COMPOSITION OF EGGS AND NEONATES OF CANADA GEESE AND LESSER SNOW GEESE

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ABSTRACT.—We collected eggs, neonates, and adults of Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) from Akimiski Island, Nunavut, during the 1996 breeding season. This was done to assess interspecific differences in egg composition, egg-nutrient catabolism, developmental maturity, tissue maturity, and body reserves, and to relate observed differences in those variables to ecological conditions historically experienced by Canada Geese and Lesser Snow Geese. Eggs of both species had identical proportional compositions, but Canada Goose embryos catabolized 13% more of their egg protein, whereas Lesser Snow Goose embryos catabolized 9% more of their egg lipid. Neonate Canada Geese and Lesser Snow Geese had similar protein reserves, relative to body size, but Lesser Snow Geese had relatively smaller lipid reserves than did Canada Geese. Relative to conspecific adults, Lesser Snow Goose goslings generally were structurally larger at hatch than were Canada Goose goslings. Neonate Lesser Snow Geese had more developmentally mature keels, wings, and breast muscles, and larger gizzards and caeca for their body size, than did neonate Canada Geese. Despite hatching from smaller eggs and having a shorter period of embryonic growth, skeletal muscles and gizzard tissues of Lesser Snow Geese were more functionally mature than those of Canada Geese. Increased lipid use during embryonic development could account for how Lesser Snow Geese hatched in a more developmentally and functionally mature state. In turn, differences in developmental and functional maturity of Lesser Snow Geese, as compared to Canada Geese, likely are adaptations that offset metabolic costs associated with their small body size, or to selection pressures associated with high arctic environmental conditions and colonial nesting and brood rearing. *Received 21 March 2000, accepted 28 February 2001.*

Composition and size of eggs influence growth and survival of young birds (see review by Williams 1994), but few studies have related egg characteristics and egg-nutrient use to body composition and development of neonatal birds (but see Ricklefs et al. 1978, Alisauskas 1986, Slattery and Alisauskas 1995). Differences in initial egg composition or embryonic use of egg nutrients affects body composition, functional maturity of tissues, and developmental maturity of internal and external body components of neonatal birds (Alisauskas 1986).

Eggs laid by precocial birds typically have higher energy densities than eggs of altricial species (Carey et al. 1980). Furthermore, compared to young of altricial birds, precocial young are more developmentally mature at hatch and have muscle tissues that are more

functionally mature, thereby enhancing the ability of hatchlings to thermoregulate (Ricklefs and Webb 1985, Visser and Ricklefs 1995), and acquire, process, and assimilate food (Ricklefs 1983). Neonate Ross' Geese (*Chen rossii*) neonates, for example, have relatively heavier gizzards and more functionally mature gizzard, breast, and leg muscle tissues than do neonate Lesser Snow Geese (*Chen caerulescens caerulescens*) and may be adaptations for more efficient thermoregulation and nutrient assimilation (Slattery and Alisauskas 1995).

Egg and body composition also affects neonate energetics and thus survival during nutritional or thermal stress (Ankney 1980, Rhymer 1988). During nutritional stress, neonates with more lipid relative to body size have more available energy and should survive better than those in relatively poorer condition (Slattery and Alisauskas 1995). Further, heavier neonates normally have lower mass-specific met-

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abolic and heat-loss rates than do lighter neo-
nates (Ricklefs 1983). Consequently, relatively
small birds living in cold environments may
possess large lipid stores or other physiological
adaptations that offset potential size related
energetic costs.

Historically, breeding ranges of dispersed-
nesting Interior Canada Geese (*Branta canaden-
sis interior*) and colonial-nesting Lesser Snow
Geese were separate, but recently Lesser Snow
Geese have expanded southward and estab-
lished breeding colonies in subarctic regions of
Hudson and James Bay, Canada, where Canada
Geese normally breed (Abraham and Jefferies
1997). Presently, the southern most known
Lesser Snow Goose colony in the world is on
Akimiski Island, Nunavut. Based on mitochon-
drial DNA sequence divergence between Can-
ada Geese breeding on Akimiski Island and
those on the adjacent mainland, Leafloor (1998)
postulated that Canada Geese began nesting
on Akimiski soon after it emerged from James
Bay (approximately 3,500–4,000 years ago;
Martini and Glooschenko 1984). Lesser Snow
Geese, however, have only been breeding reg-
ularly on Akimiski since 1968 (Abraham et al.
1999). High rates of gene flow among Lesser
Snow Geese colonies (Rockwell and Cooke
1977), suggests that individuals of northern
and southern populations are genetically sim-
ilar and thus possess the same adaptations.
Therefore, a comparison of Canada Goose and
Lesser Snow Goose neonates where they are
now syntopic may elucidate the ultimate role
that ecological conditions have on early growth
and developmental patterns in northern geese.

Our study objectives were to (1) determine if
interspecific differences in neonatal body com-
position, developmental maturity, and tissue
maturity were related to such differences in
egg composition or egg-nutrient catabolism,
and (2) test our hypothesis that two species of
geese that have evolved under different ecolog-
ical conditions would differ at hatch with re-
spect to functional maturity of their tissues and
developmental maturity of their internal and
external body components. We predicted that
neonate Lesser Snow Geese would be more de-
veloped and their tissues more functionally
mature than those of Canada Geese due to se-
lective pressures associated with high arctic
environments and their colonial lifestyle. Be-
cause Lesser Snow Geese are smaller than Can-

ada Geese and neonates living in the high arctic
may experience longer periods of energetic
stress than do subarctic neonates, we also pre-
dicted that Lesser Snow Geese would have rel-
atively larger lipid stores or more functionally
mature muscles, or both, than would Canada
Geese.

STUDY AREA AND METHODS

STUDY AREA

This study was conducted on the north shore of
Akimiski Island, Nunavut (53°11′N, 81°35′W). Ak-
imiski is the largest island in James Bay with an area
of ~3,000 km² and is classified as subarctic habitat.
The north shore is characterized by extensive coastal
mudflats and intertidal and supratidal salt marshes
(Riley 1981). Major vegetation zones are a progres-
sion of *Puccinellia phryganodes* in low marsh to *Carex
subspathacea* in high salt marsh areas and from there
grading into supratidal and freshwater marsh dom-
inated by *Festuca rubra* and *Carex aquatilus* (Leafloor
et al. 2000).

EGGS

Collections.—On 21 May 1996, 20 fresh, first-laid
eggs were collected from nests of Canada Geese and
Lesser Snow Geese. Only first-laid eggs were col-
lected to control for possible differences in compo-
sition related to laying sequence (Alisauskas 1986)
and to compare our data to those of Slattery and Al-
isauskas (1995). If one egg was present in a nest at
the time of collection, it was assumed to be the first-
laid egg, but if more than one egg was present the
most heavily stained egg was assumed to have been
laid first (Cooper 1978). Remaining eggs in a nest
were marked to avoid later collection of neonates
from those nests. Egg length and breadth (±0.1 mm)
were measured using digital calipers, and eggs were
weighed (±0.1 g), hard-boiled (Ankney 1980), re-
weighed, and frozen.

Egg composition.—Composition of eggs was deter-
mined using methods modified from Alisauskas and
Ankney (1985) and Dobush et al. (1985). Mass of al-
bumen and lean dry yolk were summed to calculate
egg protein mass (±0.01 g). Lipid was determined by
subtracting lean dry yolk mass from dry yolk mass
(±0.01 g). Egg mineral was mass of the dried egg
shell (±0.01 g).

NEONATES AND ADULTS

Collections.—During peak hatch (20–28 June 1996),
28 and 35 pipped, first-laid eggs of Canada and Less-
er Snow geese, respectively, were collected from the
areas where fresh eggs were collected. Each pipped

egg was measured and put in a portable heating unit at 37°C until it hatched ≤24 h after collection. Neonates were killed immediately upon hatching, weighed (±0.1 g), and frozen.

Following Sedinger (1986), flightless adults were collected and used as a comparative standard for assessment of gosling growth and development. From 2–5 August 1996, we collected 19 adult Canada Geese (n_{CGmale} = 10, $n_{CGfemale}$ = 9) and 19 adult Lesser Snow Geese ($n_{LSGmale}$ = 10, $n_{LSGfemale}$ = 9) during banding operations (see Leafloor et al. 2000). Molt-migrant Giant Canada Geese (*Branta canadensis maxima*) were excluded from collection using morphometric criteria developed to discriminate them from Akimiski Island Canada Geese (Merendino et al. 1994). Other criterion for collection of adults included ≥5 clear primary shafts, sheathed penis, and a distinct brood patch; characteristics suggestive of flight ability (Weller 1957) and sexual maturity (Hanson 1962), respectively.

Structural measurements.—Unless otherwise noted, structural measurements (±0.1 mm) were made by one observer (SSB) and followed Dzubin and Cooch (1992). Measurements included skull length (excluding skin), skull width (width at widest point, excluding skin), culmen, tarsus (bone), keel (after excision of muscles), plucked wing length (outstretched wing perpendicular to body, measured from body junction to tip of phalanges; ±1.0 mm), and plucked body length (±1.0 mm).

Body composition.—Thawed geese were plucked and weighed (±0.001 g for neonates and ±0.01 g for adults). Left breast muscles, left leg muscles, yolk sac (neonates), and digestive tract were excised, weighed, and saved for drying and lipid extraction. The digestive tract was dissected into gizzard, small intestine, large intestine, and left and right caeca. Length measurements of small intestine (±1.0 mm), both caeca (±1.0 mm), and gizzard (±0.1 mm) were made before removal of gut contents; empty gut components were separately weighed and saved for drying.

Adult body composition was determined using laboratory methods first described by Alisauskas and Ankney (1985) and later modified by Ankney and Afton (1988). In general, the methods above also were used to determine neonatal body composition except that ash content was determined directly from the ash content of the carcass homogenate (Badzinski 1998). Nutrient constituents of yolk sacs were determined separately from neonate body composition and later added to carcass constituents to calculate total protein and total lipid reserves; yolk-sac nutrients are not included in neonatal carcass protein or carcass lipid.

STATISTICAL ANALYSES

Egg composition.—We used *t*-tests to compare differences in egg volumes and composition between Canada Geese and Lesser Snow Geese (PROC TTEST, SAS Institute 1990). Egg size could not be used as a covariate in an Analysis of Covariance (ANCOVA) to test for interspecific differences in egg composition because volumes of only the two largest Lesser Snow Goose eggs (range: 102.7–133.1 cm³) and the smallest Canada Goose egg (range: 124.8–182.9 cm³) overlapped (i.e. 8% of eggs). Thus, proportional composition of eggs were separately calculated for Canada Geese and Lesser Snow Geese; this was done by dividing egg protein, albumen, yolk protein, egg lipid, and shell by shell-free dry egg mass or dry egg mass (percentage shell).

Egg-nutrient catabolism.—Egg volume (V) was calculated for each fresh and pipped egg using Hoyt's (1979) equation: $V = 0.51 \times$ length (cm) $\times$ breadth (cm). Data from our sample of fresh eggs (n_{CG} = 20 and n_{LSG} = 20) of known volume and composition were used to develop regression equations to estimate initial water, mineral, protein, and lipid mass of eggs from which collected neonates had hatched (r^2 = 0.22–0.96, df_{CG} = 19, df_{LSG} =19, $P <$ 0.05) (for equations see Badzinski et al. unpubl. data). Estimated mass of egg constituents and data for neonatal body composition were log10 transformed to account for mass differences between eggs and neonates of Canada Geese and Lesser Snow Geese. Multivariate Analysis of Variance (MANOVA), using species and stage (egg/neonate) as factors, was used to test for differences in catabolism of egg constituents during embryonic growth (PROC GLM, SAS Institute 1990). We used MANOVA because it is superior to several univariate tests evaluating overall group differences and it uses rather than ignores correlations among variables (Willig et al. 1986). Significance of the overall species × stage interaction indicated that patterns of egg-nutrient use differed between species (see also Slattery and Alisauskas 1995). Those differences were then determined by evaluating significance of each univariate interaction via Analysis of Variance (ANOVA) (PROC GLM, SAS Institute 1990, Hatcher and Stepanski 1994). To illustrate interspecific differences, we calculated the relative change of water, mineral, protein, and lipid during embryonic growth as Catabolized (%) = $((\bar{x}_{egg}) - (\bar{x}_{neonate}) / (\bar{x}_{egg})) \times$ 100, where $\bar{x}_{egg}$ = mean estimated mass of total egg water, mineral, protein, or lipid and $\bar{x}_{neonate}$ = mean mass of total water, ash (mineral), protein, or lipid in the neonate.

Comparison of neonatal characteristics.—Two-factor ANOVA was used to test for absolute differences in external morphology between species and sexes. Principal Component Analysis performed on the correlation matrix of skull length, skull width, tarsus, keel, wing length, and body length measurements of neonates of both species was used to obtain Principal Component one (PC1) scores which indexed structural size of each neonate (PROC PRINCOMP, SAS Institute 1990). ANCOVA, with species

and sex as class variables and PC1 scores as the co-variate, was used to assess interspecific differences in digestive organs and body composition after accounting for differences in neonatal size (PROC GLM, SAS Institute 1990). We considered digestive organs to be more developed if one species hatched with relatively longer or heavier organs for their body size.

Data used in analyses of developmental maturity were log10 transformed, so the relative change between neonate and adult values could be assessed between species. Including species, stage (neonate/adult), and species $\times$ stage as effects in MANOVA allowed for assessment of interspecific differences in overall patterns of developmental maturity of external structures and body composition (i.e. a significant species $\times$ stage interaction indicated that neonates of one species were nearer adult size [or mass] than were those of the other species). If the interaction term from the overall MANOVA was significant, we investigated significance of the univariate interactions by using ANOVA to determine which variables contributed most to interspecific differences in developmental maturity (Hatcher and Stepanski 1994). Percentage of adult size (or mass) was calculated to show the magnitude and interspecific differences in developmental maturity; mean adult values ($\pm$ SD) were weighted by sex differences in sample sizes (for values see Badzinski 1998).

Other studies have calculated a Lipid Index (lipid/total lean dry matter) to assess relative differences in energy reserves of neonatal birds (Alisauskas 1986, Aubin et al. 1986), but use of ratios in statistical analyses can be problematic (Blem 1984). Therefore, we used total lipid mass of neonates as a response variable in ANCOVA to test for differences in lipid reserves between species and sexes after correcting for lean dry carcass mass.

Maturation of skeletal muscles is correlated with decreased proportion of water, that is, a lower percentage of water content in a tissue indicates higher functional maturity of that tissue (Ricklefs and Webb 1985, Ricklefs et al. 1994). The ratio of water to lean dry muscle mass is one common index to functional maturity of tissues (Ricklefs 1979, Alisauskas 1986). However, we used the water content of a muscle or digestive organ as a response variable in an AN-COVA, using the corresponding lean dry muscle or organ mass as a covariate and species and sex as class variables, to test for differences in tissue maturity.

Type III sums of squares were used to evaluate significance of all effects in statistical models. Statistical models and effects were considered significant at $P \leq 0.05$; in all tables ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. In tables and text, unless otherwise noted, we report means and least-squares (LS) means ($\pm$SE) and breast and leg protein data from only the left side.

RESULTS

EGG COMPOSITION

Canada Geese laid larger eggs ($\bar{x}_{CG}$ = 152.3 $\pm$ 2.8 cm^3 vs. $\bar{x}_{LSG}$ = 115.3 $\pm$ 2.8 cm^3) (t = 9.52, df = 18, $P < 0.001$) with absolutely heavier ($P < 0.05$) constituents than did Lesser Snow Geese. Proportional egg composition, however, did not differ ($P > 0.05$) between species: 27% shell, 53% protein, 26% albumen, 27% yolk protein, and 47% lipid.

EGG-NUTRIENT CATABOLISM

Within each species, mean egg size did not differ between those collected for egg composition and those from which neonates were obtained (Canada Geese: t = 1.22, df = 44, $P > 0.05$ and Lesser Snow Geese: t = -0.95, df = 52, $P > 0.05$). Canada and Lesser Snow geese differed in their use of egg constituents during embryonic development (MANOVA, species $\times$ stage, F = 7.20, df = 4 and 113, $P < 0.001$) (Table 1). There were, however, no statistically significant species $\times$ stage interactions for individual egg constituents, but those for protein (P = 0.0686) and lipid (P = 0.1050) were nearly significant (i.e. these two constituents combined likely caused the significant overall MANOVA).

NEONATAL CHARACTERISTICS AND RELATIVE DEVELOPMENT

External structures.—Canada Geese had longer skull, keel, wing, and body measurements than did Lesser Snow Geese, but Lesser Snow Geese had longer bills (i.e. culmen) at hatch than did Canada Geese (Table 2). Overall developmental patterns of external structures differed between Canada Geese and Lesser Snow Geese (MANOVA, species $\times$ stage, F = 44.33, df = 6 and 92, $P < 0.001$). More specifically, wing, keel, and body length measurements of Lesser Snow Geese were closer to adult size than were those of Canada Geese, but skull length of Canada Geese was closer to adult size than was that of Lesser Snow Geese.

Digestive organs.—Relative to their body size, Lesser Snow Geese had larger gizzards and longer caeca than did Canada Geese (Table 3). Similarly, Lesser Snow Geese had relatively heavier gizzards and caeca than did Canada

TABLE 1. Egg and neonate composition and percentage of egg constituents catabolized (Change) by Canada Geese (CG) and Lesser Snow Geese (LSG) during embryonic development. Species (spp.) × stage (egg/neonate) interaction was significant (MANOVA, $F = 7.20$, df = 4 and 113, $P < 0.001$); significance of univariate spp. × stage interactions are given under P_{stage}.

Component (g)	CG ($n = 28$)			LSG ($n = 35$)			Spp. × stage
	Stage			Stage			
	Egg[a]	Neonate[b]	Change	Egg	Neonate	Change	P_{stage}
Water	100.58 (1.32)	73.88 (1.32)	−26.6%	81.48 (1.16)	59.79 (1.16)	−26.6%	NS
Mineral	16.18 (0.08)	1.49 (0.03)	−90.8%	11.82 (0.08)	1.08 (0.02)	−90.9%	NS
Protein	22.37 (0.30)	13.44 (0.30)	−39.9%	17.89 (0.26)	11.64 (0.26)	−34.9%	$P = 0.0686$
Lipid	19.97 (0.26)	12.03 (0.26)	−39.8%	15.92 (0.22)	8.94 (0.22)	−43.8%	$P = 0.1050$

[a] x̄ (± SE) egg composition estimated from gosling egg volume.
[b] x̄ (± SE) body composition of neonates including appropriate yolk-sac contribution.

Geese. Relative length and mass of small intestines, however, did not differ interspecifically.

Body composition.—Accounting for differences in neonate body size, Canada Geese had relatively heavier carcass mass and more carcass water, ash, and breast protein than did Lesser Snow Geese (Table 4). Body size and carcass lipid were positively correlated in neonates of both species, but as body size increased lipid content increased at a faster rate in Canada Geese than in Lesser Snow Geese (ANCOVA, species × body size, $F = 4.96$, df = 1, $P < 0.05$); Canada Geese (LS x̄ = 7.339 ± 0.217 g) also had, on average, more carcass lipid for their

size than did Lesser Snow Geese (LS x̄ = 5.661 ± 0.174 g). Total lipid reserves of both species were independent of body size, but Canada Geese (LS x̄ = 11.863 ± 0.367 g) had larger total lipid reserves than did Lesser Snow Geese (LS x̄ = 9.082 ± 0.341 g) (ANCOVA, species effect, $F = 23.98$, df = 1, $P < 0.001$). An analysis that controlled for lean dry body mass, rather than for body size, also showed that Canada Geese (LS x̄ = 11.335 ± 0.261 g) had relatively larger lipid reserves than did Lesser Snow Geese (LS x̄ = 9.505 ± 0.230 g) (ANCOVA, species effect, $F = 23.55$, df = 1, $P < 0.001$). After correcting for structural size, total protein reserves of

TABLE 2. Interspecific differences in structural measurements and structural development of neonate Canada Geese (CG) and Lesser Snow Geese (LSG) relative to conspecific adults. Overall species (spp.) × stage (neonate/adult) interaction was significant (MANOVA, $F = 44.33$, df = 6 and 92, $P < 0.0001$); significance of univariate spp. × stage interactions are given under P_{stage}.

Component (mm)	Mean (± SE)[a]			Development relative to adults		Spp. × stage
				% of adult		
	CG ($n = 28$)	P	LSG ($n = 35$)	CG	LSG	P_{stage}
Skull length	47.7 (0.2)	***	44.2 (0.2)	41.5	38.8	***
Culmen	16.6 (0.2)	**	17.2 (0.1)	33.3	32.3	NS
Tarsus	31.1 (0.3)	NS	31.0 (0.3)	36.6	37.7	NS
Keel	24.1 (0.3)	***	19.8 (0.3)	16.0	17.3	***
Wing length	57 (1)	**	55 (1)	12.8	13.8	**
Body length	196 (1)	***	174 (1)	27.6	29.8	***

[a] All sex effects and species × interactions $P > 0.05$.

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TABLE 3. Interspecific differences in digestive organs after correction for neonatal body size (PC1) of Canada Geese (CG) and Lesser Snow Geese (LSG).

	LS mean (± SE)[a]			Mean (± SE)	
Component	CG (n = 28)	P	LSG (n = 35)	CG (n = 28)	LSG (n = 35)
Length (mm)					
Gizzard	23.8 (0.4)	*	24.9 (0.3)	24.8 (0.3)	24.1 (0.2)
Small intestine	501 (10)	NS	514 (9)	529 (9)	493 (8)
Caeca	90 (3)	***	111 (3)	94 (2)	108 (2)
Mass (g)					
Gizzard	0.536 (0.020)	*	0.591 (0.020)	0.609 (0.018)	0.532 (0.016)
Small intestine	0.149 (0.005)	NS	0.145 (0.005)	0.163 (0.005)	0.134 (0.004)
Caeca	0.014 (0.001)	*	0.017 (0.001)	0.015 (0.001)	0.016 (0.001)

[a] All body size (PC1) effects $P < 0.005$; all sex effects and species × sex interactions $P > 0.05$.

Canada Geese and Lesser Snow Geese did not differ, but were positively correlated with their body sizes (ANCOVA, body size effect, $F = 11.08$, df = 1, $P < 0.01$).

Comparisons of body mass, breast muscles, and carcass protein suggested that Lesser Snow Geese were developmentally more advanced than were Canada Geese (MANOVA, species × stage, $F = 8.50$, df = 6 and 92, $P < 0.001$) (Table 4).

Functional maturity of tissues.—Muscle tissues of Lesser Snow Geese were more functionally mature than were those of Canada Geese (i.e. LS means of Lesser Snow Geese were lower than those of Canada Geese): gizzard (LS $\bar{x}_{LSG} = 2.658 \pm 0.018$ g vs. LS $\bar{x}_{CG} = 2.740 \pm 0.019$ g), breast (LS $\bar{x}_{LSG} = 0.625 \pm 0.013$ g vs. LS $\bar{x}_{CG} = 0.728 \pm 0.016$ g), and leg (LS $\bar{x}_{LSG} = 4.060 \pm 0.060$ g vs. LS $\bar{x}_{CG} = 4.385 \pm 0.069$ g). Lesser Snow Geese (LS $\bar{x} = 55.169 \pm 0.916$ g) also had less carcass water per gram of carcass protein than did Canada Geese (LS $\bar{x} = 62.535 \pm 1.051$ g). Sex was significant only for carcass water; males had less water per gram of lean dry mass than did females.

DISCUSSION

NEONATAL ENERGETICS

Egg composition and egg-nutrient catabolism.—Body composition and energy reserves of neonatal birds are related to egg composition or egg-nutrient catabolism (Alisauskas 1986). In this study, egg composition alone could not explain observed interspecific differences in relative body composition and energy reserves of

TABLE 4. Interspecific differences in carcass composition and energy reserves of neonate Canada Geese (CG) and Lesser Snow Geese (LSG) and development of neonate body components relative to those of conspecific adults. Overall species (spp.) × stage interaction was significant (MANOVA, $F = 8.50$, df = 6 and 92, $P = 0.001$); significance of univariate spp. × stage interactions are given under P_{stage}.

	LS mean (± SE)[a]			Mean (± SE)		Development relative to adults		
						% of adult		Spp. × stage
Component (g)	CG (n = 28)	P	LSG (n = 35)	CG (n = 28)	LSG (n = 35)	CG	LSG	P_{stage}
Body mass[b]	79.538 (1.117)	***	71.837 (0.957)	85.856 (1.289)	66.782 (1.153)	3.36	3.78	*
Breast protein	0.118 (0.003)	***	0.096 (0.002)	0.125 (0.002)	0.091 (0.002)	0.20	0.25	***
Leg protein	0.890 (1.020)	NS	0.874 (0.017)	0.995 (0.023)	0.790 (0.022)	1.96	2.16	NS
Carcass water	61.507 (0.975)	**	56.027 (0.848)	66.456 (1.051)	52.608 (0.940)	4.06	4.51	*
Carcass ash	1.374 (0.024)	***	1.167 (0.021)	1.485 (0.025)	1.083 (0.024)	1.14	1.18	NS
Carcass protein	8.824 (0.168)	NS	8.431 (0.144)	9.692 (0.184)	7.736 (0.165)	1.53	1.80	**

[a] All body size (PC1) effects $P < 0.05$. Sex effects (only breast protein and carcass water) $P < 0.05$; F > M.
[b] Plucked ingesta-free body mass (neonates without yolk sac).

neonates, because females of both species laid eggs with identical proportional compositions. Interspecific differences in egg-nutrient catabolism or embryonic metabolic rates could explain the interspecific differences we found in energy reserves and developmental and functional maturity. Canada Geese used absolutely and relatively more egg protein than did Lesser Snow Geese during their embryonic development (see Table 1). But that analysis ignores that average egg size of Canada Geese (152.3 cm³) is larger than that of Lesser Snow Geese (115.3 cm³) and Canada Geese incubate their eggs longer ($\bar{x}$ = 28 days; Raveling and Lumsden 1977) than do Lesser Snow Geese ($\bar{x}$ = 23 days; Cooke et al. 1995). After accounting for those differences, we calculated that Lesser Snow Geese actually used 11% more of their egg protein than did Canada Geese. Increased protein use by Lesser Snow Goose embryos did not result in Lesser Snow Geese hatching with relatively smaller protein reserves than Canada Geese, but they did hatch with relatively smaller lipid reserves than Canada Geese. To do this, Lesser Snow Geese catabolized more of their egg lipid during embryonic development than did Canada Geese (see Table 1), and relative to their egg sizes and incubation lengths, they used 29% more egg lipid than did Canada Geese.

The calculated egg-nutrient use values above are interesting because, on the basis of an equation in Vleck and Vleck (1996, fig. 12.2), predicted metabolic rate of Canada Goose embryos should be 19% higher than that of Lesser Snow Geese. However, after converting protein (5.65 kcal × g⁻¹) and lipid (9.50 kcal × g⁻¹) to their energy equivalents (Ricklefs 1977) and accounting for differences in egg size and incubation length, we found that energy used (kcal × [cm³]⁻¹ × day⁻¹) during embryonic growth by Lesser Snow Geese was 23% higher than that used by Canada Geese. This substantially higher metabolic rate could explain why Lesser Snow Geese had lower lipid reserves and how they hatched with some body parts that were more developmentally mature (e.g. keel, wing, and breast muscle) and with more functionally mature muscle tissues than those of Canada Geese. Slattery and Alisauskas (1995) found that neonate Ross' Geese had more functionally mature tissues and hatched closer to adult size than did Lesser Snow Geese, but proportional

use of egg protein and lipid during embryonic development did not differ between species. They argued that because both species have similar incubation periods (~23 days), female Ross' Geese incubate eggs longer relative to their egg size to hatch a more mature gosling. Our results, however, suggest that Lesser Snow Geese used relatively more egg nutrients than did Canada Geese to support more rapid embryonic growth, which enabled them to hatch in a more advanced state of development, but with smaller energy reserves.

ECOLOGICAL SIGNIFICANCE OF INTERSPECIFIC
DIFFERENCES IN NEONATAL DEVELOPMENT

Ecological and environmental differences.—In the subarctic, current and historic range of Interior Canada Geese, there are ~16 h of daylight in summer and a plant growing season (May–August) of nearly four months (Environment Canada unpubl. data for Moosonee, Ontario, 54°N). Conversely, in the high arctic, historic range of Lesser Snow Geese, there are nearly 24 h of daylight during the months of June, July, and August, but the plant growing season lasts only about two months (Environment Canada unpubl. data for Resolute, Nunavut, 75°N). The short high-arctic growing season causes temporal availability of forage plants of Lesser Snow Geese to be much more limited than plants eaten by Canada Geese; this also causes nesting and hatching activity within Lesser Snow Goose colonies to be highly synchronous. Most Lesser Snow Goose colonies are large, dense aggregations containing several hundreds of thousands, even millions, of birds. Large colonies and highly synchronous hatching likely cause much intraspecific competition for food in and around Lesser Snow Goose colonies after hatch. In contrast, dispersed nesting Canada Geese breed at much lower densities and at lower latitudes than do Lesser Snow Geese. We hypothesize that interspecific differences in developmental patterns of Canada Geese and Lesser Snow Geese are adaptations to different environmental and ecological conditions under which they evolved.

Energy reserves.—Birds catabolize both protein and lipid reserves when they experience negative protein or energy balances (Alisauskas and Ankney 1992), but lipids are more im-

portant for neonatal survival during energetic stress (Peach and Thomas 1986, Duncan 1988). In this study, both species had similar protein reserves, but Canada Geese had larger lipid reserves than did Lesser Snow Geese. This contradicted our prediction that neonate Lesser Snow Geese would have larger energy reserves to survive cold and nutritional stress in their high-arctic environments. As pointed out earlier, Lesser Snow Goose embryos appear to have much higher metabolic rates than those of Canada Geese, and increased lipid use during embryonic growth could explain why Lesser Snow Goose neonates have smaller energy reserves and greater functional maturity of muscle tissues. Functionally mature skeletal muscles are important for early thermogenesis, homeothermy, and locomotor activity in precocial neonates (Choi et al. 1993, Visser and Ricklefs 1993, 1995; Anderson and Alisauskas 2001, 2002). Thus, ability to generate heat, maintain body temperature, and search for food soon after hatch also are important for survival of neonatal birds. Therefore, higher functional maturity of muscle tissues and well developed digestive organs in Lesser Snow Geese may be physiological adaptations for more efficient thermoregulation and nutrient assimilation that offset metabolic costs associated with their small size (Slattery and Alisauskas 1995), or they are adaptations for enhanced locomotor and digestive capabilities soon after hatch. These latter two capabilities would enable neonate Lesser Snow Geese to leave the nest relatively soon after hatch to feed, thus reducing reliance on stored energy.

Dispersal ability.—Leg muscles of neonate Lesser Snow Geese were more functionally mature than were those of Canada Geese, which suggests advanced locomotor ability soon after hatch (Anderson and Alisauskas 2001, 2002). Well-developed and early locomotor ability in neonate Lesser Snow Geese may have been selected for because feeding by adults and goslings reduces the amount food on brood rearing areas within and adjacent to their nesting colonies (Cargill and Jefferies 1984, Williams et al. 1993). Such capabilities likely enable Lesser Snow Goose goslings to quickly disperse from heavily grazed feeding areas near colonies to distant brood-rearing areas with more aboveground biomass (Cooch et al. 1993). Attesting to their early propensity for dispersal, Lesser

Snow Goose broods at La Pérouse Bay, Manitoba, have been captured >50 km from nesting areas in about a month after hatching (Cooch et al. 1993). Additionally, interspecific comparison of Ross' Geese and Lesser Snow Geese provides strong evidence linking leg tissue maturity and early dispersal abilities. Leg muscles of neonate Ross' Geese were more functionally mature than were those of Lesser Snow Geese and Ross' Goose broods were seen up to 60 km from their natal colonies only 17 days after hatch; this was >2.5 × the distances traveled by syntopic Lesser Snow Goose broods (Slattery and Alisauskas 1995).

Digestive capability.—Lesser Snow Geese generally had larger digestive organs and more functionally mature digestive tissues than did Canada Geese, suggesting that their digestive capabilities were more developed at hatch. As goslings grow, their gut size increases and allows them to extract nutrients from different, often lower quality foods to offset the decline in forage quality or availability, or both, during brood rearing (Gadallah and Jefferies 1994). But, it is the first few days after hatch when larger digestive organs may be most important for increasing chances of survival to fledging. As a result, food-processing ability and digestive efficiency immediately after hatch likely are more critical for Lesser Snow Geese, because they have relatively smaller energy reserves and inhabit areas with shorter growing seasons and more intense intraspecific competition for food than do Canada Geese. Apparently, larger digestive organs of Lesser Snow Geese, as compared to Canada Geese, are not an adaptation to lower-quality food after hatch (Kehoe et al. 1987), because they require higher quality food than do Canada Goose goslings. When captive goslings that hatched from eggs taken from Akimiski Island, Nunavut, were raised on controlled diets, Lesser Snow Geese grew faster and survived to fledge on high protein, low fiber (high quality) diets, and grew poorly or did not survive on low protein, high fiber (low quality) diets, but low-quality diets had less pronounced effects on growth, development, and survival of Canada Goose goslings (J. Leafloor, S. McWilliams, and W. Karasov unpubl. data). Consequently, Lesser Snow and Canada geese are adapted to relatively higher and lower quality forage, respectively. Thus, interspecific differences in neonatal di-

gestive-organ sizes likely are not related to av-
erage forage quality at hatch, which predicts
Lesser Snow Geese to have relatively shorter
digestive organs, but does support our hypoth-
esis of early digestive and food processing ca-
pabilities of Lesser Snow Geese.

Although high-quality food is important for
both Lesser Snow and Canada geese soon after
hatch (J. Leafloor, S. McWilliams, and W. Kar-
asov unpubl. data), we suggest that food qual-
ity may be less critical for neonate Canada
Geese because they have larger lipid reserves
that can be drawn upon until digestive efficien-
cy improves (Peach and Thomas 1986) and have
more time to complete development before fall
migration. In contrast, because Lesser Snow
Geese evolved in an environment with an ex-
tremely short growing season and much com-
petition for food, we conclude that they have
undergone stronger selection for rapid embry-
onic growth and early development of muscles,
organs, and structures used for early thermo-
regulation, locomotion, or food acquisition and
processing. Although Lesser Snow Geese show
these adaptations relative to Canada Geese in
the subarctic on Akimiski Island, Ross' Geese
show even stronger adaptations relative to
Lesser Snow Geese in the central Canadian
high arctic (Slattery and Alisauskas 1995). We
further suggest that Lesser Snow Geese, and
possibly other colonial nesting species of arctic
geese, have been selected to eat as much of the
highest quality food as possible for rapid and
early development of leg and flight muscles so
they can vacate heavily grazed brood rearing
areas for others with higher per capita food
availability to continue their growth (Badzinski
et al. 2002).

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