

# Egg size as a predictor of nutrient composition of eggs and neonates of Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*)

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**Abstract:** Fresh and pipped eggs were collected to provide data on nutrient composition of eggs and neonates, respectively, of Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*). We sought to determine how well a commonly used and simple index like estimated egg volume or "egg size" predicted egg composition and neonate characteristics including body composition, structural size, and digestive-organ mass. For both species, egg constituents were positively correlated with egg size, but relations for Canada Geese consistently had higher coefficients of determination than did those for Lesser Snow Geese. These differences suggest that there is more among-female variation in nutrient composition of Lesser Snow goose eggs relative to Canada Goose eggs. Most neonatal nutrient constituents were positively correlated with egg size in both species, but the relations between nutrient constituents and egg size were consistently stronger in Lesser Snow Geese than in Canada Geese. Several measures of structural size of neonates were positively correlated with egg size in both species, but egg size was a better predictor of neonate size for Lesser Snow Geese than for Canada Geese. Egg size was a relatively poor predictor of digestive-organ mass for both species. We hypothesize that the stronger relations between neonate quality and egg size in Lesser Snow Geese are a reflection of greater stabilizing selection for embryonic metabolic rates in species that nest at high latitudes and have a short incubation period. The fact that nutrient constituents of eggs were more strongly related to egg size than were the analogous constituents of neonates suggests that variation in metabolic rates of embryos limits the utility of egg size as an accurate and precise predictor of nutrient constituents in the two study species, but especially in Canada Geese.

**Résumé :** La récolte d'œufs frais et d'œufs éclos a permis d'étudier la composition en nutriments, respectivement des œufs et des oisons à la naissance, chez la bernache du Canada (*Branta canadensis interior*) et l'oie des neiges (*Chen caerulescens caerulescens*) dans le but de vérifier dans quelle mesure un indice simple et communément utilisé, comme le volume estimé de l'œuf ou la « taille de l'œuf », peut servir à prédire la composition de l'œuf et les caractéristiques de l'oison, telles que la composition du corps, la taille structurale et la masse de l'appareil digestif. Les constituants de l'œuf des deux espèces sont en corrélation positive avec la taille de l'œuf, mais les coefficients de détermination de la relation sont toujours plus élevés chez la bernache que chez l'oie. Ces différences laissent croire qu'il y a plus de variation d'une femelle à l'autre dans la composition nutritionnelle des œufs chez l'oie des neiges que chez la bernache du Canada. La plupart des constituants nutritionnels des oisons nouveau-nés sont en corrélation positive avec la taille des œufs chez les deux espèces, mais la relation est toujours plus forte chez l'oie que chez la bernache. Plusieurs mesures de la taille structurale des oisons sont en corrélation positive avec la taille des œufs chez les deux espèces, mais la taille de l'œuf prédit mieux la taille de l'oison à la naissance chez l'oie que chez la bernache. Chez les deux espèces, la taille de l'œuf prédit mal la masse de l'appareil digestif. Nous croyons que les relations plus fortes entre la qualité de l'oison et la taille de l'œuf chez l'oie des neiges est le reflet d'une sélection stabilisante plus importante des taux métaboliques embryonnaires chez cette espèce qui niche à de hautes latitudes et qui a une période d'incubation courte. Parce que les constituants nutritionnels des œufs sont plus fortement reliés à la taille des œufs que ne le sont les constituants analogues des oisons nouveau-nés, la variation des taux métaboliques des embryons semble devoir limiter l'utilisation de la taille des œufs pour prédire avec justesse et précision les constituants nutritionnels chez ces deux espèces, mais plus particulièrement chez la bernache du Canada.

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## Introduction

Intraspecific variation in egg size in birds has implications for the quality of eggs and neonates. Neonates that hatch from larger eggs may have several advantages over conspecifics that hatch from smaller eggs, including larger structural size and (or) body mass, enhanced thermoregulatory ability, greater fasting endurance, and higher nestling growth and survival rates (see reviews by Williams 1994; Bernardo 1996). These potential benefits may be due to greater quantities or proportions of lipid and (or) protein being initially present in large eggs (Ankney 1980). Further, neonates hatching from larger eggs may have larger body reserves (Alisauskas 1986; Slattery and Alisauskas 1995), greater cold-stress resistance (Rhymer 1988), higher functional maturity of muscle tissues (Alisauskas 1986; Anderson and Alisauskas 2001), or enhanced locomotor abilities (Anderson and Alisauskas 2002) than those hatching from smaller eggs.

Many studies have shown that egg size is a reasonably good predictor of the nutrient composition of eggs (e.g., Ankney 1980; Ankney and Johnson 1985; Alisauskas 1986; Rohwer 1986; Slattery and Alisauskas 1995). Some studies, however, have reported that egg size was not a good predictor of the nutrient or energy content of eggs because most of the intraspecific variation in egg size was due to variation in egg water content rather than to variation in lipid or protein content (Ricklefs 1984; Arnold 1989). Although egg size is a relatively good predictor of the initial energy content of eggs of most species, it is usually a much poorer predictor, or index, of the quality of the end-product of incubation, i.e., the neonate (Vleck and Vleck 1987, 1996). Several studies have suggested that intraspecific variation in the duration or rate of embryo metabolism reduces the precision with which egg size predicts the nutrient composition, energy content, or structural size of neonatal birds (Alisauskas 1986; Hepp et al. 1987; Vleck and Vleck 1996; MacCluskie et al. 1997).

Despite much interest in the relation between egg size and the growth and survival of young birds (see Williams 1994), relatively few studies have investigated the relations between both egg size and egg composition and measures of quality and nutrient composition of neonatal birds (e.g., Alisauskas 1986; Hepp et al. 1987; Martin and Arnold 1991; Slattery and Alisauskas 1995; Anderson and Alisauskas 2001, 2002). Therefore, the intent of this paper is to (i) provide data on the nutrient composition of eggs and neonates of Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) and (ii) determine the strengths of the relations between egg size and egg and neonate characteristics in two species of arctic-nesting geese.

## Materials and methods

The field portion of this study was conducted on the north shore of Akimiski Island, Nunavut, Canada (53°11'N, 81°35'W), during the spring of 1996. Akimiski is the largest island in James Bay (approximately 3000 km<sup>2</sup>) and is classified as subarctic habitat (Leafloor et al. 2000). A detailed description of the island habitats and north-shore study area are provided by Leafloor et al. (2000).

Eggs and goslings were collected under the authority of scientific permits issued by the Canadian Wildlife Service of

Environment Canada to J.O. Leafloor. Neonates were dealt with in accordance with the principles and guidelines of the Canadian Council on Animal Care. On 21 May 1996, 20 fresh, first-laid Canada Goose and 20 such Lesser Snow Goose eggs were randomly collected from nests of different females. Only first-laid eggs were collected, to control for any possible differences associated with laying sequence (Alisauskas 1986). If one egg was present in a nest it was assumed to be the first-laid egg, but if more than one egg was present, the first-laid egg was determined to be the one with the most stained shell (Cooper 1978). The remaining eggs in the clutch were marked, to avoid collecting neonates from those nests later that spring. Later the same day, all eggs collected were measured (length and breadth;  $\pm 0.1$  mm), weighed ( $\pm 0.01$  g), hard-boiled, reweighed, and then frozen (Ankney 1980).

During the peak hatching period (20–28 June 1996), we returned to areas where fresh eggs were previously obtained and collected 26 and 34 pipped, first-laid Canada Goose and Lesser Snow Goose eggs, respectively. Each pipped egg was measured (as described above) and then placed immediately in a portable heating unit until it hatched. Eggs were maintained at 37°C and a wet sponge added humidity to aid in the hatching process. Immediately upon hatching, goslings were killed and body mass ( $\pm 0.1$  g) was recorded; only birds that hatched  $\leq 24$  h after being collected were included in our analyses. Neonates were then frozen until necropsy and subsequent proximate analyses were conducted at the Avian Energetics Laboratory at the University of Western Ontario.

The nutrient composition of eggs was determined using laboratory methodology outlined in Alisauskas and Ankney (1985), except that neutral lipids were extracted using petroleum ether as a solvent in a modified Soxhlet apparatus to determine lean dry mass of the yolk (Dobush et al. 1985). Masses of albumen (including shell membranes) and lean dry yolk were summed to determine egg protein; masses of all egg constituents were taken to the nearest 0.01 g. Egg lipid mass was determined by subtracting lean dry yolk mass from dry yolk mass. Eggshell mass was the mass of the dried eggshell. Egg volume (hereinafter egg size) of each fresh and pipped egg was estimated from their linear dimensions (see above) using the following equation: volume (cm<sup>3</sup>) =  $K_v \times LB^2$ , where  $K_v = 0.51$  and  $L$  (length) and  $B$  (breadth) are in centimetres (Hoyt 1979);  $K_v$  is a shape constant generally applicable to eggs of waterfowl.

Neonates were thawed, weighed ( $\pm 0.001$  g), plucked, and reweighed in the laboratory at the University of Western Ontario. Structural measurements ( $\pm 0.1$  mm) of neonates were made only by S.S.B. and followed methods described in Dzubin and Cooch (1992) and Badzinski et al. (2001). Measurements taken included skull length, culmen (culmen1), tarsal bone (tarsus), keel, wing length ( $\pm 1$  mm), and body length ( $\pm 1$  mm). Species-specific principal-component analyses were performed on the correlation matrices of the univariate size measures to develop a multivariate index of neonate structural size (PROC PRINCOMP; SAS Institute Inc. 1990). The principal component 1 (PC1) scores for each neonate represented its overall structural size relative to conspecifics in the sample.

To reduce bias and systematic error, dissections of all neonates were done by S.S.B. and followed a regimented order

for removing and weighing body parts; masses of all neonate body components were taken to the nearest 0.001 g. Left breast muscles (pectoralis and supracoracoideus), left leg muscles (muscles attached to the femur, tibiotarsus, and tarsometatarsus), and yolk sac were excised, weighed, and saved for subsequent drying and lipid extractions. The digestive tract was removed and dissected into esophagus, proventriculus, gizzard, small intestine, large intestine, and caeca. Organs were emptied of contents, stripped of adhering fat (subsequently returned to the carcass), separately weighed, and saved for drying.

Body composition of neonates was generally determined using laboratory methods described in Alisauskas and Ankney (1985) and later modified by Ankney and Afton (1988), with one exception: ash content of the carcass was determined directly from the entire carcass homogenate. Nutrient constituents of the yolk sac were determined separately from neonate body composition. Yolk-sac contributions were later added to carcass constituents (i.e., protein and lipid) to calculate total protein and total lipid stores of the neonate. Carcass water was calculated by subtracting ash, protein, and lipid masses of the carcass from plucked ingesta- and yolk-sac-free body mass. Total water was carcass water plus water contained in the yolk sac. Dry mass was used as a proxy for the protein content of the heart and digestive organs because the lipid content of these tissues was considered to be negligible. Energy content of eggs and neonates was calculated from the energy equivalents  $23.7 \text{ kJ}\cdot\text{g}^{-1}$  of protein and  $39.8 \text{ kJ}\cdot\text{g}^{-1}$  of lipid (Ricklefs 1977).

All statistical analyses were two-tailed and considered significant at  $P \leq 0.05$ . Summary statistics are reported with their standard errors ( $\pm$ SE). Student's  $t$  tests were used to determine if the sizes of fresh eggs differed from those of piped eggs (PROC TTEST; SAS Institute Inc. 1990). Ordinary least squares (OLS) (simple linear regression) was used to determine the relation between egg nutrient constituents and egg size and neonate characteristics (nutrient composition, structural size, digestive-organ mass) and egg size (PROC REG; SAS Institute Inc. 1990). The mass of each egg constituent and length or mass of each neonate characteristic ( $Y$ ) was regressed on egg size ( $X$ ) to estimate the intercept ( $a$ ) and slope ( $b$ ) for the relations. Coefficients of determination ( $r^2$ ) from OLS regressions were used as an index of how well egg size predicted egg constituents and neonate characteristics for each species. Residuals were plotted against egg size to assess if model assumptions were satisfied (Zar 1996); all models reasonably met assumptions of linear models. We acknowledge that other statistical techniques, including reduced major axis and major axis regressions, are available to determine the structural relation between an independent and a dependent variable, but presently there is no consensus as to which is most appropriate in avian nutrient composition studies (T. Arnold and A. Green, personal communication). Compared with reduced major axis and major axis regressions, OLS regression is always the most appropriate statistical technique to use for predictive purposes (T. Arnold and A. Green, personal communication). Given that our main objective was to predict nutrient contents from egg size and to assess the strengths of these relations, we believe that using arithmetic (non-transformed), as opposed to logarithmic (transformed), data

and OLS regression was most appropriate to analyze these data.

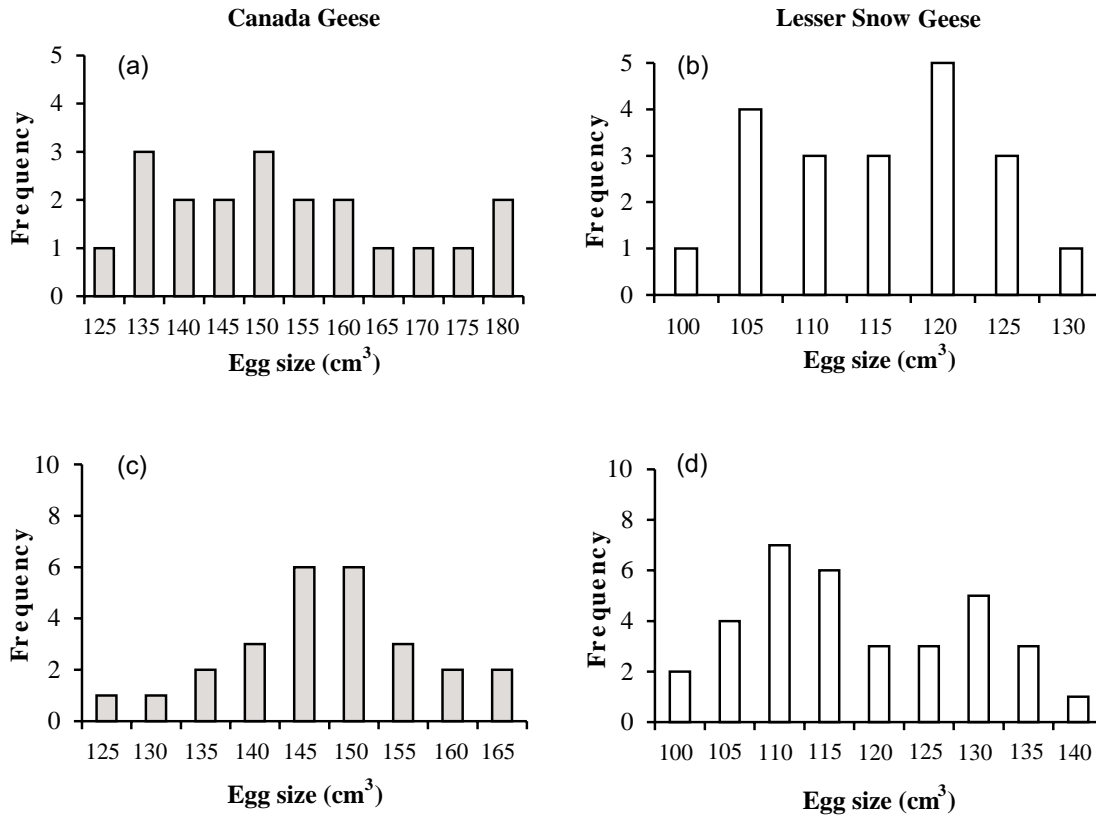
## Results

For each species, the sizes of eggs used for determining egg composition did not differ from those used to determine proximate composition of neonates (Canada Geese:  $\bar{x} = 152.33 \pm 3.46 \text{ cm}^3$  vs.  $\bar{x} = 147.46 \pm 1.97 \text{ cm}^3$ ,  $t_{[19,25]} = 1.22$ ,  $P = 0.2306$ ; Lesser Snow Geese:  $\bar{x} = 115.25 \pm 1.79 \text{ cm}^3$  vs.  $\bar{x} = 117.74 \pm 1.93 \text{ cm}^3$ ,  $t_{[19,33]} = -0.87$ ,  $P = 0.3478$ ). Frequency distributions of estimated egg sizes used in proximate analyses of fresh eggs and neonates were nearly identical, but the eggs used in Canada Goose egg composition analyses included some that were larger than those from which neonates were collected (Fig. 1).

Egg size explained 98 and 96% of the variation in mass of Canada and Lesser Snow goose eggs, respectively (Table 1). Egg size also explained >90% of the variation in water content of eggs of both species and 88 and 79% of the variation in dry egg mass for Canada and Lesser Snow geese, respectively. For Canada Geese, egg size explained nearly all (94%) of the variation in total egg protein but less of the variation in dry albumen (67%) and yolk protein (70%). Total protein of Lesser Snow goose eggs was also more highly correlated with egg size than was dry albumen or yolk protein. Dry yolk mass of Canada and Lesser Snow goose eggs was more strongly related to egg size than were its separate components, yolk protein and yolk lipid. Energy content of eggs increased with egg size in both species. Egg size explained more variation in energy content of eggs for Canada Geese ( $r^2 = 0.86$ ) than for Lesser Snow Geese ( $r^2 = 0.70$ ). Generally, egg size explained more of the variation in mass of egg constituents and energy content for Canada Geese (higher  $r^2$  for each constituent) than for Lesser Snow Geese. However, the rank order of variation in major egg constituents explained by egg size ( $r^2$ ) was the same for the two species: egg water > protein > lipid > shell.

Almost all regressions relating body composition of neonatal Canada Geese and Lesser Snow Geese to their egg sizes were significant ( $P_{b=0} < 0.05$ ); however, dry yolk sac, yolk-sac protein, and yolk-sac lipid of neonate Canada Geese were not correlated with egg size ( $P_{b=0} > 0.05$ ) (Table 2). Egg size explained 79 and 64% of the variation in body mass of Lesser Snow Geese and Canada Geese, respectively. Coefficients of determination for the remaining body components of Canada Geese were considerably lower than that for body mass and ranged from 0.51 for dry body mass to 0.27 for carcass lipid. Energy content of neonatal Canada Geese increased with egg size; egg size accounted for 41% of the variation in this relationship. With the exception of total ash and carcass lipid, body components and energy content of neonatal Lesser Snow Geese were consistently more strongly correlated with egg size than were the same components of neonatal Canada Geese. In neonatal Lesser Snow Geese, total ash ( $r^2 = 0.34$ ), total lipid ( $r^2 = 0.38$ ), carcass lipid ( $r^2 = 0.22$ ), and carcass protein ( $r^2 = 0.29$ ) were most weakly related to egg size; relations were stronger between dry mass, ash-free dry mass, total water, total protein, and egg size ( $r^2 = 0.74$ – $0.62$ ). Mass of dry yolk sac, yolk-sac lipid, and yolk-sac protein were positively, although weakly,

**Fig. 1.** Frequency distributions of sizes of Canada Goose (*Branta canadensis interior*) and Lesser Snow Goose (*Chen caerulescens caerulescens*) eggs used for egg-composition (a and b) and neonate (c and d) analyses.



correlated with egg size in Lesser Snow Geese. In contrast, yolk-sac components of Canada Geese were not correlated with egg size. Egg size explained 58% of the variation in energy content of neonatal Lesser Snow Geese. Additionally, coefficients of determination for neonatal energy content and body composition of both species were consistently lower than those of their corresponding egg constituents (see Tables 1 and 2).

Most variation in univariate measures of structural size and in overall body size (PC1) for neonates of both species was not explained by variation in egg size (Table 3). Keel length was not correlated with egg size in Canada Geese. Regressions relating culmen ( $P_{b=0} = 0.0961$ ) and tarsus ( $P_{b=0} = 0.0689$ ) measurements, two commonly used univariate indices of structural size, in Canada Geese to egg size also were not significant. Coefficients of determination in the remaining relations ranged from 0.22 to 0.29. Measures of structural size were generally more strongly correlated with egg size in Lesser Snow Geese and were most apparent when coefficients of determination for the relation between body size of Canada Geese ( $r^2 = 0.26$ ) and Lesser Snow Geese ( $r^2 = 0.46$ ) and egg size were compared.

Nearly all regressions relating masses of digestive organs of neonatal Canada Geese and Lesser Snow Geese to egg size were not significant ( $P_{b=0} > 0.05$ ) (Table 4). Only lean dry liver mass and total dry digestive organ mass of Canada and Lesser Snow geese and dry mass of esophagus and caeca of Lesser Snow Geese were positively related to egg

size ( $P_{b=0} < 0.05$ ), but coefficients of determination from these relations were relatively low ( $r^2 = 0.13$ – $0.30$ ).

## Discussion

The ability to predict egg nutrient constituents from egg size allows for estimation of female nutrient investment in a clutch of eggs or the amount of protein and lipid deposited in a single, unincubated egg of a specific size. The latter application has been used to assess egg nutrient use during embryonic growth by comparing estimated fresh egg composition with actual nutrient composition of neonates (Alisauskas 1986; Slattery and Alisauskas 1995; Badzinski et al. 2001). Clearly, the precision and accuracy with which egg size can predict different egg constituents is important for such studies. Our results suggest that egg size was a reasonably good predictor of most nutrient constituents of Canada and Lesser Snow goose eggs, but the precision and accuracy of estimates varied among egg components within and between species. Egg size predicted fresh egg mass very well for both Canada Geese ( $r^2 = 0.98$ ) and Lesser Snow Geese ( $r^2 = 0.96$ ), which agrees with the results of previous studies that used an egg-size index to estimate fresh egg mass for Brown-headed Cowbirds (*Molothrus ater*) ( $r^2 = 0.97$ ; Ankney and Johnson 1985), American Coots (*Fulica americana*) ( $r^2 = 0.93$ ; Alisauskas 1986), Ross' Geese (*Chen rossii*) ( $r^2 = 0.96$ ; Slattery and Alisauskas 1995), and Lesser Snow Geese ( $r^2 = 0.95$ ; Slattery and Alisauskas 1995). Fresh eggs of both Canada

**Table 1.** Statistics from ordinary least squares (OLS) regression of Canada Goose (*Branta canadensis interior*) and Lesser Snow Goose (*Chen caerulescens caerulescens*) egg constituents (g) on their estimated egg sizes (cm<sup>3</sup>).

Component	$r^2$	Intercept (a)	Slope (b)	SE (b)	$P_{b=0}$
<b>Canada Geese (N = 20)</b>					
Fresh mass	0.98	3.08	1.06	0.03	0.0001
Dry mass	0.88	10.14	0.33	0.03	0.0001
Shell-free dry mass	0.91	4.28	0.26	0.02	0.0001
Shell <sup>a</sup>	0.44	5.86	0.07	0.02	0.0013
Water	0.96	-7.06	0.73	0.04	0.0001
Yolk <sup>a</sup>	0.72	3.78	0.19	0.03	0.0001
Lipid	0.68	2.71	0.12	0.02	0.0001
Yolk protein	0.70	1.07	0.07	0.01	0.0001
Protein	0.94	1.57	0.14	0.01	0.0001
Albumen <sup>a</sup>	0.67	0.50	0.07	0.01	0.0001
Energy (kJ)	0.86	145.03	7.99	0.75	0.0001
<b>Lesser Snow Geese (N = 20)</b>					
Fresh mass	0.96	17.03	0.94	0.05	0.0001
Dry mass	0.79	12.08	0.28	0.04	0.0001
Shell-free dry mass	0.78	6.15	0.23	0.03	0.0001
Shell <sup>a</sup>	0.22	5.93	0.05	0.02	0.0362
Water	0.91	4.95	0.65	0.05	0.0001
Yolk <sup>a</sup>	0.49	6.52	0.16	0.04	0.0006
Lipid	0.40	4.27	0.10	0.03	0.0028
Yolk protein	0.45	2.26	0.06	0.02	0.0012
Protein	0.81	1.88	0.14	0.02	0.0001
Albumen <sup>a</sup>	0.56	-0.38	0.08	0.02	0.0002
Energy (kJ)	0.70	214.35	7.14	1.11	0.0001

<sup>a</sup>Dry mass.

and Lesser Snow geese contain about 64% water (Badzinski et al. 2001), so it was not surprising that this constituent was highly correlated with egg size in both species. Although water content is important for proper embryonic development, egg hatchability, and survival for some species, egg quality is usually assessed from the amount of lipid and protein, and thus energy, it contains (Vleck and Vleck 1996).

Egg protein mass and egg lipid mass of Canada and Lesser Snow goose eggs were positively correlated with egg size. These results agree with those from other studies of egg composition in waterfowl (e.g., Ankney 1980; Birkhead 1984, 1985; Rohwer 1986; Hepp et al. 1987; Slattery and Alisauskas 1995) which have shown that bigger eggs contain more nutrients. Egg protein was more highly correlated with egg size than was either dry yolk or lipid mass in both Canada Geese and Lesser Snow Geese. Studies on egg composition in both the American Coot and Blue-winged Teal (*Anas discors*) have shown that within-clutch variation in albumen mass was greater than that in lipid mass (Alisauskas 1986; Rohwer 1986). Therefore, because each egg in this study was collected from a different nest, the substantial variation in yolk components not explained by egg size likely was due to among-female differences in lipid deposition during rapid follicular growth. For a given size, eggs with less lipid must have more protein and water, and vice versa, because protein contains a constant fraction of water and lipid is hydrophobic; they are also proportionately the largest components of

eggs. This probably explains why protein and water were consistently more strongly related to egg size than was egg lipid in Canada and Lesser Snow geese and several other bird species (Ricklefs et al. 1978; Birkhead 1984; Ricklefs 1984; Ankney and Johnson 1985; Rohwer 1986; Martin and Arnold 1991). Despite this, egg size predicted, although less reliably, the lipid content of Canada and Lesser Snow goose eggs.

Egg constituents were more strongly related to egg size for Canada Geese than for Lesser Snow Geese. This likely was not related to interspecific differences in egg shape and the consequent inability of the constant ( $K_v$ ) to account for such differences because egg size explained only 2% more variation in fresh mass for Canada Goose eggs than for Lesser Snow Goose eggs. Thus, we conclude that there is simply more among-female variation in egg composition in Lesser Snow Geese than in Canada Geese. This greater variation could occur if egg composition has a higher repeatability in Lesser Snow Geese than in Canada Geese. Further investigation of variation in egg composition with respect to egg size, egg sequence, clutch (female), clutch size, and laying date is needed in order to better assess sources of variation in egg quality in these two and other species of birds (e.g., Rohwer 1986; Arnold et al. 1991).

Large body size and body mass of neonates may be important determinants of survival for some bird species by providing them with possible energetic advantages (Ankney

**Table 2.** Statistics from OLS regression of Canada and Lesser Snow goose neonate body constituents (g) on their estimated egg sizes (cm<sup>3</sup>).

Component	$r^2$	Intercept (a)	Slope (b)	SE (b)	$P_{b=0}$
<b>Canada Geese (N = 26)</b>					
Body mass	0.64	25.160	0.568	0.088	0.0001
Dry mass	0.51	3.452	0.214	0.043	0.0001
Ash-free dry mass	0.43	0.761	0.168	0.040	0.0003
Total ash	0.50	0.017	0.010	0.002	0.0013
Total water	0.49	21.710	0.354	0.073	0.0001
Yolk sac <sup>a</sup>	0.02	1.514	0.040	0.055	0.4717
Total lipid	0.32	-2.177	0.096	0.029	0.0024
Carcass lipid	0.46	-3.358	0.079	0.017	0.0001
Yolk-sac lipid	0.01	1.181	0.018	0.030	0.5660
Yolk-sac protein <sup>a</sup>	0.03	0.333	0.023	0.027	0.3996
Total protein	0.37	2.938	0.071	0.018	0.0009
Carcass protein	0.27	2.605	0.048	0.016	0.0069
Energy (kJ)	0.41	-17.006	5.524	1.368	0.0005
<b>Lesser Snow Geese (N = 34)</b>					
Body mass	0.79	0.124	0.748	0.069	0.0001
Dry mass	0.63	1.502	0.229	0.031	0.0001
Ash-free dry mass	0.62	-3.096	0.201	0.028	0.0001
Total ash	0.34	0.283	0.007	0.002	0.0003
Total water	0.74	-1.379	0.520	0.055	0.0001
Yolk sac <sup>a</sup>	0.41	-7.654	0.128	0.028	0.0001
Total lipid	0.38	0.559	0.071	0.016	0.0001
Carcass lipid	0.22	2.282	0.026	0.009	0.0054
Yolk-sac lipid	0.25	-1.723	0.045	0.014	0.0029
Yolk-sac protein <sup>a</sup>	0.48	-5.931	0.083	0.015	0.0001
Total protein	0.66	-3.654	0.130	0.017	0.0001
Carcass protein	0.29	2.277	0.047	0.013	0.0010
Energy (kJ)	0.58	-64.367	5.912	0.888	0.0001

<sup>a</sup>Dry mass.**Table 3.** Statistics from OLS regression of Canada and Lesser Snow goose structural measures (mm) on their estimated egg sizes (cm<sup>3</sup>).

Component	$r^2$	Intercept (a)	Slope (b)	SE (b)	$P_{b=0}$
<b>Canada Geese (N = 26)</b>					
Skull length	0.28	38.6	0.1	<0.1	0.0047
Culmen	0.11	12.6	<0.1	<0.1	0.0961
Tarsus	0.13	24.4	0.1	<0.1	0.0689
Keel	0.01	22.4	<0.1	<0.1	0.7390
Wing length	0.22	39	<1	<1	0.0146
Body length	0.25	135	<1	<1	0.0090
Body size (PC1)	0.26	-14.5	0.1	<0.1	0.0073
<b>Lesser Snow Geese (N = 34)</b>					
Skull length	0.29	37.3	0.1	<0.1	0.0012
Culmen	0.34	12.8	<0.1	<0.1	0.0003
Tarsus	0.23	23.7	0.1	<0.1	0.0040
Keel	0.24	15.3	<0.1	<0.1	0.0030
Wing length	0.30	44	<1	<1	0.0007
Body length	0.44	131	<1	<1	0.0001
Body size (PC1)	0.46	-14.0	0.1	<0.1	0.0001

**Table 4.** Statistics from OLS regression of Canada and Lesser Snow goose digestive-organ sizes (mm) on their estimated egg sizes (cm<sup>3</sup>).

Component <sup>a</sup>	r <sup>2</sup>	Intercept (a)	Slope (b)	SE (b)	P <sub>b = 0</sub>
<b>Canada Geese (N = 26)</b>					
Esophagus	0.08	0.026	<0.001	<0.001	0.1572
Proventriculus	0.09	0.005	<0.001	<0.001	0.1323
Gizzard	0.12	0.122	0.003	0.002	0.0867
Small intestine	0.03	0.101	<0.001	<0.001	0.4447
Caeca	0.06	0.004	<0.001	<0.001	0.2182
Large intestine	0.01	0.024	<0.001	<0.001	0.6426
Liver	0.30	-0.152	0.005	0.001	0.0036
Total gastrointestinal mass	0.20	0.130	0.009	0.004	0.0220
<b>Lesser Snow Geese (N = 34)</b>					
Esophagus	0.13	0.023	<0.001	<0.001	0.0340
Proventriculus	0.05	0.025	<0.001	<0.001	0.2101
Gizzard	0.10	0.241	0.003	0.001	0.0669
Small intestine	0.10	0.060	0.001	<0.001	0.0726
Caeca	0.19	<0.001	<0.001	<0.001	0.0096
Large intestine	0.01	0.022	<0.001	<0.001	0.6964
Liver	0.25	0.133	0.002	0.001	0.0029
Total gastrointestinal mass	0.20	0.504	0.006	0.002	0.0076

<sup>a</sup>Lean dry mass was used for liver analysis and dry tissue mass for all other analyses.

1980; Alisauskas 1986; Slattery and Alisauskas 1995; Anderson and Alisauskas 2002), enhanced motor performance (Anderson and Alisauskas 2001), and thermoregulatory advantages (Rhymer 1988) relative to smaller conspecifics. Numerous previous studies have shown a positive correlation between egg size and hatchling mass, but few have reported on the relation between egg size and structural size of neonates (see Williams 1994). Our results show that larger eggs of both species produced heavier and structurally larger neonates than did smaller eggs; neonates hatching from larger eggs also had more lipid, protein, total energy, and digestive tissues than those hatching from smaller eggs. These findings support those of other studies of egg size and nutrient composition done on young waterfowl (Hepp et al. 1987; Slattery and Alisauskas 1995; Anderson and Alisauskas 2002).

As in most similar studies, we also found that most nutrient constituents of neonatal Canada and Lesser Snow geese were positively correlated with egg size, but the reliability of predicting these constituents differed among body components within, and between, species. For example, some studies have shown that yolk reserves in some altricial (Rofstad and Sandvik 1987), semiprecocial (Parsons 1970; Birkhead and Nettleship 1984), and precocial (Thomas and Peach Brown 1988) birds increase with egg size. Consistent with the findings of those studies, dry yolk sac mass, as well as residual yolk lipid and yolk protein masses, were positively, but weakly, correlated with egg size in Lesser Snow Geese. The size of yolk reserves in neonatal Canada Geese, however, was independent of egg size. Many studies that related survival of hatchlings to egg size have assumed that larger eggs result in young that have larger yolk reserves (e.g., Schifferli 1973; O'Connor 1979; Ankney 1980; Bolton 1991; Grant 1991), but clearly that assumption does not hold for the *interior* subspecies of the Canada Goose. The primary function of the residual yolk, however, seems to relate to

early growth, and body lipid is more important for survival (Peach and Thomas 1986; Duncan 1988). Given our results, it appears that egg size was not an overly good predictor of energy stores for Canada or Lesser Snow geese because carcass lipid and total lipid masses were only weakly correlated with egg size. Relative to other major body constituents, lipid mass was also weakly correlated with egg size in other precocial and semiprecocial birds (e.g., American Coot (Alisauskas 1986); Arctic Tern, *Sterna paradisaea* (Østnes et al. 1997); Japanese Quail, *Coturnix japonica* (Ricklefs et al. 1978; Martin and Arnold 1991); Laughing Gull, *Larus atricilla* (Ricklefs et al. 1978); Lesser Snow Geese (Slattery and Alisauskas 1995); Ross' Goose (Slattery and Alisauskas 1995); and Wood Duck, *Aix sponsa* (Hepp et al. 1987)).

Another pattern often observed in studies that have related size of eggs to both egg and neonatal composition is that egg size explains more variation in protein and lipid masses for fresh eggs than it does for the corresponding constituents in neonates (Ricklefs et al. 1978; Alisauskas 1986; Hepp et al. 1987; Martin and Arnold 1991). This general result could be a statistical artifact because lipid necessarily decreases as an embryo develops, and correlations with smaller components would be smaller because measurement error, which is a fixed quantity, is a higher fraction of smaller components than of larger ones. Alternatively, genetically based variation in metabolic rate among embryos, further modified by maternal and environmental influences, is probably the primary factor contributing to this pattern. MacCluskie et al. (1997) found that, after controlling for maternal effects, the time required for Mallard (*Anas platyrhynchos*) embryos to reach the star-pipped stage of hatch varied considerably among clutches (females) and that there was a tendency for metabolic rates of embryos to vary among clutches. Further, the rate of lipid metabolism, an indirect measure of embryonic metabolic rate, varied considerably among American Coot

(Alisauskas 1986) and Wood Duck embryos (Hepp et al. 1987). We also observed that the correlation between lipid mass of neonates and egg size was weaker than that between egg lipid mass and egg size, which supports the idea that there is considerable variation among individual embryos of Canada and Lesser Snow geese, independent of egg size, in their rates of lipid metabolism.

In this study, coefficients of determination were also consistently higher in regressions relating nutrient constituents and energy content of neonatal Lesser Snow Geese to their egg sizes than in similar relations for Canada Geese. To further illustrate this, we calculated percent change in the coefficients of determination between corresponding egg and neonate nutrient constituents and energy content for Canada and Lesser Snow geese and found much smaller changes in the comparisons for Lesser Snow Geese than in those for Canada Geese (e.g., percent change (egg/neonate) in Canada Geese versus Lesser Snow Geese: ash-free dry mass: 53 vs. 21%; protein: 61 vs. 19%; lipid: 53 vs. 5%; energy: 52 vs. 17%). These calculations, especially those for energy content, suggest that there is more intraspecific variation in embryonic metabolic rates in Canada Geese than in Lesser Snow Geese. Badzinski et al. (2001) found that rates of egg nutrient metabolism in Lesser Snow Goose embryos were much higher than those of Canada Goose embryos and suggested that this was the proximate result of intense selection for rapid embryonic growth and development, ultimately related to unique life-history features of Lesser Snow Geese (i.e., coloniality and High Arctic environment). Selection for high metabolic / embryonic-growth rates may have simultaneously selected for reduced variability in these rates. If metabolic or embryonic-growth rates of Lesser Snow Geese are at or near their maximum, variability may be much reduced compared with that in a species which is farther from its maximum value. There is some evidence that such a relationship exists because, relative to egg mass ( $\bar{x} = 125$  g; Badzinski 1998), Lesser Snow Geese have one of the shortest incubation periods ( $\bar{x} = 23$  days; Cooke et al. 1995) within the Anatidae. Therefore, the higher variability in embryonic metabolism of protein and lipid among Canada Geese may be a consequence of more variable embryonic-growth rates, which are ultimately likely related to the average environmental conditions encountered at hatch (Badzinski et al. 2001).

A relatively large variation in neonate body mass and energy reserves has also been reported for Giant Canada Geese (*Branta canadensis maxima*) in southern Ontario (Thomas and Peach Brown 1988). Thomas and Peach Brown (1988) suggested that small goslings with low energy reserves might be able to survive at more southerly latitudes because they experience a less stressful climate and have a more readily available food supply than do arctic geese. Interestingly, the coefficient of determination relating hatchling mass of Giant Canada Geese to egg size (mass) was 0.40, which is lower than that for our more northerly breeding *interior* subspecies ( $r^2 = 0.64$ ). This suggests that metabolic rates of Giant Canada Goose embryos were even more variable than those of Canada Geese inhabiting subarctic environments and likely resulted from less intense selection pressures associated with their more "southerly" historical environments, i.e., tall-grass and mixed prairie areas of central North America (Hanson 1965). These intraspecific differences in embryonic meta-

bolic rates within *Branta canadensis* spp. support mounting evidence that many birds, particularly arctic geese, are adapted to environmental conditions they encounter at hatch and during the pre fledging growth period (Lack 1968; Sedinger 1986; Slattery and Alisauskas 1995; Badzinski et al. 2001, 2002).

We conclude that egg size, a simple index of egg volume, predicted most egg constituents of Canada and Lesser Snow geese and also, although much less reliably, the nutrient composition and energy content of neonates of both species. The differences we found between these two goose species with respect to how precisely egg size predicted nutrient reserves and composition of neonates shows the importance of assessing variation in both eggs and neonates before analyzing the relation between egg size and growth and survival of young birds. Investigation of the specific mechanisms by which egg size may confer survival advantages on young birds is an important and necessary step toward a better understanding of this general and somewhat inconsistent pattern in avian ecology.

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