INCUBATION BEHAVIOR OF EMPEROR GEESE COMPARED WITH OTHER GEESE: INTERACTIONS OF PREDATION, BODY SIZE, AND ENERGETICS

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ABSTRACT.—The incubation constancy of 11 female Emperor Geese (*Chen canagica*) was monitored electronically and behavior of both sexes was observed during incubation recesses in 1983 and 1984 at Kokechik Bay, Alaska. Average nest attentiveness of female Emperor Geese was 99.5% during 4,800 h of monitored incubation time. Recesses averaged (±SE) 13.3 ± 0.8 min, and modal recess length was 8 min (n = 107). Recess frequency was 0.54/day. This high degree of nest attentiveness exceeded that reported for any goose species. Nest attentiveness did not vary significantly through the incubation period, but increased in the last 3 days, probably in response to embryo noises and pipping. Most recesses (45%) occurred between 1200 and 1800, the warmest portion of the day. There were no significant differences in recess length at different times of day, however, and recess duration and frequency were not related to differences in daily temperature or wind speed. Females fed for only 14% of the time during their infrequent and brief recesses. Most time (43%) during recesses was spent preening and bathing. Males were alert for 49% of the time females were on recess but were present during only 56% of recesses, reflecting their relative lack of attendance during incubation. Behavior of females during recesses when males were absent did not differ significantly from when males were present.

The high incubation constancy, loss of body mass during incubation (20.7%), and relatively large average clutch size (5.2) indicate that Emperor Geese arrive on nesting grounds with an extremely high level of endogenous reserves relative to other geese. Clutch size and incubation behavior also represent trade-offs in energy investment related to body size, egg size, food availability, and feeding needs during incubation. Generally, larger species or subspecies of geese depend more on endogenous reserves than do smaller forms. We believe, however, that this relationship is not satisfactorily explained just by energetic constraints related to body size because Emperor Geese were more attentive to incubation than even larger goose species. Emperor Geese usually can defend their nests from arctic foxes (*Alopex lagopus*) but, when on incubation recesses, are apparently less efficient in defense against avian predators than sympatric-nesting smaller geese. These smaller species are more vulnerable to foxes but more agile and effective against avian predators. The incubation constancy of geese results from an interaction of predation pressures related to body size and defense capabilities. *Received 28 July 1986, accepted 18 May 1987.*

ONLY female geese incubate, relying heavily on body reserves for the energy and materials needed for clutch formation and incubation (Ankney and MacInnes 1978; Raveling 1979a, b). The level of reserves that remain after egg laying determines how a female goose will allot time between nest attentiveness and incubation breaks for feeding. Geese that are least attentive to nests lose the most eggs to predators (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977). Males play an important role in the detection and deterrence of predators (Ankney 1977, Raveling 1979a, Fox and Madsen 1981, Raveling 1981, Aldrich 1983). Therefore, the incubation behavior of a species should be strongly affected by variables such as food availability and quality, body size, predation pressure, and behavior of the male.

The average incubation constancy of geese ranges from 89.6% to 93.6% for the small Black Brant (*Branta bernicla nigricans*; Thompson unpubl. rept.) and Cackling Canada Goose (*B. canadensis minima*; Aldrich 1983) and from 97.5% to 98.5% in the larger Giant and Western Canada geese (*B. c. maxima*, Cooper 1978; *B. c. moffitti*, Aldrich and Raveling 1983). These results suggest that incubation constancy is related to body size (see also Afton 1979, 1980). We selected the intermediate-size Emperor Goose (*Chen canagica*) to study incubation behavior to provide additional comparative data for geese on nest attendance patterns in relation to body size, loss of mass during incubation, and nesting success.

METHODS

Data were collected during May and June 1983–1984 at Kokechik Bay (61°40'N, 166°0'W) on the Yukon-Kuskokwim (Y-K) Delta of Alaska (see Eisenhauer and Kirkpatrick 1977 for a description of the area).

Nest attendance.—The incubation constancy of female Emperor Geese was monitored with spring-loaded activity platforms (Cooper 1978). Sod blocks containing the nest bowls were excavated and placed on top of the platforms. Enough soil was removed from the excavation to leave nests at their original heights when platforms and nests were replaced. The presence or absence of incubating birds was sensed by electrical microswitches affixed to the platforms and connected to Rustrak strip-chart recorders driven by 12-v automotive batteries. Activity platforms were placed under 11 Emperor Goose nests beginning with days 3–9 of incubation. Platforms and recorders were inspected every 3–7 days to ensure proper operation. These inspections were made in the late evening (2200–2400) when most birds would have finished any recess activity for the day (see Results). The time spent by investigators at the nests was usually less than 5 min. The times spent off the nest by birds during these inspections or any other known disturbances caused by humans were excluded from attendance analyses except when investigating the effect of these disruptions on incubation behavior.

Behavior observations.—Emperor Geese were observed during incubation recesses with a 20–60× telescope or 9× binoculars from two, 4-m-tall towers. Nests and pairs observed were located 100–400 m from the towers. As soon as a female on recess was observed, her behavior and that of her attending male, if present, were point sampled (Altmann 1974) at 10-s intervals throughout the recess. The location of the maximum distance the female traveled from her nest during each recess was marked on an aerial photograph. After hatch, the distances from the nest to these points were measured to the nearest 5 m.

Weather observations.—Ambient temperature was monitored in 1984 with a continuously recording pen thermograph housed in a ventilated white box and placed near camp at the approximate elevation of most nests. Wind speed and direction data for 1984 were obtained from National Oceanographic and Atmospheric Administration weather observations on the coast approximately 10 km northwest of the study area. These wind data would not correspond exactly to conditions on the study area but were assumed to provide reasonable indices to test for correlations with incubation behavior.

Statistics.—Friedman's two-way ANOVA by ranks was used to compare total recess time per day for each female among 6 portions of monitored incubation periods (days 3–7, 8–11, 12–15, 16–19, 20–22, and 23–25). Chi-square tests were used to test for differences in recess frequency between halves of incubation. Differences in recess length among times of day were tested using one-way ANOVA. Two-sample t-tests were used to test for differences in maximum distance traveled from the nest by females on recesses when males were present and when males were absent. Differences in behavior between sexes and between recesses with males present or absent were compared with Mann-Whitney U-tests. Spearman ranked correlations were used to test for relationships between recess length and weather. Regressions were computed with the Minitab computer package, Pennsylvania State University. Values are reported ±SE.

RESULTS

Effects of research disturbance.—Periodic disturbances of monitored geese to maintain equipment did not appear to modify their behavior. The average total recess time on the day after a disturbance (7.7 ± 1.6 min, $n = 57$) was not significantly different from that of any other day (6.6 ± 0.8 min, $n = 143$, $P > 0.5$). The day following a disturbance was used for analysis because equipment was inspected in the late evening of the preceding day. The regression of total percentage of nest attendance for each bird considering only spontaneous recesses vs. total time off the nest because of researcher disturbance was not significant ($y = 99.6 - 0.00045x$, $r^2 = 1.5$, $P > 0.5$, $n = 11$), indicating that human-induced inattentiveness neither substituted for nor caused more spontaneous recess time.

Nest attentiveness.—Mean attentiveness to the nest for 11 females was $99.5 \pm 0.1\%$ (range 99.1–99.7%) of their monitored incubation periods ($n = 4,800$ h monitored). Modal recess length was 8 min, and longer recesses occurred approximately 3.5 times more frequently than shorter recesses. Mean recess length was 13.3 ± 0.8 min for all 107 recesses (range 2–46 min). Mean recess length of each of the 11 birds was 13.7 ± 1.8 min (range 8.6–29.1 min). Ninety-two percent of all recesses lasted 5–25 min. Recess frequency was 0.54/day of monitored time. Average recess frequency of all 11 birds was 0.54 ± 0.05 (range 0.37–0.80) per day.

The patterns of recesses varied among individual geese. One bird took no spontaneous recesses during the first 9 days it was monitored (days 4–12 of incubation), yet it eventually became the least attentive bird by taking much longer ($\bar{x}$ = 29.1 min) recesses than the mean (12.2 min) for the other 10 birds. Another bird was attentive continuously for the last 8 days of incubation. Incubation bouts averaged 37 h and lasted from 15 min to 9 days. Two hundred days of incubation were monitored in their entirety (0000-2400 h). No recesses occurred on 53% of these days, 42% had 1 recess, 4% had 2 recesses, and 1% had 3 recesses.

Recess length did not vary significantly with day of incubation ($y = 12.5 + 0.49x$, $r^2 = 0.1$, $P > 0.5$), but some individuals spent more time off their nests later in incubation. Significantly ($P < 0.05$) less time per day was spent off the nest in the last 3 days of incubation (days 23-25), however, than in all other portions except days 3-7, the earliest monitored period. All other differences among portions of incubation (see Methods) were not significant.

There was no significant difference in the proportion of days that contained no recesses in the first half (days 3-13, 50%, $n = 89$) and second half (days 14-25, 54%, $n = 111$) of incubation ($\chi^2 = 0.24$, $P > 0.5$), although 7.8% of all days in the second half contained more than one recess compared with 2.3% in the first half. The last 3 days of incubation (days 23-25, $n = 28$) had a significantly greater proportion of days without recesses (82%) than all other days (days 3-22, 52%, $n = 172$, $\chi^2 = 8.73$, $P < 0.005$). Even excluding these last 3 days, however, there was no significant difference in the proportion of continuously attentive days between the first half and the remaining days of the second half of incubation ($\chi^2 = 0.62$, $P > 0.1$).

Forty-five percent of recesses and 49% of recess time occurred between 1200 and 1800 (Fig. 1). Despite the correlation of recess frequency with time of day, differences in mean recess length among different periods of the day were not significant ($F = 0.95$, $P > 0.5$). There was no significant correlation between recess length and either wind speed ($r_s = 0.085$, $P > 0.5$) or ambient temperature ($r_s = 0.194$, $P > 0.5$) at the time of recesses during 1984. Recess frequencies were not related to differences in mean ambient temperature (t) or mean wind speed (w) among days ($y = 0.246 + 0.0319t + 0.0191w$, $r^2 = 6.5$, $P > 0.5$).

Behavior.—We observed females during 25 incubation recesses over days 10-23 of incubation. The average maximum distance traveled from the nest was 53 ± 8 m (range 25-195 m) and did not vary significantly with day of incubation ($y = 55.6 - 0.13x$, $r^2 = 0.0$, $P > 0.5$).

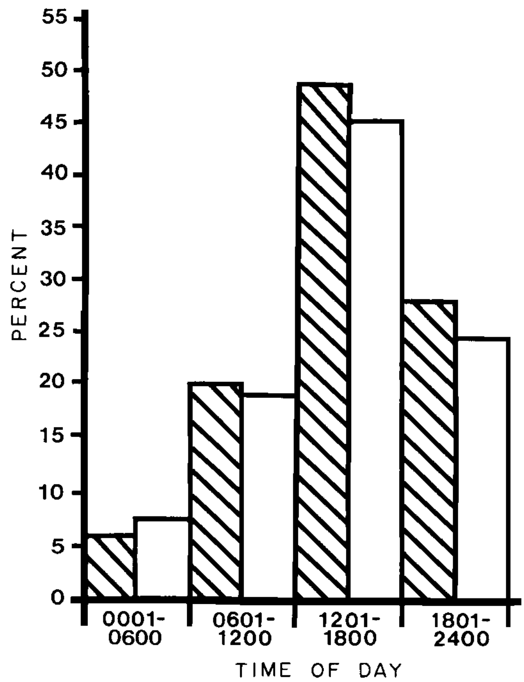

Fig. 1. Proportion of incubation recesses (open bars, $n = 107$) and total recess time (hatched bars, $n = 1{,}426$ min) taken by female Emperor Geese at different times of day.

Preening and bathing were the predominant activities of females during recesses (Table 1). Feeding, the next most frequently observed behavior, occupied only about one-third as much time. The proportion of each recess spent feeding did not vary significantly with day of incubation ($y = 4.3 + 0.565x$, $r^2 = 3.4$, $P > 0.5$).

Despite the short distances traveled during recesses, females flew on 19 of the 25 observed breaks from the nest. The flight seemed undirected because the birds flew in circles or back and forth. Other behavior such as preening, bathing, feeding, and walking appeared to be carried out at an accelerated rate compared with the same behaviors before incubation began.

Male Emperor Geese were present during 14 (56%) of the 25 observed recesses. On 7 occasions, behavior of geese was observed from the beginning of the recess. In 4 of these 7 instances, males did not arrive until 2-7 min ($\bar{x}$ = 4.2 min) after their mates had left their nests. Identification of males was confounded by a number of apparently nonbreeding or

TABLE 1. Behavior of male and female Emperor Geese during incubation recesses. Values are mean percentages of all recesses observed.

Sex	No. of recesses observed	No. of different birds observed	Total min. of recess	Precentage of time spent in: Preen/bathe	Feed	Alert	Walk[a]	Stand[a]	Swim[a]	Drink	Fly	Agonistic	Other
Male	14	7	131	9.4	4.0	48.8	7.4	5.0	20.4	0.2	1.8	0.2	2.9
				***[b]	**	***	NS	NS	*	*	NS	NS	
Female													
Male present[c]	14	7	152	46.3	14.0	4.0	10.4	6.6	8.3	2.6	2.9	0.1	4.8
				NS	NS	NS	NS	NS	NS	NS	NS	NS	
Male absent	11	5	133	39.8	15.4	6.9	10.4	8.0	7.3	2.9	3.0	0.1	6.3
Total	25	9	285	43.4	14.3	5.3	10.4	7.2	7.8	2.7	3.0	0.1	5.8

[a] When not associated with feeding.
[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant ($P > 0.05$) between adjacent values within a column (Mann-Whitney *U*-test).
[c] Behavior between sexes compared only for recesses when both sexes were present.

failed-breeding birds that remained in the study area throughout incubation and wandered near nests without being challenged by either males or females. When present during recesses, male Emperor Geese remained near (<10 m) their females and spent almost half of their time alert (Table 1). Males spent significantly less time than females in bathing, preening, and feeding during incubation recesses. Females often stood on the shores of ponds preening, bathing, and drinking while males swam in the ponds. Males spent a significantly higher proportion of time swimming than did females.

There were no significant differences in female behavior between recesses when males were present and those when they were absent (Table 1). The average maximum distance traveled by a female away from her nest did not vary significantly between when males were present (62 ± 12 m) or absent (41 ± 10 m; $P >$ 0.1).

DISCUSSION

Energy allocation and nest attentiveness by geese.—Snow Geese (*Anser caerulescens*) and Canada Geese accumulate large body stores of fat and protein before egg laying, which facilitates reproduction when and where food is initially unavailable or in low abundance and quality (Ankney and MacInnes 1978; Raveling 1979a, b). This pattern generally is thought to hold for most goose populations (cf. Owen 1980). The accumulated reserves plus any energy obtained by feeding on nesting grounds are available for reproduction. These resources should be allocated between eggs and incubation constancy in proportions that maximize fitness. Reserves can be committed to sustaining a high degree of nest attentiveness at the cost of laying fewer or smaller eggs. Alternatively, reserves can be devoted to production of more or larger eggs at the cost of less attentiveness because females would have to feed more frequently during incubation. This division of reserves is a critical balance because female geese are emaciated at the end of incubation (Ankney and MacInnes 1978; Raveling 1979a, b), and starvation may even occur (Harvey 1971, Ankney and MacInnes 1978).

Emperor Geese are by far the most attentive to their nests of all goose species yet studied by continuous monitoring methods (Table 2), and exceed even the largest geese. For Emperor

TABLE 2. Nest attentiveness of geese studied by continuous monitoring methods.

Species[a] (source)	No. of nests monitored	Total % time incubating (range)	Modal recess length (min)	Mean recess length (min)	Mean recesses/day	Mean recess time/day (min)[b]
Giant Canada Goose (Cooper 1978)	15	98.5 (96.7–99.7)	10	15	1.4	20
Western Canada Goose (Aldrich and Raveling 1983)	13	97.5 (95.3–98.6)	15	13[c]	2.8[c]	36
Emperor Goose (this study)	11	99.5 (99.1–99.7)	8	13	0.5	7
Cackling Canada Goose (Aldrich 1983)	12	93.6 (89.1–96.6)	15	26[c]	3.5[c]	92
Black Brant (Thompson unpubl. rept.)	4	89.6 (87.3–94.9)	22	22	6.7	148

[a] Listed in order of decreasing body mass of females at beginning of incubation.
[b] May vary slightly from product of mean recess length × mean recesses per day because of rounding-off effects.
[c] Derived from published regression.

Geese, the average recess time per day and the recess frequency are 65% and 60% less, respectively, than the next most attentive species. This extremely high attentiveness by Emperor Geese implies commitment of a large portion of energy reserves to sustaining incubation. Emperor Geese, however, also produce large clutches relative to other arctic species and populations of geese (Table 3). In comparison, the loss of mass by Snow Geese between prelaying and hatching is similar to that of Emperor Geese, but Snow Geese allot relatively less energy to eggs and lose a larger proportion of their mass during incubation. Although quantitative data are lacking, Snow Geese also are believed to be extremely attentive to their nests (Harvey 1971, Ankney and MacInnes 1978), and weather on their nesting grounds is thought to be colder and windier typically than on the Y-K Delta, possibly accounting for the greater mass loss during incubation in this species. Western Canada Geese allot a relatively small proportion of their reserves to eggs and lose a large amount of mass (Table 3) during their highly attentive incubation (Table 2).

At the other extreme are the smaller Cackling Canada Geese and Brant, which have larger expenditures in eggs relative to body mass than the heavier geese (Table 3). Consequently, relatively frequent and long recesses by these small geese allow them to feed extensively during incubation (Tables 2 and 4). Brant differ from Cackling Canada Geese in that their level of reserves on arrival at the nesting grounds is lower and they depend more on local food sources for egg production and incubation (Ankney 1984). This difference is further indicated by clutch mass, which exceeds the body mass lost during egg laying; by the relatively small amount of mass lost during incubation (Table 3); and by the observation that Brant feed more during incubation than other species of geese (Table 4).

The relative investment in eggs by the smaller goose species is larger, but fewer eggs generally are produced than by the larger geese (Table 3). This is because the size of their eggs is larger relative to body size and presumably reflects selection in the small species toward maximizing gosling size. Larger goslings can survive starvation longer than smaller ones in the days immediately after hatching (Ankney 1980) and probably can withstand cold better than smaller goslings.

Emperor Geese and Snow Geese have shorter average incubation periods than some species of smaller geese (Table 3), in exception to the general direct correlation of body size, egg size, and length of incubation periods in geese (see Owen 1980: 202–203). It therefore appears that the length of incubation is related not only to body and egg size, but also to the proportion of the incubation period spent actually incubating. Aldrich and Raveling (1983) found that the individual Western Canada Geese with the shortest incubation periods were those most attentive to their nests.

The lack of variability in nest attentiveness we observed through most of the incubation period in Emperor Geese differed from the de-

TABLE 3. Clutch size and mass (g), and changes in body mass (g) of female geese.

Species	Prelaying mass	Begin incubation mass	% loss at end of laying	Mass at hatching	% mass loss in incubation	Mean clutch size	Mean egg mass	Mean clutch mass	Clutch as % of prelaying mass	Clutch as % of begin incubation mass	Incubation period (days)
Western Canada Goose	4,822[a]	4,305[b]	10.7	3,137[b]	27.1	5.3[c]	164[d] (3.8)[e]	869	18.0	20.2	28[b]
Lesser Snow Goose	2,950[f]	2,530[f]	14.2	1,710[f,g]	32.4	3.9[c]	122[h] (4.8)	476	16.1	18.8	23[f]
Emperor Goose	2,950[i]	2,233[j]	24.3	1,770[j]	20.7	5.2[k]	121[l] (5.4)	629	21.3	28.2	25[k]
Cackling Canada Goose	1,890[m]	1,387[m]	26.6	1,095[m]	21.1	4.8[m]	97[m] (7.0)	466	24.7	33.6	26[m]
Atlantic Brant	1,384[n]	1,143[n]	17.4	1,013[n]	11.4	3.9[n]	84[n] (7.4)	328	23.7	28.7	24[n]

[a] Akesson 1980.
[b] Aldrich and Raveling 1983.
[c] Bellrose 1976.
[d] Raveling unpubl. data.
[e] Egg mass as percentage of body mass at beginning of incubation.
[f] Ankney and MacInnes 1978.
[g] Mass in late incubation.
[h] Ankney and Bisset 1976.
[i] K. Laing pers. comm. ($n = 6$).
[j] M. Petersen unpubl. data.
[k] Eisenhauer and Kirkpatrick 1977.
[l] Owen 1980.
[m] Raveling 1979a.
[n] *Branta bernicla hrota*; Ankney 1984.

TABLE 4. Incubation recess time spent feeding by female geese.

Species	Percentage of recess time feeding	Mean time off nest/day (min)	Mean feeding time/day (min)
Giant Canada Goose	38[a]	20[a]	8
Western Canada Goose	40[b]	36[d]	14
Emperor Goose	14	7	1
Cackling Canada Goose	77[c]	92[c]	71
Black Brant	64[d]	148[d]	95

[a] Cooper 1978 (some birds had access to artificially provided food).
[b] Aldrich and Raveling 1983 (captive birds provided food *ad libitum*).
[c] Aldrich 1983.
[d] Thompson unpubl. rept. (feeding percentage based on 3 recesses).

crease in attentiveness as incubation progressed in Cackling Canada Geese (Aldrich 1983) and Western Canada Geese (Aldrich and Raveling 1983). Increases in recesses by Canada Geese were attributed to an increasing need to feed brought about by depletion of body energy reserves. Embryo thermogenesis and higher embient temperatures late in incubation may facilitate this decreased attentiveness by slowing egg cooling. Although Emperor Geese lost significant body mass during incubation, the proportion of recess time spent feeding did not increase as in the two subspecies of Canada Geese. This suggests that most Emperor Geese did not approach a critical low mass, as did Canada Geese.

Increased attentiveness by Emperor Geese during the last three days of incubation was presumably a response by females to tapping, vocalizations, and, finally, pipping by embryos. Cooper (1978) observed a similar response in Giant Canada Geese during the final two days of incubation. This response, however, was not seen in Western Canada Geese (Aldrich and Raveling 1983) and was not observed until the last day of incubation in Cackling Canada Geese (Aldrich 1983). These differences in behavior may reflect differences in the resolution of the conflict between the increasing stimuli from eggs and the need to feed.

Differences occur among species in the distances females travel from their nests during recesses. Most recesses by female Emperor Geese were taken within 50 m of the nest. Aldrich (1983) found that female Cackling Canada Geese traveled more than 100 m from their nests and left their territories in over half of all recesses.

We observed female Brant more than 100 m from their nests in 6 of 8 recesses. Many female Brant and Cackling Canada Geese apparently seek better food sources away from their nesting territories because of their greater reliance on feeding during incubation. The little amount of time female Emperor Geese spent feeding illustrates their relative independence from food during incubation compared with other species (Table 4).

Influence of weather on incubation behavior.—Eggs cool more quickly than they can be rewarmed (Drent 1970); consequently, the time and energy spent to return eggs to an optimum temperature for embryo development should influence the timing and duration of incubation recesses to maximize hatching success. Emperor Goose females took most recesses in the afternoon (Fig. 1), when ambient temperatures were usually highest and egg cooling rates would be lowest, but recesses at other times of the day were not shorter, as in Western Canada Geese (Aldrich and Raveling 1983). The incubation behavior of Emperor Geese did not appear to be influenced significantly by variations in weather among different days, as indicated by the lack of correlation between recess length and either wind speed or ambient temperature at the time of recess or between recess frequency and either average daily wind speed or temperature. Ambient temperature was a significant factor related to recess length in other waterfowl studies (Caldwell and Cornwell 1975, Cooper 1978, Afton 1980). We believe that variations in heat loss from eggs during the short and infrequent recesses of Emperor Geese were not important enough to result in predictable variability in response to prevailing weather conditions during this one season.

Predation.—Nest attentiveness and reliance on endogenous reserves is generally greatest in larger species and subspecies of geese, whereas smaller geese invest more in eggs relative to their body size (Tables 2 and 3). Emperor Geese exceeded even larger goose species in nest attentiveness, which suggests a more complex relationship that involves several interacting factors.

Female geese that are least attentive to their nests suffer the greatest rate of clutch loss to predation (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977). Incubation behavior therefore should be related to the vulnerability of the nest and incubating female to predators and the ability of the female or the pair to repel these threats.

The primary nonhuman, terrestrial predator of geese and eggs on the Y-K Delta is the arctic fox (*Alopex lagopus*). The nesting patterns of the goose species breeding there reflect the importance of this predator and the species' abilities to defend against it. Cackling Canada Geese consistently nest on pond islands (Mickelson 1975), which are relatively inaccessible to foxes. Cackling Canada Geese nesting on shorelines or islands that became connected to the shore lost 80% (n = 100) of their nests to predators, mainly foxes, compared with 40% (n = 385) of the nests located on islands (Raveling unpubl. data). Brant also prefer island nest sites (Mickelson 1975) but nest in dense colonies of up to 15/ha (Eisenhauer 1977), where predator swamping is probably beneficial (cf. Wittenberger and Hunt 1985).

The larger Emperor and Greater White-fronted (*Anser albifrons*) geese nest in a dispersed manner at mainland sites (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Ely and Raveling 1984). Despite their accessibility to foxes, Emperor and Greater White-fronted geese have relatively low rates of nest predation by foxes. Presumably, their larger size enables them to repel foxes effectively (e.g. see Mickelson 1975, Eisenhauer and Kirkpatrick 1977).

Goose nests are also vulnerable to destruction by avian predators. Glaucous Gulls (*Larus hyperboreus*) and Parasitic Jaegers (*Stercorarius parasiticus*) are common on the Y-K Delta, but seldom are able to destroy an entire clutch of goose eggs at one time if one or both goose parents are in the near vicinity. They are quick to find unattended nests, however, and effective repulsion of these avian predators requires adept aerial pursuit by geese.

The relatively stocky-bodied, short-winged Emperor Goose is "clumsy" in flight compared with the smaller, faster, and more agile Brant and Cackling Canada Goose. We believe Emperor Geese lack the speed and maneuverability to keep avian predators away effectively if parents are not in the immediate vicinity of their nest. Group vigilance and defense in Brant colonies seem to deter avian predators further (pers. obs.).

Male Brant and Cackling Canada Geese remain close to their nests while females are away (Eisenhauer 1977, Aldrich 1983) and are therefore in position to defend their nests from avian predators and facilitate the feeding excursions of females. When present, male Emperor Geese behaved as guardians of their females during recesses, following them from the nest. Males could, therefore, defend both females and nests because females remained close to nests during recesses. This strategy did not appear to be well developed, however, because males were not present during all recesses and the behavior of females during recesses was not influenced by the presence or absence of males.

The alert and defensive behaviors of male geese are thought to be important during reproduction both as an antipredator response and to allow females to devote maximum time to feeding (Ankney 1977, Raveling 1979a, Fox and Madsen 1981, Raveling 1981, Aldrich 1983). Because feeding was of almost negligible importance to incubating female Emperor Geese and they remained close to their nests during recesses, the defensive role of males was diminished compared with other geese. Male Emperor Geese presumably gain some greater benefit by spending little time near the nest, probably through use of better food resources away from the nest. Indeed, on three occasions we saw males depart the vicinity of the nest and join groups of feeding Emperor Geese hundreds of meters away (also see Dementiev and Gladkov 1967: 282, Palmer 1976: 178–179). Male geese are also important defenders after hatch, which allows emaciated females and growing goslings maximum time to feed (Ankney 1977, Harwood 1977, Lazarus and Inglis 1978). Any reserves gained before hatch would allow males to devote more time to vigilance during brood rearing.

We conclude that female Emperor Geese are extremely attentive to their nests because they usually can repel foxes and prevent avian predation by maintaining a physical presence on the eggs. This also minimizes the necessity of inefficient aerial pursuit. The Emperor Goose maintains sufficient reserves to incubate almost continuously. In contrast, Cackling Canada Geese and Brant can be less attentive because their presence or absence often may make little difference should a fox reach their nests, but they are efficient at aerial pursuit. These smaller species thus depend on nest placement and male behavior to protect the nest and invest maximally in eggs by supporting incubation through relatively frequent and long recesses for feeding.

The larger Canada Geese, like the smaller Cackling Canada Geese, most commonly nest on islands (e.g. Klopman 1958, Raveling and Lumsden 1977, Cooper 1978). The larger subspecies of Canada Geese are also extremely attentive to their nests, although less so than Emperor Geese (Table 2). The incubation patterns of these populations evolved in the presence of coyotes (*Canis latrans*) and wolves (*C. lupus*). Flying agility is also probably not as important an antipredator factor related to incubation behavior among large Canada Geese because they do not have to cope with jaegers.

Energetic constraints affect the evolution of proximate control of clutch size in geese (Ryder 1970, Raveling and Lumsden 1977, Ankney and MacInnes 1978, Raveling 1979a). We suggest that predator pressure is an additional agent controlling clutch size in geese by influencing the proportion of reserves devoted to eggs vs. retention of those reserves for successful attentive incubation. Constancy of attentiveness is related to vulnerability to different types of predators.

Energetic considerations.—The different patterns of incubation relative to body size and predation are facilitated by different patterns of energy use. The larger geese have lower metabolic and heat loss rates relative to body mass (LeFebvre and Raveling 1967) and, therefore, use endogenous reserves more efficiently and have greater fasting endurance (e.g. Calder 1974; Afton 1979, 1980). On the other hand, the smaller Brant and Cackling Canada Geese have greater mass-specific metabolic requirements and deplete body reserves more rapidly, but have lower absolute requirements than larger forms. Lower absolute energy requirements could be filled more easily by limited food available during incubation. Therefore, these smaller geese can commit a larger portion of these reserves to clutch formation and depend more on food sources to support incubation. Larger species of geese would have to feed longer during recesses to gain equal nutritional benefits relative to absolute needs, which may not be viable given the costs of exposure of eggs to predation, rewarming eggs, and increased activity. Hypothetically, for a goose to increase its attentiveness to incubation, it would have to decrease the number of eggs it lays and channel that energy into sustaining incubation. Because the smaller species lay larger eggs relative to body size, in smaller clutches, reduction of clutch size by one egg would more greatly diminish their reproductive output than in larger species with larger numbers of eggs. These energy relationships seem to have produced a maximization of egg investment rather than incubation constancy in smaller species.

Comparison with other Anatidae.—Most ducks depend heavily on food on their nesting grounds for egg production and incubation (e.g. Krapu 1974, Krapu and Swanson 1975, Afton 1979) and generally exhibit a larger investment in eggs compared with geese. Ducks lose mass during incubation but also feed extensively on much longer and more frequent incubation breaks than taken by geese (e.g. Caldwell and Cornwell 1975; Miller 1976; Afton 1978, 1979, 1980; Ringelman et al. 1982; Hohman 1986). Ducks conceal their nests, and the presence of the female on the nest would do little to deter most terrestrial predators. Thus, most incubation time in excess of that needed for timely embryo development is better spent feeding than protecting the nest, allowing a larger investment in eggs. Also, most ducks nest in milder weather conditions than geese, which facilitates less attentiveness. Frequent incubation breaks limit adult mass losses and assist renesting by most ducks if nests are predated; northern goose species do not renest (see review by Bellrose 1976). An exception to this pattern is the Common Eider (*Somateria mollissima*), which lays a small clutch relative to other ducks and uses a large portion of its endogenous reserves to support nearly continuous incubation. This pattern of reproduction is thought to have arisen in response to the threat of avian predation to largely exposed nest sites (Milne 1976, Korschgen 1977). Thus, the pattern of energy use and incubation in the Common Eider resembles that of geese rather than of other ducks.

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