ECOLOGICAL AND PHYSIOLOGICAL FACTORS AFFECTING BROOD PATCH AREA AND PROLACTIN LEVELS IN ARCTIC-NESTING GEESE

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Abstract.—We investigated effects of ecological and physiological factors on brood patch area and prolactin levels in free-ranging Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter "Snow Geese") and Ross's Geese (*C. rossii*). On the basis of the body-size hypothesis, we predicted that the relationships between prolactin levels, brood patch area, and body condition would be stronger in Ross's Geese than in the larger Snow Geese. We found that brood patch area was positively related to clutch volume and inversely related to prolactin levels in Ross's Geese, but not in Snow Geese. Nest size, nest habitat, and first egg date did not affect brood patch area in either species. Prolactin levels increased as incubation progressed in female Snow Geese, but this relationship was not significant in Ross's Geese. Prolactin levels and body condition (as indexed by size-adjusted body mass) were inversely related in Ross's Geese, but not in Snow Geese. Our findings are consistent with the prediction that relationships between prolactin levels, brood patch area, and body condition are relatively stronger in Ross's Geese, because they mobilize endogenous reserves at faster rates than Snow Geese. *Received 4 August 2004, accepted 23 July 2005.*

Key words: body condition, body size, brood patch, geese, incubation, prolactin.

Factores Ecológicos y Fisiológicos que Afectan el Área del Parche de Incubación y los Niveles de Prolactina en Gansos Nidificantes del Ártico

Resumen.—Investigamos los efectos ecológicos y fisiológicos sobre el área del parche de incubación y los niveles de prolactina en gansos silvestres de las especies *Chen caerulescens caerulescens* y *C. rossii*. Basándonos en la hipótesis del tamaño corporal, predijimos que la relación entre los niveles de prolactina, el tamaño del parche de incubación y la condición corporal sería más fuerte en *C. rossii* que en *C. caerulescens*. Encontramos que el tamaño del parche de incubación estaba relacionado positivamente con el volumen de la puesta e inversamente relacionado con los niveles de prolactina en *C. rossii*, pero no en *C. caerulescens*. El área del parche de incubación no fue afectada por el tamaño del nido, el hábitat del nido ni la fecha de la puesta del primer huevo en ninguna de las dos especies. Los niveles de prolactina aumentaron a medida que la incubación

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progresó en *C. caerulescens* pero esta relación no fue significativa en *C. rossii.* La condición corporal y los niveles de prolactina (corregidos por el tamaño corporal) se relacionaron inversamente en *C. rossii* pero no en *C. caerulescens.* Nuestros resultados concuerdan con la predicción de que las relaciones entre los niveles de prolactina, el tamaño del parche de incubación y la condición corporal son relativamente más fuertes en *C. rossii*, debido a que estos gansos movilizan las reservas endógenas a tasas más rápidas que *C. caerulescens.*

Most birds develop brood patches (also called "incubation patches") prior to incubation (see reviews by Drent 1975, Lea and Klandorf 2002). The brood patch is a featherless area on the breast and belly that facilitates heat transfer from parents to eggs (Jones 1971, Drent 1975). Only the incubating sex develops a brood patch (Wiebe and Bortolotti 1993), which is restricted to females among Northern Hemisphere ducks and geese (Kear 1970, Afton and Paulus 1992). Birds generally shed feathers from brood patches during a process similar to molt (Wiebe and Bortolotti 1993). By contrast, female geese and ducks use their bills to pluck down and contour feathers from breast and belly areas and place them in their nests; nest down insulates eggs from ambient air during incubation recesses (Caldwell and Cornwell 1975, Cole 1979, Thompson and Raveling 1988). Breast plucking occurs throughout incubation in some goose species (Hanson 1959, Inglis 1977, Cole 1979); female Canada Geese (*Branta canadensis*) pluck new nest down from their belly after wind blows older down from their nests (Cooper 1978).

Female waterfowl generally feed little and, thus, lose weight during incubation (Ankney and MacInnes 1978, Ankney and Afton 1988, Afton and Paulus 1992). However, smaller goose species generally take more frequent and longer incubation recesses than larger species; feeding is the primary purpose for incubation recesses (Afton and Paulus 1992). These behavioral differences commonly are linked to the observation that mass-specific metabolic rate increases with decreasing body size in birds (Kendeigh 1970). Thus, larger species generally have a higher fasting endurance than smaller species, which must rely more on foraging opportunities to support their metabolism during incubation (body-size hypothesis; Skutch 1962, Afton 1980, Thompson and Raveling 1987, Afton and Paulus 1992).

Featherless body parts, such as brood patches, are areas of increased heat loss and can thus be energetically costly to maintain (Haftorn and Reinertsen 1985, Midtgård 1989), especially for smaller birds (cf. Brummermann and Reinertsen 1991). In Bantam Hens (*Gallus domesticus*), smaller females exhibited a stronger decrease in body temperature during experimental cooling of the brood patch, which indicates a relatively greater responsiveness to heat loss through brood patches in smaller individuals (Brummermann and Reinertsen 1991). Heat loss through the brood patch can induce shivering thermogenesis in muscles (Tøien 1989), which, in turn, should increase catabolism of energy reserves.

Some authors have reported a positive relationship between clutch size and brood patch area (see review by Wiebe and Bortolotti [1993]). Numerous egg-addition experiments have tested the assumption that brood patch area has evolved to accommodate clutch size (Beer 1965, Wiebe and Bortolotti 1993). Waterfowl have large, central brood patches and can enlarge them as needed to incubate larger clutches (see Wiebe and Bortolotti 1993). Brood patches of Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter "Snow Geese") and some Ross's Geese (*C. rossii*) undergo enhanced vascularization (Jónsson et al. 2006), and the resulting increased blood flow enhances heat transfer from the female to eggs (Midtgård et al. 1985).

Changes in hormone levels and environmental stimuli initiate brood-patch formation (Hanson 1959, Jones 1971, Lea and Klandorf 2002). Prolactin is an important hormone associated with reproduction in birds (Goldsmith 1983, 1991; Johnson 2000, Scanes 2000, Vleck 2002). Prolactin in birds has at least three possible functions: (1) prolactin stimulates nesting activity and incubation behavior, and tactical stimulation of the brood patch stimulates release of prolactin (Kern 1979, Hall and Goldsmith 1983, El Halawani and Rozenboim 1993, Lea

and Klandorf 2002); (2) prolactin accelerates gonadal regression at the end of incubation and also is required for inducing postnuptial molt (Dawson and Sharp 1998, Dawson et al. 2001); and (3) prolactin stimulates foraging activity and weight gain in Ringed Turtle-Doves (*Streptopelia risoria*; Buntin and Figge 1988, Buntin et al. 1999). Although prolactin has been determined to be a stress hormone in mammals, there seems to be little or no direct evidence that it plays such a role in birds (Maney et al. 1999; but see Hazelwood 2000). If the above functions of prolactin are present in incubating Snow and Ross's geese, they may confound each other; female geese lose weight as incubation progresses (Ankney and MacInnes 1978), whereas they reduce their sitting behavior (incubation constancy) simultaneously to increasing time spent feeding (Afton and Paulus 1992, Gloutney et al. 2001). The body-size hypothesis (cf. Afton and Paulus 1992) predicts that female Ross's Geese mobilize their energy reserves at a faster rate than Snow Geese. Thus, we hypothesized that any relationship between prolactin levels, brood patch area, incubation stage, and body condition would be stronger in Ross's Geese than in Snow Geese.

Nest-site selection is an important factor affecting microclimate of parents and eggs, particularly in cold environments (Dawson and O'Connor 1996, Gloutney and Clark 1997, McCracken et al. 1997). Nesting habitats of Snow and Ross's geese at Karrak Lake differ in exposure to wind and availability of nest materials; habitats were classified by their wind exposure (from the least to the most sheltered) and their nesting materials (rock, moss, mixed, and heath; see detailed descriptions in Ryder 1972, McLandress 1983, McCracken et al. 1997). At Karrak Lake, larger nests provide greater insulation for eggs; nests of both species were smallest in rock habitats, intermediate in mixed habitats, and largest in moss habitats (Ryder 1972, McCracken et al. 1997). Furthermore, McCracken et al. (1997) reported that rim height, wall thickness, circumference, and outer diameter were relatively larger in Ross's Goose nests than in those of Snow Geese.

We hypothesized that brood patch area of geese is affected by clutch size and clutch volume but is also limited by energetic needs of incubating females (a possible parent–offspring conflict; Trivers 1974, Clutton-Brock 1991). Specifically, we hypothesized that brood patch

area is (1) adapted to accommodate the size and volume of the clutch, as observed in other birds (Beer 1965, Wiebe and Bortolotti 1993); and (2) limited by female body condition (as indexed by size-adjusted body-mass; see below), prolactin levels, availability of nest materials, and nest size. Our hypothesis assumes that (1) the amount of heat loss through the brood patch is positively correlated with brood patch area (after Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991), and (2) selection of a good nest site and nest building can reduce such heat loss (McCracken et al. 1997). Our hypothesis predicts that brood patch area is positively correlated with (1) clutch size, because larger clutches need larger brood patch areas (Wiebe and Bortolotti 1993); (2) incubation stage, because geese will replace older nest down as incubation progresses (Cooper 1978); (3) body condition, because birds in poorer condition refrain from plucking their brood patches (after Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991); (4) prolactin levels, because prolactin induces sitting behavior in birds and prolactin levels have a positive relationship with tactile stimulus of the brood patch (Lea and Klandorf 2002); (5) nest size, because geese that build larger nests are better sheltered from wind chill (McCracken et al. 1997); and (6) nesting habitat, because geese that use the more sheltered nest habitats (McLandress 1983, McCracken et al. 1997) are better protected from wind chill and, thus, can pluck a larger brood patch area.

We studied implications of body size on brood patch formation in two closely related, free-ranging, Arctic-nesting geese because of its perceived importance to fitness in relatively harsh high-latitude environments; Ross's Geese are approximately two-thirds the size of Snow Geese (MacInnes et al. 1989). Our first objective was to test the hypothesis that observed brood patch area is an optimum between clutch size and ecological and physiological variables (i.e. body condition, prolactin levels, nest size, and nest habitat), which we measured for individual female Snow and Ross's geese. Our second objective was to determine whether increased circulating levels of prolactin in incubating geese are correlated with female body condition. Our third objective was to test the hypothesis that these relationships would be stronger for Ross's Geese than for Snow Geese.

Methods

Data Collection

We collected 30 female Ross's Geese and 30 female Snow Geese from the nesting colony at Karrak Lake, Nunavut (67°14′N, 100°15′W; Ryder 1972, McLandress 1983) during incubation from 15 to 30 June 1996. Karrak Lake is the largest goose colony in the Queen Maud Gulf Bird Sanctuary (Slattery and Alisauskas 1995, McCracken et al. 1997). Immediately following collection, we took blood samples and drew outlines of brood patches on Saran Wrap (Dow Chemical Company, Midland, Michigan), using a permanent marker. In the lab, we measured (±0.01 mm^2) brood patch area on films with a Li-Cor 3100 leaf area meter (Li-Cor, Lincoln, Nebraska).

We measured prolactin levels (ng mL^{-1}), in a single assay, following methods described in Bluhm (1983a, b). The prolactin assay RIA for Wild Turkey (*Meleagris gallopavo*), described in Burke and Papkoff (1980), was validated for use with goose serum by comparing the dose–response relationship of serum from incubating Snow Geese with that of purified Wild Turkey prolactin; both gave parallel slopes (Bluhm et al. 1983a, b). We used this type of assay to measure prolactin in our blood samples; the within-assay coefficient of variation for the prolactin assay was 7%. We were unable to estimate prolactin levels for three Snow Geese and six Ross's Geese, because their blood samples had insufficient liquid serum for the hormone assay. In our statistical analyses, we only included geese with successful prolactin assays; thus, all our findings are based on 27 Snow Goose and 24 Ross's Goose females.

We classified nesting habitat for our specimens (cf. McCracken et al. 1997). Ross's Geese rarely nest in rock nesting habitat (McCracken et al. 1997); thus, our nest habitats for this species included only heather (*n* = 8), mixed (*n* = 9), and moss (*n* = 7) habitats (McLandress 1983, McCracken et al. 1997). For Snow Geese, our nest habitats included rock (*n* = 3), heather (*n* = 8), mixed (*n* = 9), and moss (*n* = 7). We measured outer diameter, wall thickness, circumference, rim height, bowl depth, and inner diameter (±1 mm) of all nests (McCracken et al. 1997).

We recorded clutch size and measured (±0.1 mm) maximum length and width of all eggs in each clutch (Slattery and Alisauskas 1995, Alisauskas et al. 1998). We calculated clutch volume by adding volumetric measurements of each egg in a clutch, using the equation given by Hoyt (1979; see also Flint and Sedinger 1992): egg volume = 0.507 × length × width^2. We estimated incubation stage by candling all eggs in each clutch (Weller 1956); incubation stage ranged from 5 to 24 days in Snow Geese and from 7 to 22 days in Ross's Geese. We estimated first egg date by backdating, assuming a laying rate of 1 egg per 1.3 days and a 23-day incubation for both species (Ryder 1972). We measured fresh body mass (±1 g) and head, wing, culmen, and tarsus length (±0.1 mm; Dzubin and Cooch 1992).

Data Analysis

Summary statistics.—We used *P* = 0.05 as the critical value (α) in all statistical analyses. We first examined whether explanatory variables other than body size, size-adjusted body mass, incubation stage, and nest habitat differed between female Snow and Ross's geese. We used analysis of variance (ANOVA; PROC MIXED, SAS Institute 1999) to compare prolactin levels and clutch size between species as a fixed effect in this analysis. We used multivariate analysis of variance (MANOVA; PROC GLM, SAS Institute 1999), with the PDIFF option in LSMEANS, to compare nest-size measurements between species (McCracken et al. 1997).

Calculations of explanatory variables.—We wanted to account for variation in body mass from sources other than body condition (Ankney and Afton 1988, Alisauskas and Ankney 1994). We anticipated that fresh body mass would be affected by (1) incubation stage, because females lose weight during incubation (Afton and Paulus 1992); (2) body size, which accounts for a significant proportion of variation in fresh body mass (Ankney and Afton 1988, Alisauskas and Ankney 1994); and (3) prolactin levels, because prolactin levels are related to body condition in other birds (Buntin and Figge 1988, Buntin et al. 1999, Hazelwood 2000, Criscuolo et al. 2002). Accordingly, we conducted a principal component analysis (PCA; PROC PRINCOMP, SAS Institute 1999), separately for each species, on the correlation matrix of head, culmen, tarsus, and wing length. We then used the first principal component (PC1) to index body size in subsequent statistical models. The PC1 explained

64% and 61% of the body-size variation in Snow and Ross's geese, respectively. We calculated size-adjusted body mass (SBM) using a multiple regression for each species separately (PROC REG, SAS Institute 1999), with fresh body mass as the dependent variable and body size indexed by PC1, incubation stage (i), and prolactin levels (y) as explanatory variables. We used backwards stepwise selection procedure to determine our final regression models (Alisauskas and Ankney 1994, Gloutney et al. 2001). Prolactin levels were not significant in the regression for Snow Geese ($P = 0.275$). The final regression models were:

$$\text{SBM}_{\text{Snow Geese}} = 2111.2 + 69.2(PC1) - 19.1(i)$$
$$(r^2 = 0.67, P < 0.001) \qquad (1)$$

$$\text{SBM}_{\text{Ross's Geese}} = 1466.5 + 34.6(PC1) - 11.4(i) - 0.6(y)$$
$$(r^2 = 0.70, P < 0.001) \qquad (2)$$

We calculated size-adjusted body mass for each female by adding individual residuals from the multiple regressions above to the mean fresh body mass of each species (see Ankney and Afton 1988).

We divided measurements of each nest with the square root of clutch volume to account for individual variation, because of egg and clutch size (McCracken et al. 1997). McCracken et al. (1997) reported that Ross's Geese built proportionately larger nests than Snow Geese. First, we confirmed this difference in our data by comparing all six nest measurements with a MANOVA (see below). We needed an index of nest size that would include interspecific differences because they also represent the value of nest building as insulation (McCracken et al. 1997). We indexed nest size by reducing dimensionality of nest measurements using PCA on all six nest measurements, and then we used MANOVA with LSMEANS to examine which PCA scores differed between Snow and Ross's geese. Multivariate analysis of variance showed that PC1 ($P = 0.001$) and PC3 ($P = 0.021$) differed between species; thus, we used PC1 and PC3 to index nest size. These cumulatively explained 61% of the nest-size variation. In our analysis, nest habitat accounts for insulation properties of nest materials (i.e. rock, heather, mixed, and moss habitats), because selection of nest materials reflected nest habitat and did not differ between species within a nest habitat (Ryder 1972, McCracken et al. 1997).

Statistical tests of hypotheses.—We used an analysis of covariance (ANCOVA; PROC MIXED, SAS Institute 1999) to determine which ecological and physiological variables affected brood patch area. We ran separate ANCOVAs for each species, because they did not overlap in size-adjusted body mass (Table 1). For this analysis, nesting habitat was the only categorical variable and covariates were clutch volume, incubation stage, size-adjusted body mass, prolactin levels, nest size (PC1 and PC3), and first egg date. Habitat type was a fixed effect, but all covariates were random effects because they were a sample from a large population (Kuehl 2000). We determined final models by backwards stepwise selection procedure (Alisauskas and Ankney 1994, Gloutney et al. 2001).

We tested our hypothesis that relationships between size-adjusted body mass, incubation stage, and prolactin levels are stronger in Ross's Geese than in Snow Geese. We did a multiple regression (PROC MIXED, SAS Institute 1999) for each species, with prolactin levels as a response variable and size-adjusted body mass and incubation stage as explanatory variables. Because prolactin level was a response variable, we recalculated size-adjusted body mass of Ross's Geese by removing prolactin levels from regression Equation (2); this was not necessary for Snow Geese because prolactin levels were not significant in Equation (1). We examined whether removing incubation stage would alter final findings, because we were concerned that adjusting for incubation stage might inflate our estimate of the relationship between prolactin levels and incubation stage. However, we obtained the same final models, whether incubation stage was included in the regression or not. Thus, we present only the analysis without incubation stage, and we refer to size-adjusted body mass from Equations (3) and (4) as body condition (BC):

$$\text{BC}_{\text{Snow Geese}} = 1842.7 + 82.1(PC1)$$
$$(r^2 = 0.41, P = 0.0002) \qquad (3)$$

$$\text{BC}_{\text{Ross's Geese}} = 1184.7 + 40.0(PC1)$$
$$(r^2 = 0.25, P = 0.0036) \qquad (4)$$

We determined final models by backwards stepwise selection procedure (Alisauskas and Ankney 1994, Gloutney et al. 2001). Also, we repeated the ANCOVAs for brood patch area

Table 1. Summary statistics for female Snow Geese and Ross's Geese, collected at Karrak Lake, Nunavut, in June 1996.

	Snow Geese				Ross's Geese				
	n	Mean ± SD [a]	Min	Max	n	Mean ± SD [a]	Min	Max	P
Clutch size	30	4.2 ± 1.0	2	6	30	3.9 ± 0.8	2	5	0.371 [b]
Clutch volume (mm³)	30	445.7 ± 103.7	202	654	30	348.8 ± 62.2	222	461	NA
Incubation stage (days)	30	15.1 ± 5.6	5	24	30	14.2 ± 5.1	7	22	NA
Prolactin levels (ng mL^{-1})	27	169.1 ± 67.9	64	372	24	167.3 ± 54.9	55	249	0.700b
Size-adjusted body mass (g)	30	1,741.8 ± 96.6	1,565	1,914	30	1,184.7 ± 67.8	1,020	1,312	NA
Nest measurements									
Outer diameter [c]	30	15.2 ± 2.4	12	21	30	16.0 ± 1.8	13	21	0.127 [d]
Inner diameter [c]	30	7.1 ± 0.5	6	8	30	7.3 ± 0.4	7	9	0.100 [d]
Wall thickness [c]	30	4.8 ± 1.1	3	7	30	5.4 ± 1.0	4	8	0.040 [d]
Rim height [c]	30	2.9 ± 0.8	1	4	30	4.2 ± 0.9	3	6	<0.001 [d]
Bowl depth [c]	30	3.5 ± 0.6	3	6	30	3.7 ± 0.5	2	5	0.147 [d]
Circumference [c]	30	89.3 ± 20.0	66	148	30	96.6 ± 10.8	73	120	0.082 [d]

[a] Means and standard deviations (SD) are based on LSMEANS in SAS (SAS Institute 1999).
[b] P-values from ANOVA.
[c] Measurements (mm) divided by the square root of clutch volume.
[d] P-values from MANOVA.
NA = not applicable.

with body condition (Equations [3] and [4]) replacing size-adjusted body mass (Equations [1] and [2]) as an explanatory variable; both sets of ANCOVAs arrived at the same final models.

We also performed a multiple regression, with brood patch area as the dependent variable and various covariates as explanatory variables (PROC REG, SAS Institute 1999). We used this accompanying regression to examine multicollinearity among covariates, using variance inflation factors (VIF), following Freund and Wilson (1997), who suggested that multicollinearity is present when VIF ≥ 10. Also, we compared our findings from backwards model selections with findings from model selection using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In all cases, both methods arrived at the same final model. Here, we present results from backwards model selection.

Visual inspection of the data led us to consider the possibility that the species relationship between incubation stage and prolactin levels was nonlinear. Thus, we tested for polynomial relationships between these variables using a *post-hoc* polynomial regression (Dowdy et al. 2004). We used PROC REG (SAS Institute 1999) to run linear, quadratic, and cubic models. We performed *F*-tests on each model and then selected the model with the highest *F*-value for inference, provided that the overall *F*-test for that model was significant at the $P = 0.05$ level (Dowdy et al. 2004).

<div align="center">RESULTS</div>

Analysis of variance indicated that clutch size ($F = 0.81$, df = 49, $P = 0.371$) and prolactin levels ($F = 0.15$, df = 49, $P = 0.700$) were similar between

species (Table 1). Overall nest size differed between Snow and Ross's geese (MANOVA: $F = 7.77$, df = 6 and 53, $P < 0.001$). Comparisons of LSMEANS indicated that Ross's Goose nests had higher rims and thicker walls than those of Snow Geese (Table 1).

Analysis of covariance detected no relationship between brood patch area of Snow Geese and any of the explanatory variables; the accompanying regression confirmed the absence of multicollinearity (all VIFs ≤ 1.1). The final regression model for prolactin levels in Snow Geese included only incubation stage ($t = 4.12$, df = 23, $P < 0.001$):

$$y_{\text{Snow Geese}} = 81.7 + 5.3(i) \qquad (5)$$

Prolactin levels were positively related to incubation stage in Snow Geese (Fig. 1A), though we detected two outliers that had extremely high prolactin levels (unfilled symbols in Fig. 1A). Nevertheless, we arrived at the same final models for Snow Geese whether or not these outliers were included. The linear model (Equation [5]) had the highest *F*-value in the polynomial regression and, thus, was the most appropriate model for the relationship between prolactin levels and incubation stage in Snow Geese (Table 2).

The final ANCOVA model for brood patch area (BPA) in Ross's Geese included clutch volume (CU) ($t = 2.55$, df = 21, $P = 0.019$), and prolactin levels ($t = -2.79$, df = 21, $P = 0.011$):

$$BPA_{\text{Ross's Geese}} = 142.3 - 0.2(y) + 0.2(\text{CU}) \qquad (6)$$

Brood patch area in Ross's Geese was positively related to clutch volume (Fig. 1B), but inversely related to prolactin levels (Fig. 1C);

TABLE 2. *Post-hoc* polynomial regression for the relationship between prolactin levels (y) and incubation stage (i) for female Snow Geese and Ross's Geese, collected at Karrak Lake, Nunavut, in June 1996.

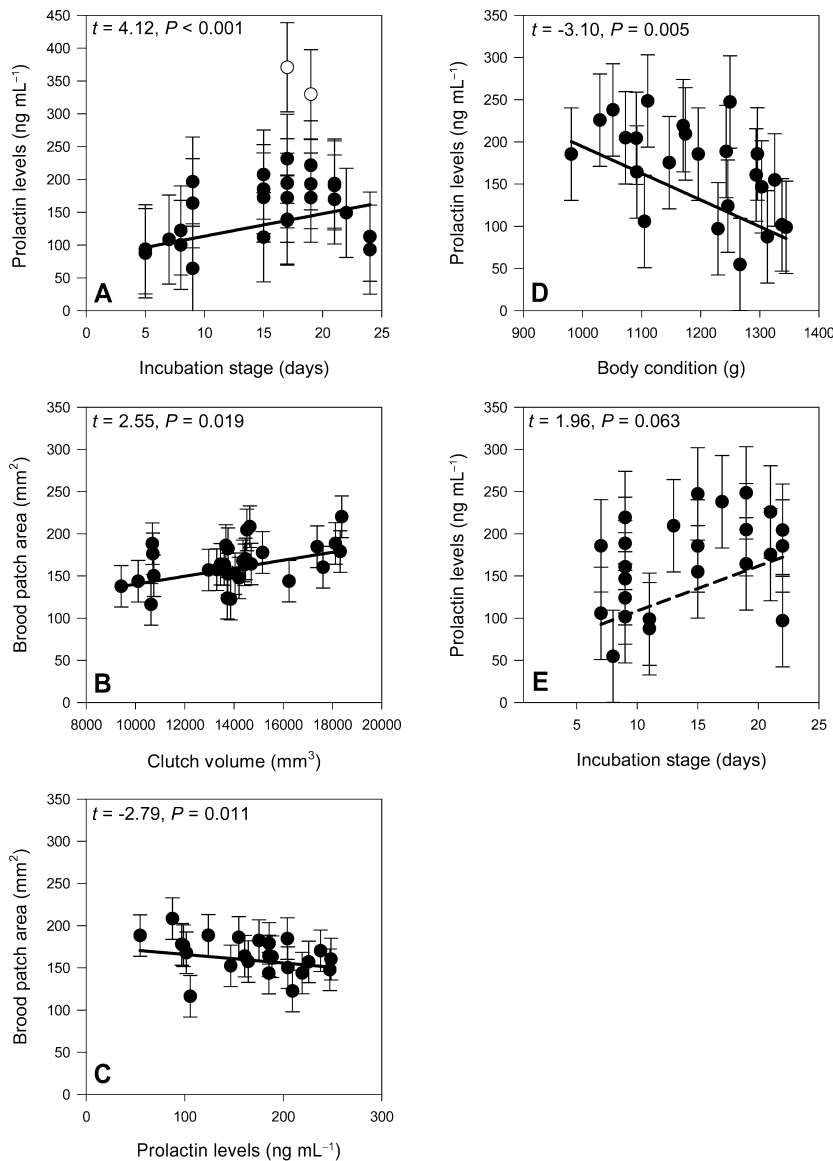| Model	Equation	F	r^2	Mean square error	P
		Snow Geese			
Linear	$y = 77.1 + 5.7(i)$	17.97	0.439	1260.5	0.001
Quadratic	$y = 8.0 + 18.1(i) - 0.5(i^2)$	10.59	0.491	1195.8	0.001
Cubic	$y = 61.6 + 3.5(i) + 0.7(i^2) - 0.1(i^3)$	6.87	0.495	1241.3	0.002
		Ross's Geese			
Linear	$y = 115.8 + 3.51(i)$	3.13	0.13	2712.1	0.092
Quadratic	$y = -20.9 + 24.5(i) - 0.70(i^2)$	2.99	0.23	2519.2	0.073
Cubic	$y = 123.2 - 7.9(i) + 1.5(i^2) - 0.05(i^3)$	2.02	0.24	2611.7	0.145

Fig. 1. Relationships of brood patch area and prolactin levels with various explanatory variables in (A) Snow Geese and (B–E) Ross's Geese at Karrak Lake in June 1996. Values for *P* and *t* are at significance levels from final ANCOVA and regression models performed in PROC MIXED. Error bars are 1 SD from the mean of each response variable (see Table 1). Unfilled symbols signify suspected outliers (see text for details). Broken line in (E) indicates that a linear relationship was suggested but not statistically significant (see text for details).

the accompanying regression indicated that there was no evidence of multicollinearity between explanatory variables (all VIFs ≤ 1.5). The final regression model for prolactin levels in Ross's Geese included only body condition ($t = -3.10$, df = 22, $P = 0.005$):

$$y_{\text{Ross's Geese}} = 312.1 - 0.3(\text{BC}) \qquad (7)$$

Prolactin levels were inversely related to body condition in Ross's Geese (Fig. 1D). A linear relationship was suggested (Fig. 1E), but not statistically significant, between prolactin levels

and incubation stage in Ross's Geese (t = 1.96, df = 22, P = 0.063). Linear and quadratic models yielded similar F-values in the polynomial regression analysis; however, F-tests indicated that linear, quadratic, and cubic models were not significant at the P = 0.05 level (Table 2).

Discussion

None of the factors that we predicted would limit brood patch area were statistically significant for Snow Geese, and only clutch volume and prolactin levels were significant for Ross's Geese. Brood patch area in Ross's Geese conformed to their clutch volume (Fig. 1B). Nest size and nest habitat did not affect brood patch area in either species. Both species lost weight as incubation progressed (Equations [1] and [2]; also see Ankney and MacInnes 1978, Aldrich and Raveling 1983, Afton and Paulus 1992). Snow and Ross's geese differed in that prolactin levels had a significant, inverse relationship with brood patch area (Fig. 1C) and body condition (Fig. 1D) in Ross's Geese, but not in Snow Geese. Prolactin levels increased in Snow Geese as incubation progressed (Fig. 1A), but although this relationship was suggestive, it was not significant in Ross's Geese (Fig. 1E), possibly because during the first half of incubation, prolactin levels in Ross's Geese (Fig. 1E) were highly variable compared with those of Snow Geese (Fig. 1A).

Which factors limit brood patch area in geese? — Our results confirmed that female Ross's Geese adjusted brood patch area in relation to clutch volume, as reported for other birds (Beer 1965, Wiebe and Bortolotti 1993). By contrast, our findings on Snow Geese indicate that they do not limit breast-plucking to exposing a bare area of skin that snugly conforms to their clutch size. Perhaps, Snow Geese that lay smaller clutches (2–4 eggs) pluck a larger brood patch area than needed to warm the clutch, which allows them to warm all their eggs simultaneously and thereby reduce the need to re-arrange eggs. Arguably, some Snow Geese in our study may have suffered partial clutch loss before collection, which could confound the relationship between brood patch area and clutch volume. However, we have no evidence that such egg loss was more likely among Snow Geese than among Ross's Geese at Karrak Lake in 1996.

Brood patch area was unrelated to incubation stage in both species, perhaps because replacement down was unnecessary as incubation progressed (see Cooper 1978). Wind frequently blew down from nests at Karrak Lake, and geese were observed salvaging wind-blown down to use for lining of nests (A. D. Afton pers. obs.). Snow and Ross's geese may supplement lost nest down by breast-plucking when wind-blown down is scarce. Alternatively, breast-plucking during incubation may have been of feathers grown after the initial breast-plucking (i.e. "trimming" of brood patch) at the start of incubation. We suspect that breast-plucking occurs throughout incubation in Snow and Ross's geese, as observed in Canada Geese (Cooper 1978), though observational studies are needed to confirm this behavior.

The absence of a relationship between brood patch area and nest habitat or nest size does not indicate that heat loss through brood patches (Haftorn and Reinertsen 1985) is not important in Snow or Ross's geese; instead, we can only conclude that nesting in relatively sheltered habitats and the building of larger nests seemingly did not encourage females to pluck larger brood patch areas. Our findings on interspecific differences in nest size were similar to those of McCracken et al. (1997); we attribute subtle differences in significance levels between the two studies to (1) our smaller sample size (51 nests, compared with 105 in McCracken et al. [1997]), and (2) annual variations in either nest building or availability of nest materials or both.

Relationship between body condition and prolactin. — Circulating prolactin levels increased during late incubation in Snow Geese (Fig. 1A), and possibly in Ross's Geese (Fig. 1E). This finding agrees with the generalized effects of prolactin on terminating reproduction as summarized by Dawson and Sharp (1998). This hypothesis posits that a positive relationship between incubation stage and prolactin levels occurs because prolactin triggers either gonadal regression or brood patch regression or both, all of which are part of terminating reproduction and inducing postnuptial molt (Dawson and Sharp 1998, Dawson et al. 2001). Under this hypothesis, the inverse relationships between (1) body condition and prolactin levels (Fig. 1D) and (2) prolactin levels and brood patch area (Fig. 1C) in Ross's Geese are attributable to earlier gonadal regression because of body size constraints

and the concomitant lesser ability to maintain endogenous reserves.

Elevated prolactin levels during late incubation also are consistent with a second hypothesis, which posits that high levels of prolactin in late incubation stimulate foraging behavior (Buntin et al. 1999). Waterfowl typically take longer and more frequent incubation recesses during late incubation when females are forced to feed because of weight loss incurred during incubation (Afton and Paulus 1992, Gloutney et al. 2001, Criscuolo et al. 2002). The mechanism involved in Snow and Ross's geese may be similar to that found in Ringed Turtle-Doves, where increased levels of prolactin stimulate an increase in foraging activities (Buntin and Figge 1988, Buntin et al. 1999). Furthermore, this hypothesis explains the inverse relationship between size-adjusted body mass and prolactin levels in Ross's Geese (Fig. 1D) and its absence in Snow Geese; and it is consistent with the body-size hypothesis, which predicts that Ross's Geese mobilize endogenous reserves at faster rates than Snow Geese (Afton and Paulus 1992).

A third hypothesis posits that females in poorer body condition have higher prolactin levels, because they fed more prior to collection than females in better body condition. Our results are somewhat similar to those found in an experimental study of Common Eiders (*Somateria mollissima*), where (1) females subjected to shortened incubations had higher body masses and higher prolactin levels than control birds and (2) females subjected to prolonged incubations started to feed and had lower body masses and higher prolactin levels than control birds (Criscuolo et al. 2002). Thus, Criscuolo et al. (2002) concluded that feeding during late incubation enhanced prolactin secretion, which stimulated females to complete incubation despite being in poor body condition. This third hypothesis is interesting because Snow and Ross's geese at Karrak Lake feed during late incubation but are unable to ingest much food because the colony area is denuded of food plants (Gloutney et al. 2001, Alisauskas et al. 2006). Gloutney et al. (2001) considered alternatives to explain possible functions of feeding behavior other than nutrient acquisition, such as territorial defense, maintenance of gut flora, and search for egg shells as a calcium source. We suggest that the hypothesis of Criscuolo et al. (2002) also should be considered for Ross's Geese at Karrak Lake.

In summary, the relationship between high circulating prolactin levels and deteriorating body condition was documented previously in Ringed Turtle-Doves (Buntin et al. 1999) and Common Eiders (Criscuolo et al. 2002). That relationship is particularly intriguing in species that have little or no feeding opportunities during incubation, such as Snow and Ross's geese nesting at Karrak Lake. We encourage future studies to differentiate among the three hypotheses proposed here to explain the relationship between body condition and high circulating prolactin levels. Importantly, repeated measurements of prolactin levels from individual females throughout incubation would be useful for examining further this relationship in incubating Snow and Ross's geese. The functional significance of high levels of prolactin late in incubation (Criscuolo et al. 2002, present study) may be in preparing the females for brooding behavior of the young after hatch. Dittami (1981) found that, in female Bar-headed Geese (*Anser indicus*), presence of goslings was correlated with elevated prolactin levels posthatch, as compared with prolactin levels maintained in females with no goslings.

Effects of smaller size of Ross's Geese.—We found that the brood patch area of Ross's Geese was affected by more variables than that of Snow Geese (Fig. 1); thus, we speculate that more factors regulate brood patch area in Ross's Geese than in Snow Geese. This interspecific difference is consistent with the body-size hypothesis (Afton and Paulus 1992), regardless of whether elevated prolactin levels (1) stimulate gonadal regression, feeding behavior, or both, or (2) prolactin levels are stimulated by feeding or other behaviors; all these explanations account for the interplay between body condition and incubation stage. We speculate that the relationship between prolactin levels and body condition observed in Ross's Geese also would occur in some Snow Geese during springs when body condition is poor, because incubating Snow Geese likely would then deplete endogenous reserves earlier and at faster rates than we observed in 1996.

Our data are consistent with the idea that the smaller Ross's Geese are more sensitive to heat loss through brood patches than Snow Geese (cf. Brummermann and Reinertsen 1991), because (1) clutch volume linearly predicted the brood patch area of

Ross's Geese but not of Snow Geese, and (2) Ross's Geese built relatively larger nests than Snow Geese (McCracken et al. 1997, present study). We argue that the limited food availability at Karrak Lake (cf. Gloutney et al. 2001, Alisauskas et al. 2005) makes energy conservation particularly important for incubating females, and that conservation of energy reserves is relatively more important to Ross's Geese than to Snow Geese. We speculate that Ross's Geese conserve endogenous reserves by limiting brood patch area, thereby reducing heat loss through brood patches.

Interestingly, incubation periods of Snow and Ross's geese (23 days) are shorter than those of other goose species (Ryder 1972, Owen and Black 1990, Afton and Paulus 1992, Jónsson et al. 2006). Presumably, this is an adaptation to accelerate development of embryos and hatchlings during short Arctic summers (Poussart et al. 2000). A brood patch area larger than the minimum area required by the clutch could allow incubating females to transfer heat more efficiently to eggs, by reducing resettling rate and increasing contact area between brood patch and eggs. However, a larger-than-minimum brood patch area may not be as beneficial to Ross's Geese as it would be to Snow Geese, because (1) Ross's Goose neonates potentially need less thermal protection during late incubation than Snow Geese, given that Ross's Geese are relatively more developed at hatch (Slattery and Alisauskas 1995), and (2) Ross's Goose embryos produce more heat and grow faster during early incubation than those of Snow Geese (Craig 2000).

Acknowledgments

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