2 \pm 0.2 (5-7)	7.6 \pm 0.3 (5-10)	7.7 \pm 0.4 (6-10)
Inner diameter	18.1 \pm 0.5 (17-20)	18.0 \pm 0.6 (15-23)	17.6 \pm 0.4 (14-21)	17.6 \pm 0.7 (15-21)
Nest mass ^a	561.0 \pm 103.7 (404-951)	1,002 \pm 181.0 (324-1,606)	919.9 \pm 104.0 (340-1,944)	1,378 \pm 216.1 (662-2,558)

^a Heath, $n = 5$; Rock, $n = 8$; Mixed, $n = 19$; Moss, $n = 9$.