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SHORT NOTE

Does body size influence nest attendance? A comparison of Ross's geese (*Chen rossii*) and the larger, sympatric lesser snow geese (*C. caerulescens caerulescens*)

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Abstract The body-size hypothesis predicts that nest attendance is positively related to body size among waterfowl and that recess duration is inversely related to body size. Several physiological and behavioral characteristics of Ross's geese (*Chen rossii*) suggest that females of this species should maintain high nest attendance despite their relatively small body size. Accordingly, we used 8-mm films to compare the incubation behavior of Ross's geese to that of the larger, closely-related lesser snow geese (*C. caerulescens caerulescens*; hereafter, snow geese) nesting sympatrically at Karrak lake, Nunavut, Canada in 1993. We found that nest attendance averaged 99% for both species. Our results offer no support for the body-size hypothesis. We suggest that temperature requirements of embryos in relation to short incubation duration and a low foraging efficiency of females select for high nest attendance in both snow geese and Ross's geese.

Keywords Body size · Endogenous reserves · Geese · Incubation · Nest attendance

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Introduction

Arctic-nesting geese arrive in the spring when breeding areas are often covered with snow and, consequently, they must depend heavily on endogenous reserves for breeding (Ankney and MacInnes 1978). These endogenous reserves are accumulated during stopovers on spring migration (Arzel et al. 2006; Drent et al. 2006; Newton 2006). Many waterfowl feed little and lose weight during incubation but sustain themselves on endogenous reserves (termed capital breeders; Ankney and MacInnes 1978; Ankney and Afton 1988; Parker and Holm 1990). Conversely, species or populations that can forage during incubation are termed income breeders (Meijer and Drent 1999).

During incubation, periods spent off nests are termed *recesses*, whereas periods spent on nests are termed *sessions* (Skutch 1962). In addition, in terms of incubation strategy studies, several variables are used to measure nest attendance in swans, ducks and geese (Afton and Paulus 1992); these include: (1) *incubation constancy*, which is the average time spent on nests each day by the hen; (2) *recess duration*, which is the average time taken per recess (in minutes). In capital-breeding species (Meijer and Drent 1999), conspecifics with larger endogenous reserves generally nest earlier, lay larger clutches, spend more time attending their nests, and have higher nest success (Ankney and MacInnes 1978; Aldrich and Raveling 1983; Eicholz and Sedinger 1999; Lepage et al. 2000; Drent et al. 2006). Capital breeders fast to maintain high nest attendances (Parker and Holm 1990; Afton and Paulus 1992; Meijer and Drent 1999), which presumably minimize egg predation (Korschgen 1977; Thompson and Raveling 1987). The number and timing of incubation recesses is important in minimizing egg predation risk (Bolduc and Guillemette 2003). Furthermore, ambient temperatures are inversely related to nest attendance; rain, snow, and fog lead to increased nest attendance, and incubation recesses are generally rare during cooler periods or the dark hours of night (Afton and Paulus 1992).

Lesser snow geese (hereafter snow geese; *Chen caerulescens caerulescens*) have some access to exogenous nutrients at many nesting locations, such as LaPerouse Bay (Cooke et al. 1995; Meijer and Drent 1999) and, therefore, feed during the incubation recesses. However, increased grazing pressure from rapidly increasing goose populations has led to devegetation in many colonies, including Karrak lake, Nunavut (Gloutney et al. 1999, 2001; Alisauskas et al. 2006). Available evidence suggests that white geese [lesser snow geese and Ross's geese (*C. rossii*)] nesting at Karrak lake are obligate capital breeders, i.e., they rely almost entirely on endogenous reserves from egg-laying until brood-rearing and have very limited opportunities to ingest food during incubation (Gloutney et al. 1999; Alisauskas et al. 2006).

Ross's geese are about two-thirds the size of snow geese (MacInnes et al. 1989). Across species, incubation constancy is positively correlated to body size in several bird families (Skutch 1962), including swans, ducks and geese (Afton and Paulus 1992). This relationship (hereafter the body-size hypothesis; compare Skutch 1962; Afton 1980) is interpreted as follows: larger species have a greater fasting endurance than smaller species because larger species are capable of storing larger amounts of endogenous reserves – relative to body size (Afton and Paulus 1992). This relationship is consistent with the inverse relationship between mass-specific metabolic rate and body size (Calder 1996), effectively predicting that smaller species deplete their energy reserves relatively faster than larger species and will therefore probably starve before the latter, assuming that both species live in the same environment. Thus, the body-size hypothesis (compare Skutch 1962; Afton 1980; Afton and Paulus 1992) predicts that, relative to snow geese, Ross's geese should: (1) exhibit a lower average incubation constancy or nest attendance, and (2) spend more minutes away each time they leave the nest (i.e., have higher average recess duration).

Despite the general relationship between nest attendance and body size, exceptions do occur, especially among larger species (Afton and Paulus 1992). However, Ross's geese, which are among the smallest of the goose species, are believed to maintain higher nest attendance than expected, based on their body size, for several reasons:

1. Incubation duration (no. of days) correlates with body size in geese (Jónsson et al. 2006a), and high nest attendance is necessary to minimize incubation periods (Poussart et al. 2000). However, average lengths of incubation (23 days) are the same for snow geese and Ross's geese.
2. Ross's goose embryos grow faster and generate more metabolic heat during early incubation than do snow goose embryos (Craig 2000).
3. Ross's goose embryos are relatively more developed at hatch, as evidenced by their relatively larger pectoralis muscles, larger gizzards, and lower water content in tissues (Slattery and Alisauskas 1995).
4. LeSchack et al. (1998) reported that female snow geese and Ross's geese at Karrak lake spent the same amount of time attending nests; however, estimates of incubation constancy and recess duration were not reported.

All of these factors suggest that Ross's geese may maintain high nest attendance (compare Poussart et al. 2000)

Environmental variables, such as weather and food availability, affect nest attendance in waterfowl (Afton 1980). Waterfowl species are confronted with different climates, habitat types, and food availability, and they migrate variable distances with different energetic costs. We chose snow geese and Ross's geese for comparison because when these two species are compared within the same nesting colony and/or wintering area, they can be observed in the context of a natural experiment in which phylogeny as well as temporal, weather-related, and environmental effects are controlled (Gloutney et al. 2001; Jónsson 2006a, b). Snow geese and Ross's geese that nest together at Karrak lake utilize the same food resources and generally use the same nesting habitats with similar nesting chronologies (McLandress 1983; McCracken et al. 1997). We used films of both species to test the body-size hypothesis and compared the incubation behavior of these species breeding within the Karrak lake goose colony.

Methods

Study area

We studied incubating snow geese and Ross's geese of the Karrak lake goose colony on Camp Island, Nunavut, Canada (67°15′N, 100°15′W). This colony represents one of the largest goose colonies within the Queen Maud Gulf

Bird Sanctuary (Slattery and Alisauskas 1995; McCracken et al. 1997). The landscape at Karrak lake consists of rock outcrops, sedge meadows, and tundra ponds (Slattery and Alisauskas 1995); as such, it offers only limited shelter for incubating females and their nests (McCracken et al. 1997). Karrak lake and its surroundings have been described in detail by Ryder (1972) and McLandress (1983).

Data collection

We used Super-8 mm cameras (2 Minolta XL401 and 2 Minolta XL601; Konica Minolta Photo Imaging USA, Mahwah, N.J.) to record the presence and absence (hereafter, nest attendance) and recess durations (minutes) of eight pairs of snow geese and seven pairs of Ross's geese at Karrak lake from 22 June through to 13 July 1993. Daylight is continuous at this latitude during this time of year. Each camera was mounted in a fixed position throughout this period and filmed two to five nests. The eight snow goose nests hatched between 4 and 10 of July, whereas the seven Ross's goose nests hatched between 8 and 12 of July. Cameras were set up on 22 June and were allowed to run continuously, recording images at 1-min intervals until females left their nests. We changed camera batteries and replenished film every 48 h and took precautions to prevent incubating females from abandoning their nests.

Film analysis

We used the films to determine the presence and absence of incubating females throughout incubation (one frame per minute). For analysis, we estimated individual daily values of two variables: (1) nest attendance, which we indexed as the percentage of frames each 24 h period (day) that females were observed sitting on nests, and (2) recess duration (±1 min), estimated from the number of frames that each female was absent during each recess.

We recorded, on average (±SE), a total of 223 ± 19.2 h (1 day = 24 h of daylight) and 204 ± 12.0 h of data for an individual female snow goose and Ross's goose, respectively (see also Appendix 1). On occasion, the films were too dark to determine the presence or absence of females from their nests because of lower light during night hours and/or rain, heavy cloud cover, and fog. The length and frequency of these dark periods varied between nests. We evaluated whether this affected our results by running three repeated analyses in which: (1) all data points were included, (2) data for a given nest from days with more than 6 of 24 h missing were excluded, and (3) data for a given nest from days with more than 10 of 24 h missing were excluded. These analyses yielded the same findings; thus, we present here data from the original analysis with all data points included. Data recordings were equally affected in both species, and we assume that our comparison is unbiased by missing data. For the analysis of recess duration, we only included incubation recesses where the entire recess was visible. Thus, we assume that: (1) our comparative estimate of nest attendance is a valid index of incubation constancy, and (2) our estimates of recess duration are unbiased.

In the laboratory, we screened and subsequently analyzed films with an Elmo 912 film editor (Elmo USA, Planview, N.Y.). The film editor has a 9 × 12-cm-wide monitor that allows frame-by-frame viewing of Super-8 films, which are inserted into the editor and rolled manually by the operator. Before data recording, we placed a plastic transparency on the monitor, screened each film, and marked the position and number of each nest with a marker. The markings on the plastic transparency helped ensure the accurate recording of data for each individual female and to ensure that females were not confused with their mates, which spend 61% of their time sitting by their nests (Jónsson 2005).

Statistical analysis

We used mixed linear models with repeated measures (PROC MIXED; SAS Institute 1999; Littell et al. 1996) to analyze: (1) nest attendance (percentage of frames per day) and (2) recess duration (min). We included species and incubation stage as explanatory variables in both models. We calculated incubation stage by individually backdating from the hatch dates observed for each female, assuming a 23-day incubation period for both species (Ryder 1972). Individual females (subjects), nested within species, were the repeated measures effect in both models, and incubation stage represented the time effect (compare Littell et al. 1996). We used $p = 0.05$ as the critical value (α) for all tests. We present least-square mean estimates (hereafter LSMEAN; SAS Institute 1999) for nest attendance and recess duration for each species.

Results

Nest attendance did not differ between species ($F = 0.02$, $df = 1.14$, $p = 0.89$), was inversely related to incubation stage ($F = 1.70$, $df = 18, 205$, $p = 0.04$), and declined, on average, 0.06% per day of incubation (Fig. 1). Nest attendances of both species averaged 99% (Table 1). Recess duration did not differ between species ($F = 0.78$, $df = 1.14$, $p = 0.39$) or incubation stage ($F = 1.53$, $df = 17, 58$, $p = 0.11$), and it ranged from 1 to 78 min for snow geese and from 3 to 43 min for Ross's geese (Fig. 2).

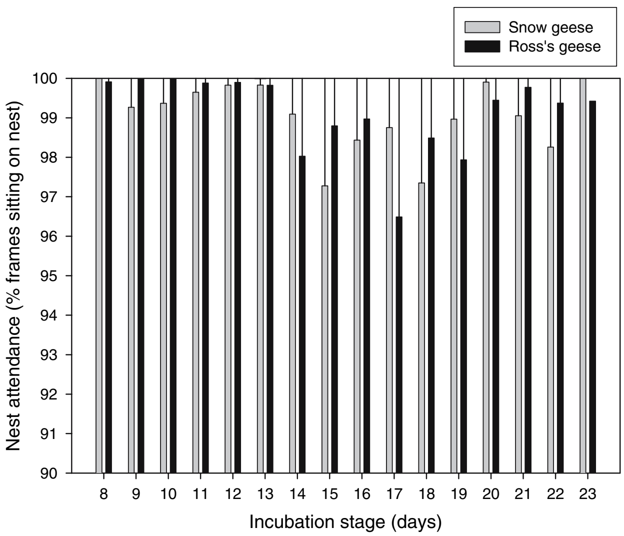

Fig. 1 Average nest attendances (percentage of frames/day) of lesser snow geese (n = 8 females) and Ross's geese (n = 7 females) nesting sympatrically at Karrak lake, Nunavut, Canada in 1993. *Error bars* are one standard deviation. Note the magnified scale on the y-axis

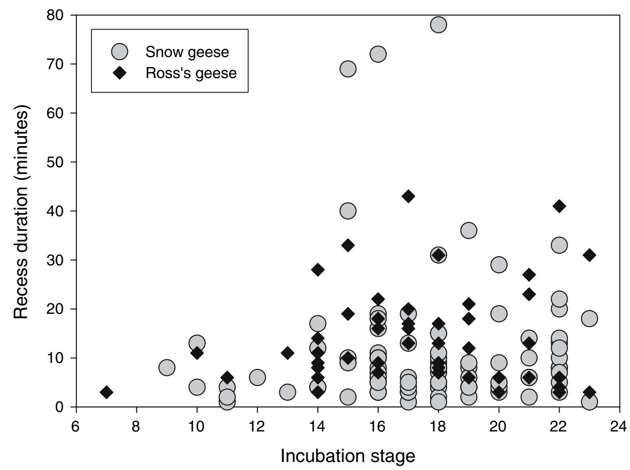

Fig. 2 Recess durations of lesser snow geese (n = 8 females) and Ross's geese (n = 7 females) nesting sympatrically at Karrak lake, Nunavut, Canada in 1993. All observed incubation recesses are included

Discussion

We found that nest attendance and recess duration of snow geese and Ross's geese were similar at Karrak lake in 1993 and did not agree with predictions of the body-size hypothesis. The mixed colonial nesting by snow geese and Ross's geese probably has led to similar selection pressures on their incubation behavior and, consequently, nest attendance might be expected to be similar in areas where the two species nest together. Equal nest attendances in snow geese and Ross's geese are in agreement with equal average lengths of incubation (23 days; see Jónsson et al. 2006a) and also agree with the findings of LeShack et al. (1998). The relatively high developmental rate of Ross's geese (Slattery and Alisauskas 1995; Craig 2000) probably could not be supported without high nest attendance by their parents.

Although there may be a possibility that our estimates of nest attendance are biased because we were unable to record female presence continuously throughout the incubation period on our films, any potential bias due to missing data should have affected both species equally and, consequently, should not have biased our interspecific comparison. Furthermore, most missing values in our data set were due to periods of rain and fog, i.e., when incubation recesses were least likely to occur (compare Afton and Paulus 1992); thus, missing data probably did not markedly bias our estimates towards high values. However, we suggest that future studies use methods that are not sensitive to weather or low light intensity because behavioral responses to those conditions are certainly of interest. A combination of cameras and nest data loggers are useful to avoid missing data due to varying light intensities (Hoover et al. 2004).

Another important caveat is that our analysis was limited to a single breeding season. As time-budgets of geese vary annually, 1-year studies should be interpreted with caution (Giroux and Bédard 1990). Mean nest initiation date for Ross's geese at Karrak lake was relatively late in 1993, whereas the mean for snow geese was near the

Table 1 Summary statistics for nest attendance and recess duration of lesser snow geese and Ross's geese nesting at Karrak lake, Nunavut, Canada, during the summer of 1993

Variable	Lesser snow geese (n = 8 females)		Ross's geese (n = 7 females)	
	Least-square mean estimates	SE	Least-square mean estimates	SE
Nest attendance (% frames/day observed for each individual female)	99.0	0.002	99.2	0.002
Recess duration in minutes (n, no. of recesses observed)	11.5 (91)	1.3	13.8 (48)	1.9

overall mean for the period 1991–2001 (Alisauskas 2001). Late nesting and subsequent limited time for brood-rearing may have favored higher nest attendance in individuals in our study in order to ensure that incubation would be completed as quickly as possible.

Our findings offer two suggestions about Ross's geese. First, in certain years Ross's geese are able to incubate at as equal high constancies as the larger snow geese. Secondly, individuals in the best body condition can attain high nest attendances (Eichholz and Sedinger 1999) and among Ross's geese, these are the individuals that are most likely to attain high nest attendances that are similar to those of the larger snow geese. We do not believe that our sample of Ross's geese was biased towards high-quality individuals because: (1) nest initiation dates did not differ ($p = 0.1043$) between Camp Island and the rest of the Karrak lake colony, and (2) clutch size was slightly lower ($p = 0.0355$) at Camp Island (2.9 on average) than in the rest of the colony (3.2 on average) (Ray Alisauskas, unpublished data).

Predation may select for high nest attendance relative to body size. Thompson and Raveling (1987) reported an incubation constancy of >99% for the intermediate-size emperor geese (*C. canagicus*), which was high relative to their body size. Apparently, the high nest attendance of emperor geese is a proximate selective response to predation pressure by foxes and gulls (Thompson and Raveling 1987), both of which also prey upon eggs, goslings, and adult geese at Karrak lake (McLandress 1983; Samelius and Lee 1998; Samelius and Alisauskas 2006). We speculate that predation pressure may partially explain the high nest attendance observed in geese nesting at Karrak lake. The two species differ in their abilities to defend their nests against predators; the bulkier snow geese are better able to fend off foxes, whereas the lighter Ross's geese are relatively more agile in flight and can effectively fight avian predators (McLandress 1983; see also Thompson and Raveling 1987; Samelius and Alisauskas 2001, 2006).

High nest attendance is beneficial because it minimizes incubation periods (Poussart et al. 2000). The optimal foraging theory predicts that when foraging becomes too costly or non-beneficial, abandoning foraging altogether can be the most beneficial option (Krebs and Davies 1993). We speculate that the high nest attendances of snow geese and Ross's geese are partially a result of the limited amount of food presently available at this colony (Gloutney et al. 1999; Alisauskas et al. 2006). Thus, as a result of poor foraging efficiency, incubating females may minimize foraging effort, especially in years when geese arrive in good body condition following hyperphagia on spring stopover areas (Alisauskas 2002; Arzel et al. 2006; Drent et al. 2006). High incubation constancies and a heavy reliance on endogenous reserves during incubation may have evolved because foraging availability is often limited during incubation, particularly in colonially nesting species like snow geese and Ross's geese. More rigorous studies of incubating snow geese and Ross's geese are needed to evaluate potential factors that favor high nest attendances.

Zusammenfassung

Beeinflusst die Körpergröße die Anwesenheit am Nest? Ein Vergleich von Zwergschneegans (*Chen rossii*) und Kleiner Schneegans (*C. caerulescens caerulescens*).

Gemåß der Körpergrößen-Hypothese sind bei Wasservögeln die Anwesenheit am Nest positiv mit der Körpergröße korreliert, die Brutpausen dagegen negativ. Mehrere Charakteristika der Zwergschneegans in Physiologie und Verhalten legen nahe, dass die Weibchen ungeachtet des relativ kleinen Körpers hohe Nest-Anwesenheiten aufrechterhalten können. Im Jahre 1993 nutzten wir 8 mm Filmaufnahmen, um das Inkubationsverhalten von Zwergschneegans und der grösseren Kleinen Schneegans zu vergleichen, die am Karrak See, Nunavut, Kanada sympatrisch bråten. Bei beiden Arten fanden wir mittlere Nest-Anwesenheiten von 99%, und die Befunde unterståtzen die Körpergrössen-Hypothese nicht. Wir vermuten, dass Anspråche des Embryos an die Temperatur in Bezug zur kurzen Inkubationsdauer sowie eine geringe Effizienz der Weibchen bei der Nahrungssuche die hohen Nest-Anwesenheiten beider Arten bedingen.

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Appendix 1

Table 2.

Table 2 Number of hours of readable film within each 24-h day and total number of hours that incubating female white geese were filmed at Karrak lake, June–July 1993

Female no.	Species	Observed hatch date	Backdated first day of incubation	1 22 June	2 23 June	3 24 June	4 25 June	5 26 June	6 27 June	7 28 June	8 29 June	9 30 June
1	ROGO	8 July	15 June	6.6	6.6	7.5	8.5	8.1	0.1	10.3	8.7	7.5
2	ROGO	9 July	16 June	6.6	6.6	7.5	8.5	8.1	0.1	9.1	8.7	7.5
3	ROGO	9 Jul	16 June	6.6	6.6	7.5	8.5	8.1	0.1	9.1	8.7	7.5
4	ROGO	8 July	15 June	0.2	0.9	8.3	6.8	9.3	6.6	0.7	10.0	24.0
5	ROGO	9 July	16 June	0.2	0.9	8.3	6.8	9.3	6.6	0.7	10.0	4.0
6	ROGO	10 July	17 June	0.2	0.9	8.3	6.8	9.3	6.6	0.7	10.0	4.0
7	ROGO	8 July	15 June	0.2	10.8	0.2	10.7	8.4	18.6	10.9	11.3	11.5
8	LSGO	7 July	14 June	0.2	10.8	0.2	10.7	8.4	18.6	10.9	11.3	11.5
9	LSGO	6 July	13 June	0.2	10.8	0.2	10.7	8.4	18.6	10.9	11.3	11.5
10	LSGO	9 July	16 June	0.2	10.8	0.2	10.7	8.4	18.6	10.9	11.3	11.5
11	LSGO	5 July	12 June	0.2	10.8	0.2	10.7	8.4	18.6	10.9	11.3	11.5
12	LSGO	10 July	17 June	0.1	10.3	8.9	12.2	10.2	9.1	1.9	13.6	11.7
13	LSGO	9 July	16 June	0.1	10.3	8.9	12.2	10.2	9.1	1.9	13.6	11.7
14	LSGO	4 July	11 June	0.1	10.9	13.6	16.8	15.9	11.6	9.6	13.6	12.4
15	LSGO	4 July	11 June	0.1	10.8	12.4	17.6	11.5	11.1	6.9	13.6	11.7

Female no.	Species	10 1 July	11 2 July	12 3 July	13 4 July	14 5 July	15 6 July	16 7 July	17 8 July	Total hours
1	ROGO	17.3	11.0	6.7	12.4	14.8	15.4	0.0	0.0	141.4
2	ROGO	17.3	11.0	6.7	12.4	14.8	15.4	0.0	0.0	140.3
3	ROGO	17.3	11.0	6.7	12.4	14.8	15.4	0.0	0.0	140.3
4	ROGO	24.0	24.0	24.0	24.0	24.0	24.0	24.0	24.0	248.7
5	ROGO	8.4	8.3	13.1	6.1	17.2	10.8	11.3	11.5	133.4
6	ROGO	8.4	8.3	13.1	6.1	17.2	10.8	11.3	11.5	133.4
7	ROGO	15.7	17.6	16.7	20.1	0.0	5.1	14.2	0.0	171.9
8	LSGO	15.7	17.6	16.7	20.1	0.0	5.1	14.2	0.0	171.9
9	LSGO	15.7	17.6	16.7	20.1	0.0	5.1	14.2	0.0	171.9
10	LSGO	15.7	17.6	16.7	20.1	0.0	5.1	14.2	0.0	171.9
11	LSGO	15.7	17.6	16.7	20.1	0.0	5.1	14.2	0.0	172.0
12	LSGO	11.8	8.7	17.7	20.1	9.1	11.1	10.0	8.1	174.4
13	LSGO	11.8	8.7	17.7	0.0	0.0	0.0	0.0	0.0	116.1
14	LSGO	12.4	9.5	18.3	0.0	0.0	0.0	0.0	0.0	144.6
15	LSGO	12.8	10.5	18.3	20.1	9.8	11.1	0.0	0.0	178.4

ROGO, Ross's geese; LSGO, lesser snow geese

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