Nest insulation and incubation constancy of arctic geese

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Introduction

Proper and timely development of avian embryos depends upon maintenance of incubation temperatures within relatively narrow limits (e.g. Lundy 1969; Drent 1975). For many birds, especially species nesting in cold environments, insulation of nests conserves heat transferred to eggs and minimises the cost of incubation to parent birds. Various species of birds nesting at high elevations or latitudes have bulkier or better insulated nests than close relatives nesting at lower elevations or latitudes (Pearson 1953; Corley Smith 1969; Collias and Collias 1971; Møller 1984). Furthermore, the amount of nest insulation may be negatively correlated with nest attentiveness (White and Kinney 1974).

In many species, the incubating bird leaves the nest for a period (a recess) to obtain food and/or engage in other maintenance activities. Nest insulation can reduce the rate of heat loss from eggs and thereby increase the length of recess without causing harm to embryos, and minimise the time and energy expended to rewarm the eggs. Species with single-sex incubation tend to have large, well insulated nests compared with species in which both sexes incubate on a rotational basis (O'Conner 1978). It may therefore be expected that variation in the insulation of nests among similar species in a given environment may be related to differences in incubation rhythms. Conversely, predation may limit nest insulation by selecting for cryptic nests as better insulated nests may be more conspicuous (Møller 1984).

In geese (Anserini), only females incubate. Nests are constructed in shallow depressions on the ground which are usually lined with dry vegetation collected from the area immediately around the nest (Owen 1980). Finally, the nest is lined with down and a few contour feathers from the breast of the female. When leaving the nest, geese cover their eggs with a blanket of material pulled from the lining of the nest.

Female geese rely heavily on endogenous reserves to sustain incubation (e.g. Ankney and MacInnes 1978; Raveling 1979a, b) and are extremely attentive to their nests (Cooper 1978; Aldrich and Raveling 1983; Thompson and Raveling 1987). There is, however, considerable variation in patterns of incubation. For example, Emperor Geese *Anser canagicus*, Cackling Canada Geese *Branta canadensis minima* and Black Brant *B. bernicla nigricans* all nest on the Yukon-Kuskokwim Delta of Alaska, but exhibit a two-fold difference in recess lengths and a thirteen-fold difference in recess frequencies, resulting in a twenty-fold difference in daily recess time between the least and most attentive species (Table 1). These differences are thought to be primarily related to the abilities of the different-sized goose species to repel different types of predators (Thompson and Raveling 1987).

There are evident differences in nest structure among Emperor Geese, Cackling Geese and Brant (Figure 1). Brant nests

Table 1. Nest attentiveness of Emperor Geese, Cackling Canada Geese and Black Brant, from, respectively, Thompson and Raveling (1978), Aldrich (1983) and Thompson (unpubl.).

Species	N	Total % time incubating (range)	Modal recess length (min)	Mean recess length (min)	Mean recesses per day	Mean recess time/d (min)
Emperor Goose	11	99.5 (99.1 – 99.7)	8	13	0.5	7
Cacking Canada Goose	12	93.6 (89.1 – 96.6)	15	26*	3.5*	92
Black Brant	4	89.6 (87.3 – 94.9)	22	22	6.7	148

*Derived from published regression.

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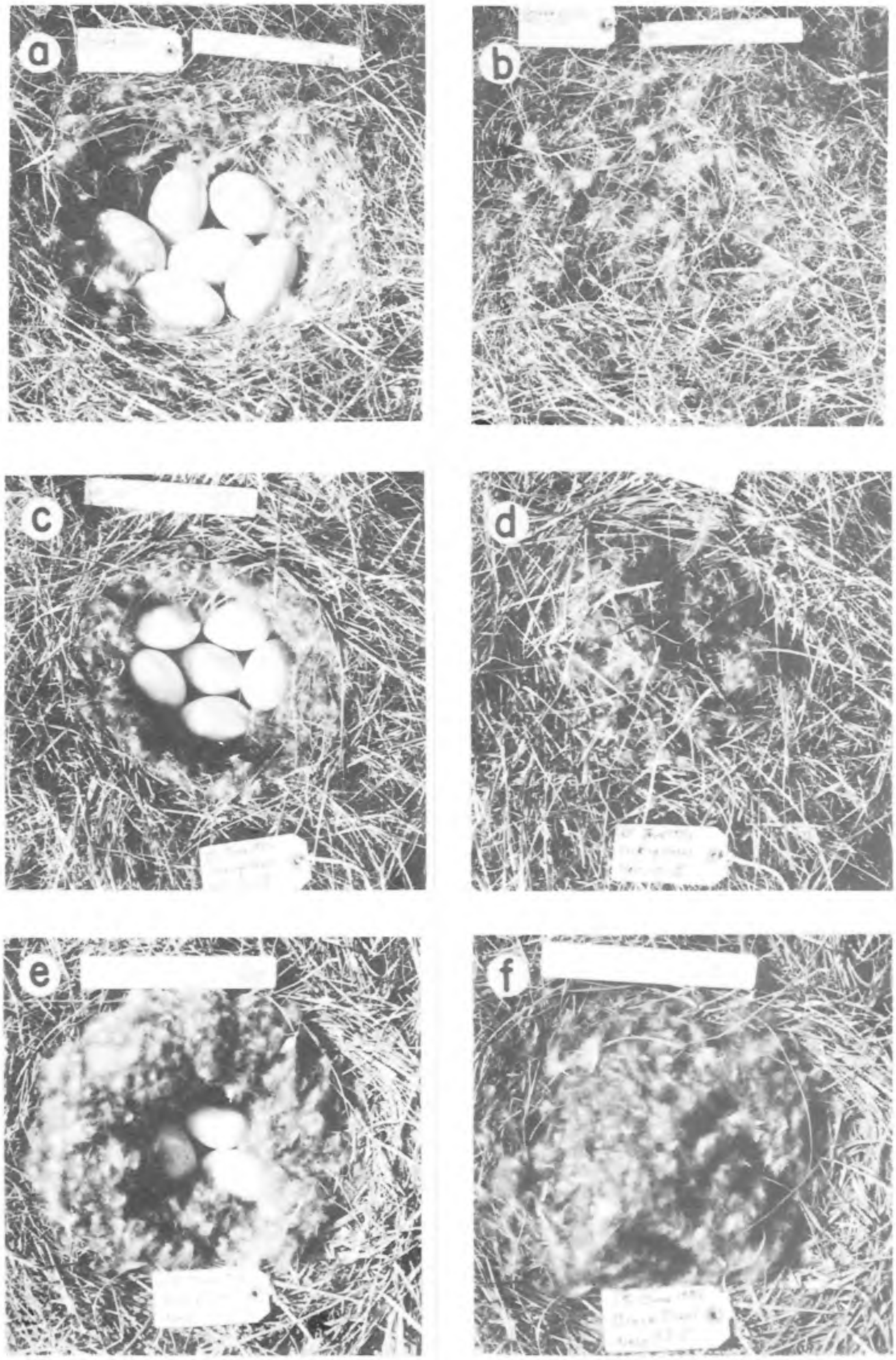

Figure 1. Typical natural nests illustrating eggs exposed and covered of Emperor Goose (a,b), Cackling Goose (c,d) and Brant (e,f).

contain by far the greatest quantities of down and feathers, whereas Emperor Goose nests contain the least amounts; the intermediate amounts in Cackling Geese nests differ more from Brant than from Emperor Geese.

The purpose of this study was to compare differences in nest insulation quality of the three species by measuring the cooling rates of eggs in their nests, and to relate those differences to the incubation constancy of each species. The possible role of predation as an agent selecting for differences in conspicuousness and vulnerability of the nests was also considered.

Methods

Six nests each of Emperor Geese, Cackling Geese and Black Brant were collected, at Kokechik Bay on the Yukon-Kuskokwim Delta, Alaska, after depredation late in incubation or after hatch, to be certain that little or no more material would have been added. Only nests judged to be relatively undisturbed by wind or predators were taken, and returned to the University of California, Davis (UCD), where they were weighed to the nearest gram on an electric balance.

Eggs from the three goose species were emptied and then refilled with paraffin. This gave eggs with heating and cooling properties similar to those of natural eggs (Schwartz *et al.* 1977), but approximately 15% less in mass. The paraffin tended to expand upon heating and crack the shells of eggs. Despite this problem, eggs retained their original mass and shape and provided valid results for the comparative purposes of this study. Clutches were assembled of 6 eggs of Emperor Geese, 5 of Cackling Geese, and 4 of Brant. These were typical of natural clutches and eggs (Table 2).

Thermistor probes (YSI model 400) were implanted in 3 eggs of each clutch by drilling a hole down the long axis to the centre of each egg, inserting the probe, and sealing it in place with melted paraffin.

Experiments were conducted in a coldroom at approximately 6°C, providing ambient thermal conditions typical of those at Kokechik Bay (Eisenhauer and Kirkpatrick 1977). Each nest was arranged in a 5 cm deep depression in moist sand of the approximate natural dimensions reported by Mickelson (1975). Although the sand was different from the material available to geese on the Delta, it provided a standardised substrate.

Clutches were heated in a drying oven at approximately 40°C until internal egg temperatures reached approximately 38°C, close to natural incubation temperatures (Drent 1975). The clutch was then immediately placed in a nest and covered with the nest lining from the edges of the nest bowl. Cooling of eggs was then monitored for 30 minutes using strip chart recorders connected to the thermistors. Air temperature in the coldroom was simultaneously measured by a probe placed 10 cm from the edge of the nest. Individual eggs of each species were placed in approximately the same positions (Figure 2) in all tests to minimise the effect of differences among eggs. These positions simulated those in natural nests. Each of the 6 nests of each species was tested to discern the effects of nest insulation relative to the combined effect on cooling of different clutch and egg sizes. Thus, each Emperor Goose nest was tested containing, in random order, the clutches of Emperor Goose eggs, Cackling Goose eggs, and Brant eggs. Each nest-egg combination was tested in "calm" air (no wind speed detectable with a Dwyer anemometer) and with a 10 km/h air flow over the nest ("windy"). This was provided by

Table 2. Sizes and masses of praffin-filled eggs in experimental clutches.

	All eggs				Thermistor-probed eggs			
Species	n	Mean egg mass (g)	Mean egg length (mm)	Mean egg width (mm)	n	Mean egg mass (g)*	Mean egg length (mm)	Mean egg width (mm)
Emperor Goose	6	103	81	52	3	102	81	52
Cackling Goose	5	86	75	50	3	86	76	50
Black Brant	4	75	71	48	3	75	70	48

*Before insertion of thermistor probes.

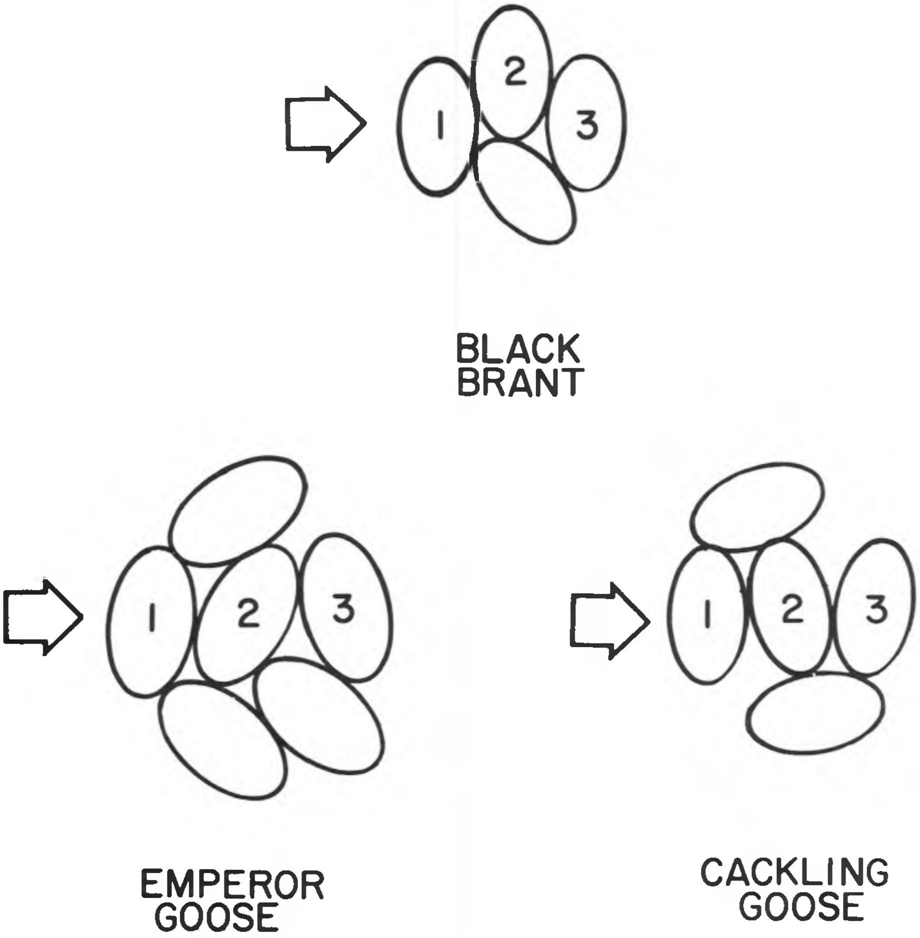

Figure 2. Arrangements of paraffin-filled eggs of Emperor Geese, Cackling Geese and Brant in experimental nests. Numbered eggs are those with thermistors. Arrows indicate direction of air flow over nests under windy conditions.

a standard household box fan placed 50 cm from the nest edge. Each nest was left empty of eggs for at least an hour between tests, adequate for nest and substrate to return to the ambient temperature.

Differences among values of initial egg temperatures, egg cooling, coldroom temperatures and nest masses were investigated by Analysis of Variation (ANOVA), and significance of differences between means tested by the T-method.

Results

The mean mass ($\bar{x}$±s.e.) of Black Brant nests (38.3±2.7 g) was significantly less than that of either Emperor Goose (243.2±24.3 g) or Cackling Goose nests (193.2±42.0 g) ($P<0.001$), but differences in mass between the nests of the latter two species were not significant ($P>0.05$). The differences in mass were primarily due to the varying amounts of vegetation present (Figure 1).

Mean coldroom temperature during tests was 6.41±0.04°C and did not vary significantly during tests of nest, egg or wind type. Average initial temperature of eggs was 38.7±0.1°C, and slight variations during tests for nest, egg or wind type or egg positions were not significant.

ANOVA showed that relative differences among nest types were the same regardless of the species of eggs they contained (Table 3). Variation in cooling of

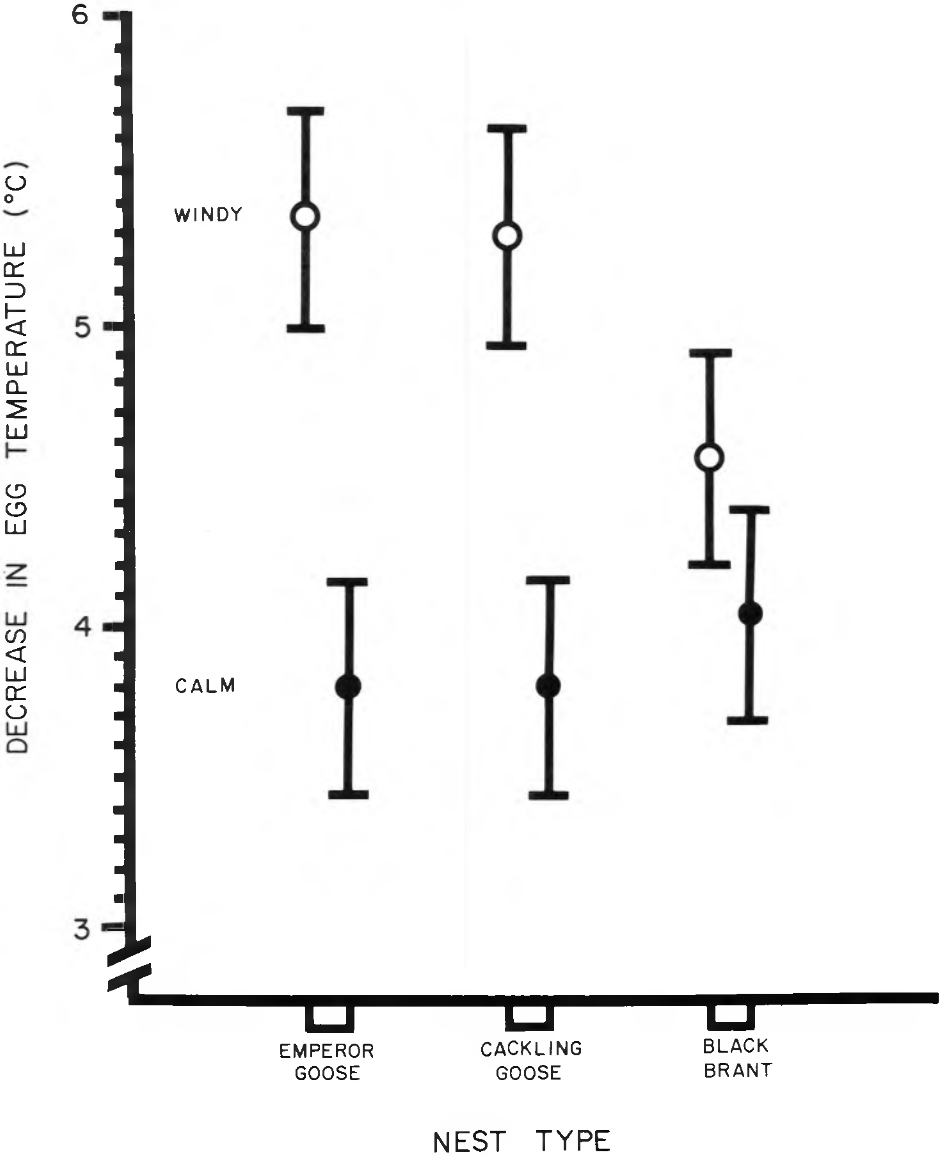

Figure 3. Combined average decrease in temperature of eggs of all species in the nests of Emperor Geese, Cackling Geese and Brant under windy (open circles) and calm (closed circles) conditions. Bars represent 95% confidence intervals based on pooled standard deviations (N = 324 for all tests).

eggs (all species therefore combined) among nest types over the 30 minute test intervals was significant when compared between wind types (Table 3). The difference in average temperature decline between windy and calm conditions was approximately three times as great in Emperor Goose and Cackling Goose nests as that in Brant nests (Figure 3).

ANOVA showed that nest types and wind conditions did not significantly influence relationships among species of egg (Table 3). Emperor Goose eggs cooled significantly less (4.09±0.14°C) than the eggs of either Cackling Geese (4.54±0.13°C) or Brant (4.84±0.13°C) ($P<0.001$). There was no significant difference in cooling between the eggs of Cackling Geese and Brant.

Cooling of eggs in different positions in

Table 3. ANOVA table for main factors and factor interactions in cooling of eggs involving nests of different species ("Nest") and eggs of different species ("Eggs") of Emperor Geese, Cackling Geese and Black Brant, windy and calm conditions ("Wind"), and different relative positions of eggs in nests ("Position") (see Figure 1 and methods).

Factor	n*	df	F	P
Nest	108	2	0.65	>0.5
Nest × Egg	36	4	0.90	>0.1
Nest × Wind	54	2	7.44	<0.01
Nest × Position	36	4	1.33	>0.1
Egg	108	2	12.39	<0.01
Egg × Wind	54	2	0.33	>0.5
Egg × Position	36	4	1.58	>0.1
Wind	162	1	90.26	<0.01
Wind × Position	54	2	23.90	<0.01
Position	108	2	22.63	<0.01

*Number of individual egg temperature measurements comprising each compared mean.

nests varied similarly regardless of species of eggs or nest (Table 3). Eggs in the windward (No. 1) position (see Figure 2) cooled on average approximately 1.5°C more than eggs in the other two positions (Figure 4). There were no significant differences in cooling in the different positions under calm conditions.

Discussion

Nest insulation

The observation that eggs under windy conditions cooled approximately 15% less in the nests of Brant than those in the other nests (Figure 3) at least partially supports the hypothesis that differences in incubation constancy are reflected in the insulative characteristics of their nests. Brant are by far the least attentive geese. The fact that there were no significant differences among nests under calm conditions does not necessarily refute the hypothesis because calm conditions are rare on the Alaska breeding grounds (personal observations over 13 years). Indeed, wind speeds often exceeded that used in the experiments. Convective heat loss is apparently a large factor contributing to the cooling, as evidenced by the difference between windy and calm conditions, especially of those eggs on the windward side of a nest.

Egg-covering behaviour when leaving their nests is prevalent in waterfowl and reduces heat loss from eggs (Caldwell and Cornwall 1975; Cooper 1978). The presence of down (abundant in Brant nests) is especially important because of its ability to "loft", creating spaces of still air that resist convective heat loss (Wainwright *et al.* 1976; Hansell 1984; Collias 1986). In swan species, where the sexes share incubation, the eggs are only briefly exposed. They tend to have little down in their nests (Howey *et al.* 1984; personal observations of *Cygnus columbianus*).

The apparent lack of difference in insulative quality between nests of Cackling Geese and Emperor Geese, despite the large differences in incubation constancy (Table 1), does not support the hypothesis. Other selection factors that affect nest insulation must therefore be considered.

Predation

Parasitic Jaegers *Stercorarius parasiticus* and Glaucous Gulls *Larus hyperboreus* are ever-present threats to unattended eggs on the Delta. The nest material covering eggs while female geese are away may camouflage them from such visually searching predators (Broekhuysen and Frost 1968; Cooper 1978). The effectiveness of camouflage, however, is probably related to the amount and colour of feathers incorporated into the nest (Møller 1984). The downs of Emperor Geese (light grey), Cackling Geese (dark grey) and Brant (dark grey) differ considerably from the adjacent vegetation.

Selection for nest crypticity should be least in the Brant. They nest colonially and the high concentration of nesting birds

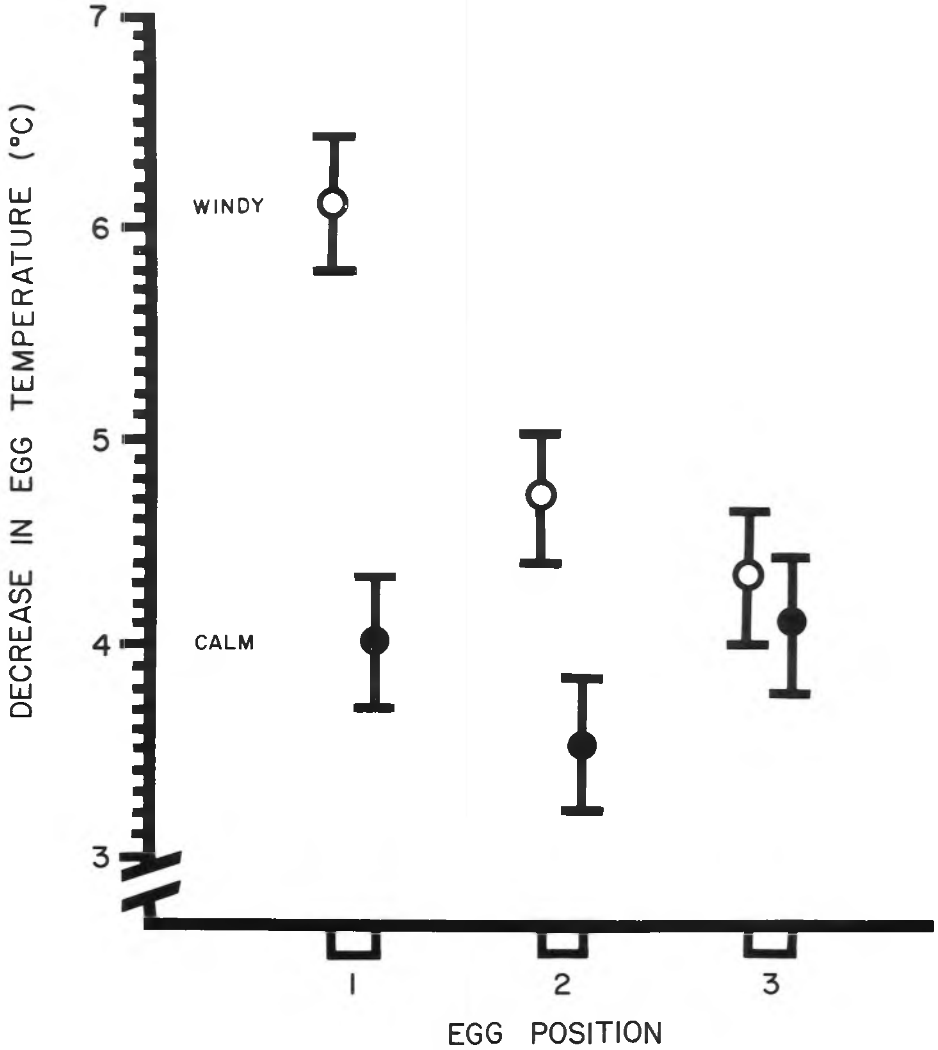

Figure 4. Combined average decrease in temperature of eggs of all species (Emperor Goose, Cackling Goose and Brant) in different positions in nests (see Figure 2) of all species under windy (open circles) and calm (closed circles) conditions. Bars represent 95% confidence intervals based on pooled standard deviations (N = 324 for all tests).

would inhibit predation through group defence (e.g. Wittenberger and Hunt 1985). Male Brant and Cackling Geese remain near their nests while the females are away (Eisenhauer 1977; Aldrich 1983). The flying agility of these small goose species also assists in deterring avian predators. In contrast, male Emperor Geese spend little time near their mate's nest and are relatively inefficient at deterring avian predators (Thompson and Raveling 1987). The nearly continuous incubation by female Emperor Geese is their primary defence against predation.

In contrast to the colonial Brant, both other species are dispersed nesters and thus may benefit more by concealing their nests. The greater amount of vegetation interspersed with less down, makes their nests less conspicuous, at least to humans, than those of Brant (Figure 1).

Egg size and number

As larger and/or more numerous eggs cool more slowly, their requirements for insulation are reduced. But these factors were only significant for the comparison of Emperor Goose eggs with those of Cackling Geese and Brant, and not between the latter two species. The dummy eggs used in this experiment had no internal heat source whereas natural eggs contain developing embryos which produce heat and, therefore, influence their cooling rates (White and Kinney 1974). Larger embryos produce more heat (Drent 1970). The average amount of recess by Emperor Geese, however, was only 8% and 4% as much as Cackling Geese and Brant, respectively, whereas the cooling of Emperor Goose eggs, although significantly less, was still 90% and 85% that of Cackling Geese and Brant, respectively. Overall, therefore, it seems unlikely that the small differences in egg cooling due to different egg sizes and numbers were an important factor in nest insulation.

Conservation of body heat

A nest can also reduce heat loss directly from an incubating parent's body (Calder 1973; Walsberg and King 1978a, b). Thus, small birds, because of their higher relative metabolic demands, appear to have better insulated nests than larger birds (Møller 1984). This relationship is unlikely to be a significant factor among the much larger geese that appear to have only a small portion of their surface enclosed by the nest. Rewarming eggs represents a larger relative decrement to the energy balance of the smaller geese. But, here again, energy expended rewarming eggs is more directly related to the amounts of time spent off the nest than to metabolic differences related to body size.

Conclusion

Differences in insulative efficiency among goose nests are primarily the result of conflicting selective forces. The need to minimise egg cooling selects for abundant insulation and is inversely related to the constancy of incubation. On the other hand, the threat of avian predation limits the amount of feathers by selecting for cryptic nests, and is also related to the nesting pattern (colonial vs dispersed) and defence capabilities of different species.

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Summary

Nest structure and the average proportion of time spent on nests by incubating geese on the Yukon-Kuskokwim Delta, Alaska, varies as follows: Black Brant *Branta bernicla nigricans* – profuse down and feathers with little vegetation, and 89.9% attentive; Cackling Canada Geese *B. canadensis minima* – abundant down mixed with vegetation, and 93.6% attentive; Emperor Goose *Anser canagicus* – sparse down and mostly vegetation, and 99.5% attentive.

The cooling of eggs in the nests of these species under "calm" and "windy" conditions was monitored in a coldroom. Eggs in Brant nests under windy conditions cooled significantly less than those in Emperor or Cackling Goose nests. The larger and more numerous eggs of Emperor Geese cooled significantly less, but this is of lesser importance than incubation constancy. The amount of insulation in a goose nest seems primarily the result of counteracting selection between the degree of egg cooling associated with incubation constancy, and the minimisation of avian predation on eggs through nest crypticity. The colonial nesting of Brant and attendance by males provide additional defence against avian egg predators.

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