



ALLOCATION OF NUTRIENTS TO REPRODUCTION AT HIGH LATITUDES: INSIGHTS FROM TWO SPECIES OF SYMPATRICALLY NESTING GEESE

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ABSTRACT.—Understanding factors that determine sources of nutrients for reproduction is vital to interpreting different life-history strategies used among species, within species, and among taxa. We used stable carbon isotope analysis ($\delta^{13}\text{C}$) to compare the relative use of endogenous and exogenous nutrients during egg synthesis between two species of geese, Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*), nesting on Akimiski Island, Nunavut. We estimated that Canada Geese used $49 \pm 1.1\%$ (SE), $61 \pm 1.3\%$, and $51 \pm 1.1\%$ endogenous nutrients for albumen, yolk protein, and yolk lipid, respectively. Lesser Snow Geese used significantly less endogenous nutrients during clutch formation, allocating only $25 \pm 1.2\%$, $36 \pm 1.5\%$, and $34 \pm 1.7\%$ endogenous nutrients for albumen, yolk protein, and yolk lipid, respectively. Although the proportion of endogenous nutrients allocated to eggs did not vary by year in Canada Geese, proportions varied significantly among years in Snow Geese. We discuss how access to exogenous nutrients appears to be an important factor in determining nutrient allocation strategies during egg production in geese and conclude that, although body size is likely an important ultimate factor in determining overall breeding strategies in birds, proximate factors that influence access to nutrients during egg production appear to be more important in shaping nutrient allocation to egg synthesis. Thus, interactions between physiological and morphological constraints and local environmental conditions can promote the use of flexible strategies in animals that migrate to breed. Received 5 February 2012, accepted 5 September 2012.

Key words: breeding strategies, Canada Goose, capital–income continuum, carbon-13, endogenous and exogenous nutrients, egg formation, Lesser Snow Goose, life history strategies.

Allocation des nutriments à la reproduction en haute altitude : aperçu de deux espèces d'oies sympatriques

RÉSUMÉ.—La compréhension des facteurs qui déterminent les sources de nutriments pour la reproduction est essentielle pour interpréter les différentes stratégies du cycle vital utilisées sein des espèces, entre les espèces et entre les taxons. Nous avons analysé des isotopes stables de carbone ($\delta^{13}\text{C}$) afin de comparer l'utilisation relative des nutriments endogènes et exogènes au cours de la synthèse des œufs entre deux espèces d'oies nichant sur l'île Akimiski, au Nunavut, soit *Branta canadensis interior* et *Chen caerulescens caerulescens*. Nous avons estimé que *B. canadensis interior* utilisait $49 \pm 1,1\%$ (SE), $61 \pm 1,3\%$ et $51 \pm 1,1\%$ des nutriments endogènes pour l'albumen, les protéines vitellines et les lipides vitellins, respectivement. *C. caerulescens caerulescens* utilisait significativement moins de nutriments endogènes au cours de la production des œufs, allouant seulement $25 \pm 1,2\%$, $36 \pm 1,5\%$ et $34 \pm 1,7\%$ de nutriments endogènes pour l'albumen, les protéines vitellines et les lipides vitellins, respectivement. Bien que les proportions des nutriments endogènes alloués aux œufs n'aient pas varié entre les années chez *B. canadensis interior*, elles ont varié significativement entre les années chez *C. caerulescens caerulescens*. Nous discutons de la façon dont l'accès aux nutriments exogènes semble être un facteur important pour déterminer les stratégies d'allocation des nutriments au cours de la production des œufs chez les oies. Nous concluons que, malgré que la taille corporelle soit probablement un facteur important pour déterminer les stratégies globales de reproduction chez les oiseaux, les facteurs proximaux influençant l'accès aux nutriments au cours de la production des œufs semblent être plus importants dans le processus d'allocation des nutriments à la synthèse des œufs. Ainsi, les interactions entre les contraintes physiologiques et morphologiques et les conditions environnementales locales peuvent promouvoir l'utilisation de stratégies flexibles chez les animaux qui migrent pour se reproduire.

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VARIATION IN LIFE history strategies reflects differences in how organisms obtain and use resources (Stearns 1992, Jönsson 1997, Bonnet et al. 1998). During breeding, resource use can vary considerably among species (Thomas 1988, Lawson 2006), within species (Mainguy and Thomas 1985), and among related taxa (Jönsson 1997, Bonnet et al. 1998). A fundamental way in which animals can differ in their nutrient allocation strategies is in allocating different proportions of stored versus locally obtained nutrients to reproduction (Drent and Daan 1980).

At one extreme, animals can rely fully on nutrient stores accumulated prior to breeding (capital breeders) to support reproduction; by contrast, income breeding involves the use of nutrient sources acquired locally (Stephens et al. 2009). Species rarely exhibit either extreme strategy, but instead fall along a continuum between pure capital and pure income breeders (Owen and Reinecke 1979, Thomas 1988). Strategies can also be flexible, depending on conditions encountered prior to or during reproduction in a given year (Klaassen et al. 2006, Warner et al. 2008). Both proximate and ultimate factors can affect how members of a species allocate nutrients to reproduction.

Access to resources at the time of reproductive investment is important in shaping strategies of nutrient allocation (Thomas 1988, Bonnet et al. 1998). Numerous vertebrate taxa show a clear link between resource availability and breeding strategy; examples include marine mammals (Costa 1993, Houston et al. 2007, Wheatley et al. 2008), ectothermic vertebrates (Bonnet et al. 1998, Lourdais et al. 2002), and migratory birds (Ryder 1970, Ankney and MacInnes 1978, Thomas 1988, Meijer and Drent 1999). Income strategies can be used only by organisms that have sufficient access to exogenous nutrients, whereas use of stored nutrients for reproduction allows individuals to breed without depending on local resources at the time of breeding (Lindstedt and Boyce 1985, Jönsson 1997, Johnson 2006). Body size can influence an organism's ability to use endogenous nutrients for reproduction, especially in birds that travel to breed and must carry endogenous resources with them. Across a variety of related taxa (fishes: Jager et al. 2008; insects: Johnson 2006; birds: Meijer and Drent 1999, Klaassen et al. 2006), it appears that only relatively large species have the ability to rely exclusively on endogenous nutrients to fuel reproduction.

In a recent review of capital–income breeding, Stephens et al. (2009) noted that comparative studies have generally not provided adaptive explanations to questions of capital–income breeding and that most studies have simply identify an organism's placement on the capital–income continuum. In the present study, we determine the position on the income–capital continuum of Interior Canada Geese (*Branta canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting on Akimiski Island, Nunavut, and consider interspecific variation in nutrient allocation to the eggs in discussing how factors such as body size and access to exogenous nutrients influence nutrient allocation strategies during egg production. We predicted that Lesser Snow Geese would rely on exogenous nutrients for egg production to a greater degree than Canada Geese because of their smaller size and greater access to exogenous nutrients on the breeding grounds. Our comparison of sympatrically breeding Canada and Lesser Snow geese provided an excellent model that offered insight into factors that influence nutrient allocation strategies in high-latitude breeding geese.

METHODS

Study area.—Akimiski Island is the largest island in James Bay (3,800 km²) and is located 20 km offshore from the mouth of the Attawapiskat River (O et al. 2006). Canada Geese nest ubiquitously across the island, but the north shore (53°11'N, 81°30'W) has the highest nest densities recorded anywhere for Interior Canada Geese, averaging ≥ 26 nests km⁻² on Akimiski Island (Leafloor et al. 2000). A small Lesser Snow Goose colony (~2,000 pairs) is situated on the north shore between the Stitt and Manning rivers (local names; 53°11'N, 81°28'W; Abraham et al. 1999). Weather data were retrieved online from the Environment Canada Wemindji A weather station, located ~140 km east of Akimiski Island on the eastern shore of James Bay. Because of missing data, maximum temperatures for 12, 19, and 29 April and 1, 5, and 8 May 2008 are from the Eastmain weather station, situated ~80 km south of the Wemindji A station.

Field methods.—Adult female Canada Geese and Snow Geese were collected annually by shotgun in the vicinity of their nests under permit from 2005–2008 along the north shore of Akimiski Island at the end of laying or beginning of incubation. Canada Geese were collected from a sympatric breeding area (i.e., where the two species breed together) and a Canada Goose–only breeding area in 2006 and 2007; the two breeding areas were separated by 14 km of coastline. However, because resource allocation to eggs did not differ between areas (C. M. Sharp unpubl. data), females and clutches from these two breeding sites were combined for our analysis. In 2005 and 2008, Canada Geese and their clutches were collected only from the sympatric breeding area. In 2005, five females of each species were collected with their clutches, and four additional clutches of each species were collected without the female.

Upon collection, females were immediately tagged with a nest number. Eggs were collected and marked with a unique combination of nest number and egg sequence number, using natural staining to define laying order, starting with the most soiled egg (no. 1) to the cleanest egg in the nest (Raveling and Lumsden 1977, Cooper 1978). Nests were aged in the field by floating eggs to determine incubation stage (Walter and Rusch 1997; ± 2.3 [SE] days for Canada Geese and ± 2 days for Lesser Snow Geese). In 2007 and 2008, we also aged embryos during egg sampling, using criteria presented in Cooper and Batt (1972; ± 1.5 days for Canada Geese and ± 1.2 days for Lesser Snow Geese, assuming that embryo development occurs in the two species at similar rates in relation to the total incubation period). Nest initiation dates were back-calculated using the following formula: nest initiation date = collection date – age of egg – (clutch size \times laying rate). Laying rates of 1.5 eggs day⁻¹ and 1.3 eggs day⁻¹ were used for Canada Geese and Snow Geese, respectively (Alisauskas and Ankney 1992). Dates of albumen production for individual eggs were calculated using the following formula: albumen production date = nest initiation date – (laying rate \times [clutch size – egg sequence number]). All eggs and females were collected during the first half of their incubation period, to avoid small changes in egg isotopic values associated with embryo development (Sharp et al. 2009). Ninety-eight percent of Lesser Snow Goose eggs were collected within 3 days of the start of incubation, and 85% of Canada Goose clutches were collected within 9 days of the start of incubation; thus, the potential influence of incubation stage on the isotopic values of albumen

TABLE 1. Canada Goose (*Branta canadensis interior*; CAGO) and Lesser Snow Goose (*Chen caerulescens caerulescens*; LSGO) breeding phenology and sampling on Akimiski Island, Nunavut, during the 2005–2008 breeding seasons.

Year	Mean start of laying		Range of initiation dates		Number of females collected ^a			Dates of collection
	CAGO	LSGO	CAGO	LSGO	CAGO	LSGO	Total	
2005	26 April	8 May	23 April–1 May	5–9 May	9 ^b	9 ^b	18	14–15 May
2006	26 April	5 May	18 April–2 May	2–7 May	44 ^c	9	53	6–12 May
2007	28 April	6 May	20 April–4 May	29 April–9 May	41 ^c	13	54	9–14 May
2008	29 April	8 May	19 April–6 May	3–10 May	19	19	38	13–16 May

^a Number of females collected with an associated clutch.

^b Only 5 females with clutches were collected for each species; 3 and 4 additional complete clutches were collected for CAGO and LSGO, respectively.

^c CAGO collected from sympatric and CAGO-only breeding areas combined.

was negligible and ignored (Sharp et al. 2009). In total, 113 Canada Goose clutches and 50 Lesser Snow Goose clutches were collected (Table 1). Clutch size ranges in 2005–2008 were 2–7 eggs in Canada Geese and 2–6 eggs in Snow Geese.

Female body measurements (mass, and head and tarsus lengths) were taken according to Dzubin and Cooch (1992). From each female, we collected samples of pectoral muscle, abdominal fat, digestive tract, and reproductive tract (ovary, developing follicles, and oviduct). Tissues were sampled within 8–24 h of collection, and carcasses were kept on ice before dissection in the field. Esophageal contents were rinsed with deionized water and stored frozen in individual plastic bags for transport. Eggs were boiled (~20 min) following collection to facilitate transport (Gloutney and Hobson 1998). Oviducal eggs, if present, were included in clutches and were assigned an egg number. All tissues were stored in plastic bags on ice while in the field and were frozen at –20°C upon return to Trent University until preparation for isotope analysis (Gauthier et al. 2003). Ovaries were examined for developing follicles. If present, follicles were included in clutch size and received the next egg number in sequence but could not be included in the multivariate analysis because they contained yolk but no albumen.

Vegetation samples were collected to provide representative isotopic endpoints of forage species on Akimiski Island (i.e., exogenous nutrients). To determine which vegetation to sample, we examined the contents of goose digestive tracts, observed the behavior of feeding geese, and reviewed the literature (Prevett et al. 1985, Dignard et al. 1991, Gates et al. 2001, Gleason 2003). Vegetation samples included above- and belowground plants collected in the immediate vicinity of goose collections or where geese were observed feeding. Vegetation samples were rinsed with deionized water and stored frozen in separate plastic bags until isotope analysis.

Isotope analysis and calculations.—Samples of pectoral muscle from females, as well as whole yolk and albumen from eggs, were freeze dried to constant mass. Vegetation and esophageal samples were rinsed in deionized water and oven dried at 65°C to constant mass. Following drying, all samples were ground with mortar and pestle to a fine powder. Lipids from pectoral muscle and yolk were extracted using a solution of 2:1 chloroform:methanol (Bligh and Dyer 1959). Abdominal fat was soaked in the same solvent mix for 48 h to allow lipids to enter solution. To recover lipids, extracts from yolk and abdominal fat were evaporated under a fume hood at room temperature for 1 week or until all the solvent had evaporated.

Body and egg tissues (1.0 ± 0.1 mg) and vegetation samples (5.0 ± 0.1 mg) were weighed into tin capsules for isotope analysis. Lipid-free dry pectoral muscle, abdominal fat extract, dry albumen, lipid-free yolk, and yolk lipid extract were analyzed for δ¹³C values. All isotope analyses were conducted using continuous-flow isotope-ratio mass spectrometry (CFIRMS). Samples from 2005–2007 were analyzed at the Environment Canada Stable Isotope Hydrology and Ecology Research Laboratory in Saskatoon, Saskatchewan, and 2008 samples were analyzed at the University of California Davis Isotope Facility. Inter-laboratory check samples (albumen standard) confirmed no effect of laboratory on stable isotope measurements. On the basis of in-house laboratory organic (protein) standards (albumen and pea grain), we estimated measurement precision within runs to be ±0.1‰ for δ¹³C measurements.

Although available, δ¹⁵N values were not used as part of the mixing models because various authors have indicated that tissue δ¹⁵N values are very sensitive to periods of fasting (Hobson et al. 1993, Hobson 1995, Cherel et al. 2005) and fluctuation in dietary protein quality (Robbins et al. 2005). Periods of fasting and fluctuations in protein quality are known to occur in Canada and Lesser Snow geese during egg formation, laying, and incubation (Afton and Paulus 1992, Alisauskas and Ankney 1992). We decided that a δ¹³C-only model was more reliable than a model using both δ¹³C and δ¹⁵N, given the potential issues associated with interpretation of δ¹⁵N values for birds at our site. Stable carbon isotope values are more robust indicators of baseline foodweb values because of their lower sensitivity to trophic effects and because, to our knowledge, they are not affected by fasting and nutritional stress (Hobson et al. 1993, Rubenstein and Hobson 2004). Moreover, we anticipated birds arriving from staging areas with higher tissue δ¹³C values than those formed from local C-3 breeding-ground foodwebs due to potential use of corn (a C-4 plant) at spring staging–wintering areas farther south (Gates et al. 2001).

Mixing-model calculations.—The isotopic discrimination factors that we used to adjust δ¹³C values for conversion of dietary isotope values to those of egg constituents are presented in Table 2. Discrimination factors corresponding to the conversion of endogenous reserves to egg components have not been established experimentally for herbivorous birds. However, Gauthier et al. (2003) reasoned that mobilizing nutrients from endogenous reserves to eggs is similar to the mobilization of exogenous muscle tissue to eggs in carnivorous birds. Therefore, we used isotopic discrimination values from Hobson's (1995) carnivore model for falcons feeding on quail muscle to infer isotopic discrimination

TABLE 2. Stable-carbon-isotope discrimination factors used in conversion of nutrients from exogenous (diet) and endogenous (body stores) sources to egg components.

Egg component	Factor	SE	Source
Exogenous (diet to egg)			
Albumen	+1.4‰	0.6‰	Hobson 1995 (Mallard, first clutch)
Yolk protein	-0.1‰	0.5‰	Hobson 1995 (Mallard, first clutch)
Yolk lipid	-2.7‰	0.5‰	Hobson 1995 (Mallard, first clutch)
Endogenous (tissue to egg)			
Albumen	+0.9‰	0.5‰	Hobson 1995 (various falcons, as suggested by Gauthier et al. 2003)
Yolk protein	+0.1‰	0.5‰	Hobson 1995 (various falcons as suggested by Gauthier et al. 2003)
Yolk lipid	0.0‰	0.0‰	Gauthier et al. 2003

for the conversion of breast muscle to lipid-free yolk and albumen (Table 2). Because little metabolic breakdown occurs to convert stored fat into yolk lipid, no isotopic discrimination is thought to occur between abdominal fat and yolk lipid (Gauthier et al. 2003). As a result, we assumed there was no fractionation between abdominal fat and yolk lipids.

We calculated the proportion of biomass in each egg component originating from endogenous sources (% endogenous) using a $\delta^{13}\text{C}$ -only, Bayesian mixing-model approach conducted in Stable Isotope Analysis in R (Parnell et al. 2010). We used the `siarsolomc-mcv4` command to calculate percent endogenous estimates for individual eggs. Goose tissue isotope (endogenous source) values used in the individual mixing models were matched with each female's eggs in all years except 2005, when not all eggs had a matching female. In the case in which eggs did not have matching females, we used population means for endogenous values in the mixing model. In these cases, the SD for the means was included in the model. Although percent endogenous values were calculated for individual eggs, the percent endogenous contributions of all eggs within a clutch were averaged to determine a percent endogenous contribution for the entire clutch. In 2008, only first and last eggs of Canada Goose clutches were analyzed isotopically; thus, the percent endogenous contribution to these two eggs was used to determine the percent endogenous contributions of the clutch.

Statistical analysis.—Variation in nutrient allocation (proportion of endogenous nutrients) between species and year was analyzed using a multivariate analysis of variance (MANOVA). Mean percent endogenous contributions for albumen, lipid-free yolk, and yolk lipid for a given nest were the dependent variables, species and year were included as categorical predictors, and relative nest initiation date (initiation date minus mean initiation date for that year; Table 1) and relative clutch size (clutch size at time of collection minus mean clutch size for that species; 4 for Snow Geese, 5 for Canada Geese) were included as covariates. Because relative initiation date and relative clutch size were correlated ($r = -0.42$), clutch size corrected for initiation date (residuals of clutch size vs. initiation date) was used in the analyses

to avoid multicollinearity. Because the interaction term between year and species was significant ($P < 0.001$), the MANOVA was separated by species to ensure proper interpretation of each main effect. Because multivariate assumptions of homogeneity are more likely to be met when univariate assumptions are met (Quinn and Keough 2002), we examined only univariate homogeneity of variances and normality because multivariate homogeneity of variances and covariance are difficult to verify. The data did not violate assumptions of homogeneity of variances and normality. In addition, Wilks' lambda was used because it is robust to any deviations in variance for multivariate homogeneity and covariance (Quinn and Keough 2002).

The association between maximum daily temperature and nutrient allocation in Snow Geese was analyzed using an analysis of covariance with percent endogenous contributions to albumen for individual eggs used as the dependent variable. Maximum daily temperature for the date of albumen production for each egg was included as a continuous predictor, and nest identity was included as a random factor to control for non-independence between eggs originating from the same nest. Information regarding initiation date and clutch is included in "Nest ID"; therefore, these factors could not be included in the model. Percent endogenous contributions to yolk protein and yolk lipids could not be included in this analysis because their production occurs over a significantly longer period (10–12 days) and, thus, could not be assigned a maximum daily temperature. All statistical analyses were completed using STATISTICA, version 6.1 (StatSoft 2003). Means (\pm SE) are presented unless otherwise mentioned; results were considered significant at a $P < 0.05$.

RESULTS

Nutrient allocation.—As predicted, the $\delta^{13}\text{C}$ values of endogenous nutrient sources of Canada and Snow geese were isotopically distinct from those of local forage plants (exogenous nutrient source; Table 3 and Fig. 1) and indicated a substantial use of C-4 plants on staging areas prior to arrival. Female Canada Geese used more

TABLE 3. Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; means \pm SE) of endogenous stores of Canada Geese (*Branta canadensis interior*) and Snow Geese (*Chen caerulescens caerulescens*), and forage plants from Akimiski Island, Nunavut.

Nutrient source	Tissue	Mean $\delta^{13}\text{C}$ (‰)
Endogenous		
Canada Goose	Muscle	-18.8 \pm 0.1
($n = 103$)	Abdominal fat	-15.0 \pm 0.2
Snow Goose	Muscle	-21.0 \pm 0.1
($n = 46$)	Abdominal fat	-22.2 \pm 0.4
Forage plants		
<i>Carex aquatilis</i> ($n = 3$)		-28.4 \pm 0.6
<i>Puccinellia phryganodes</i> ($n = 6$)		-26.7 \pm 0.6
<i>Senecio congestus</i> ($n = 8$)		-27.1 \pm 0.3
Other plants ^a ($n = 20$)		-26.9 \pm 0.8
Mean local vegetation		-27.0 \pm 0.4

^a *Equisetum* spp., *Glaux maritima*, *Hippuris* spp., and *Potentilla egedii*.

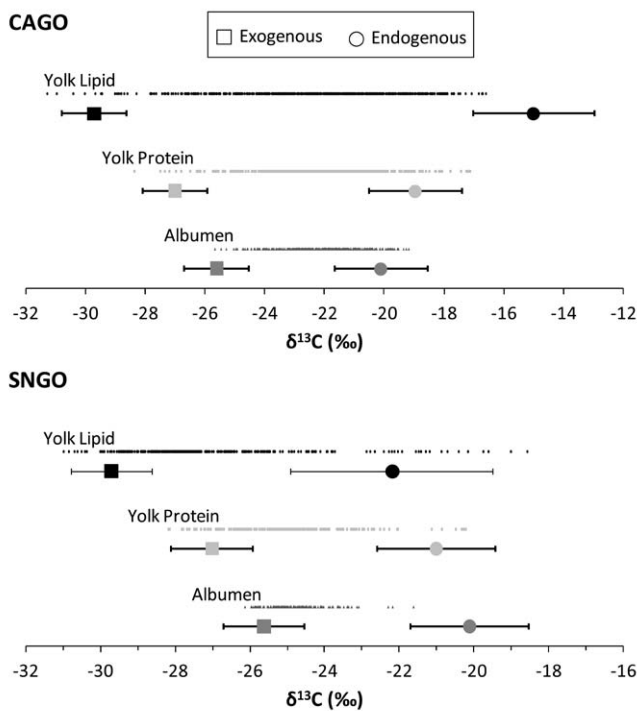
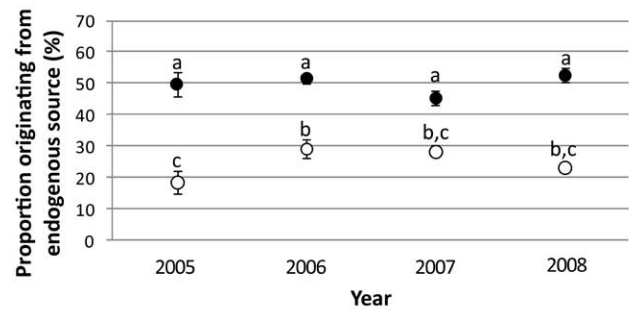


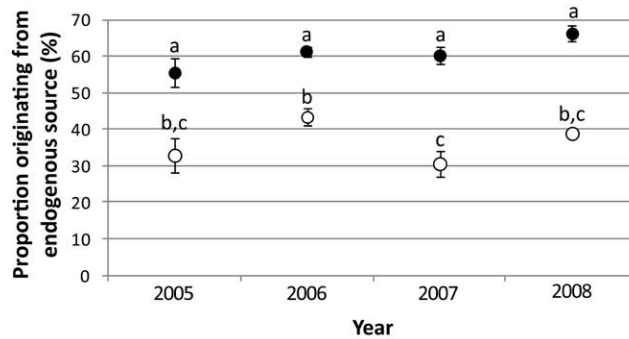
FIG. 1. Values of $\delta^{13}\text{C}$ for albumen, yolk protein, and yolk lipid from individual eggs of Canada Geese (CAGO) and Lesser Snow Geese (SNGO) nesting on Akimiski Island, Nunavut, 2005–2008, as well as values for exogenous sources (mean of plants on Akimiski Island; squares; see Table 3) and endogenous nutrient sources (muscle for albumen and yolk protein, abdominal fat for yolk lipid; circles). Dots represent individual egg isotope values. Nutrient sources have been corrected for isotopic discrimination (Table 2) and represent expected mean (\pm SD) goose isotope values that would result from an exclusive dependence on those nutrient sources.

endogenous nutrients for clutch formation in each year than Snow Geese (Wilks' $\lambda = 0.47$, $F = 56.23$, $df = 3$ and 153 , $P < 0.001$; Fig. 2). Results from the mixing models indicated that female Canada Geese, on average, used $49 \pm 1.1\%$, $61 \pm 1.3\%$, and $51 \pm 1.1\%$ endogenous nutrients for albumen, yolk protein, and yolk lipid, respectively (Table 4). Female Snow Geese allocated, on average, only $25 \pm 1.2\%$, $36 \pm 1.5\%$, and $34 \pm 1.7\%$ endogenous nutrients for albumen, yolk protein, and yolk lipid, respectively (Table 4). Clutch size had no effect on nutrient allocation to the clutches of Canada Geese (Wilks' $\lambda = 0.99$, $F = 0.1572$, $df = 3$ and 107 , $P = 0.925$) or Snow Geese (Wilks' $\lambda = 0.92$, $F = 1.13$, $df = 3$ and 44 , $P = 0.344$). The proportion of endogenous nutrients allocated to the clutches also decreased with initiation date in Canada Geese (Wilks' $\lambda = 0.87$, $F = 4.87$, $df = 3$ and 107 , $P = 0.003$), but not in Snow Geese (Wilks' $\lambda = 0.95$, $F = 0.67$, $df = 3$ and 44 , $P = 0.13$). In Canada Geese, initiation date had an effect on the relative proportion of endogenous nutrients allocated to yolk lipids ($F = 6.30$, $df = 1$ and 107 , $P = 0.013$) but not to albumen or yolk protein (albumen: $F = 2.69$, $df = 1$ and 107 , $P = 0.10$; yolk protein: $F = 0.75$, $df = 1$ and 107 , $P = 0.39$). The proportion of endogenous nutrients did not change among years in Canada Geese for any egg component but varied among years in Snow Geese (Wilks' $\lambda = 0.42$, $F = 4.65$, $df = 9$ and 98 , $P < 0.001$ for all

Albumen



Yolk protein



Yolk lipid

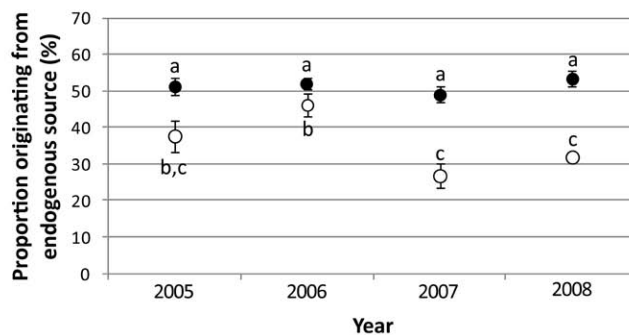


FIG. 2. Proportion (mean \pm SE) of albumen, yolk protein, and yolk lipid originating from endogenous stores in Canada Geese (*Branta canadensis interior*; filled circles) and Lesser Snow Geese (*Chen caerulescens caerulescens*; open circles) breeding on Akimiski Island, Nunavut, 2005–2008. Within species, years with differing letters are significantly different ($P \leq 0.05$).

three egg components; albumen: $F = 3.51$, $df = 3$ and 44 , $P = 0.02$; yolk protein: $F = 3.57$, $df = 3$ and 44 , $P = 0.02$; yolk lipid: $F = 7.36$, $df = 3$ and 44 , $P < 0.001$) (Fig. 2). Allocation of endogenous nutrients to albumen in Snow Goose eggs was greater in 2006 ($29\% \pm 3.2\%$) than in 2005 ($18\% \pm 3.5\%$; Tukey's HSD test for unequal n , $P = 0.03$; Fig. 2). Snow Geese also allocated more endogenous nutrients to yolk protein in 2006 ($43 \pm 2.3\%$) than in 2007 ($31 \pm 3.6\%$, Tukey's HSD test for unequal n , $P = 0.049$; Fig. 2). Finally, Snow Geese allocated more endogenous nutrients to yolk lipids in 2006 ($46 \pm 3.2\%$) than in either 2007 or 2008 ($27 \pm 3.4\%$, Tukey's HSD test for unequal n , $P < 0.001$ and $32 \pm 1.5\%$, Tukey's HSD test for unequal n , $P < 0.02$ for 2007 and 2008, respectively; Fig. 2).

TABLE 4. Body masses and relative contribution of endogenous nutrients to egg production in Arctic and sub-Arctic breeding geese.

Species	Breeding grounds	Body mass (g)	Percent endogenous nutrients			Study
			Yolk protein	Yolk lipid	Albumen	
<i>Branta canadensis interior</i>	Akimiski Island, Nunavut	4,050	55–67	46–51	45–51	Present study
<i>Chen caerulescens atlanticus</i>	Bylot Island, Nunavut	3,100	31–34	16–25	26–28	Gauthier et al. 2003
<i>Anser canagicus</i>	Yukon-Kuskokwim Delta, Alaska	2,950	65	—	—	Schmutz et al. 2006
<i>C. c. caerulescens</i>	Akimiski Island, Nunavut	2,340	18–41	23–35	9–24	Present study
<i>C. c. caerulescens</i>	Cape Churchill, Manitoba	2,340	28–42	44–71	27–38	Hobson et al. 2011
<i>B. leucopsis</i>	Breøyane Islands, Kongsfjorden / Northern Svalbard	1,590	23–65	32–73	25–88	Hahn et al. 2011
<i>B. bernicla</i>	Yukon-Kuskokwim Delta, Alaska	1,350	41	—	—	Schmutz et al. 2006

Weather.—Average daily maximum temperatures during egg production were similar across all years of the study, ranging between 5.3°C (2008) and 8.3°C (2006). However, in 2006 and 2008, during the period of Snow Goose yolk synthesis, there was a 3-day period during which maximum daily temperatures did not rise above freezing (Fig. 3). The period in 2006 also overlapped the period of albumen synthesis in Snow Geese on Akimiski Island. There was a similar period of prolonged cold weather in 2006 during the period of yolk and albumen synthesis in Canada Geese (Fig. 3). Daily maximum temperature on the date of albumen production did not have a significant effect on the proportion of endogenous nutrients used in albumen synthesis ($F = 1.27$, $df = 1$ and 131, $P = 0.26$).

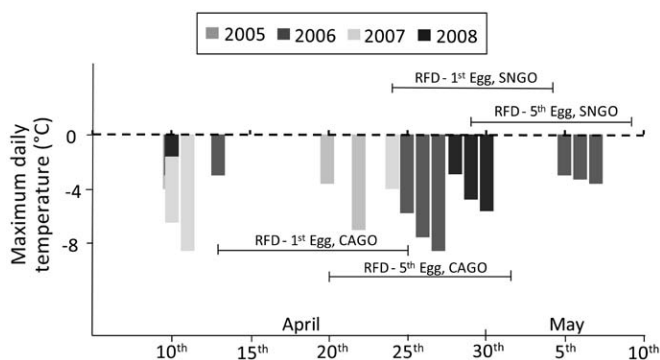


FIG. 3. Periods of freezing temperatures when maximum daily temperatures did not rise above freezing during the period of rapid follicle development (RFD) and albumen synthesis for Canada Geese (*Branta canadensis interior*; CAGO) and Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) on Akimiski Island, Nunavut. Examples of egg development stage are based on a female laying her first egg on 26 April and 5 May for CAGO and LSGO, respectively. The period of RFD was assumed to be 12 days for CAGO (Alisauskas and Ankney 1992) and 10 days for LSGO (Hamann et al. 1986). In both scenarios, clutch size was considered to be 5 eggs. A laying rate of 1.5 eggs day⁻¹ and 1.3 eggs day⁻¹ was used for CAGO and LSGO, respectively (Alisauskas and Ankney 1992), to determine the period of RFD for the fifth egg. The period of albumen synthesis was considered to be the period following RFD of the first egg to one day after RFD of the fifth egg.

DISCUSSION

Female Snow Geese nesting on Akimiski Island relied primarily on exogenous nutrients for clutch formation, whereas Canada Geese generally allocated larger amounts of endogenous nutrients to their eggs. The proportions of endogenous and exogenous nutrient sources used by Canada Geese did not vary among the 4 years. By contrast, the use of exogenous and endogenous resources by Snow Geese differed among years, revealing considerable flexibility in their ability to allocate nutrients to egg production. Overall, the breeding strategy of Snow Geese more closely resembled an income strategy than that of Canada Geese did, but both species clearly used a mixed capital–income strategy. Within Canada Geese, females that initiated nests earlier allocated relatively more endogenous nutrient to the formation of yolk lipids; initiation date did not influence nutrient allocation in Snow Geese.

Annual variation and flexibility in nutrient allocation strategies.—Variation in nutrient allocation strategy of Snow Geese was not attributable to overall spring phenology on the breeding grounds because Akimiski Island had similar spring melt phenology in all 4 years of our study, and mean nest initiation dates varied by only 3 days in both species (Table 1). Instead, we speculate that the increase in use of endogenous stores for albumen and yolk protein synthesis by Snow Geese in some years was linked to fluctuations in daily temperature during yolk and albumen synthesis, which influenced access to exogenous nutrients. In both 2006 and 2008, there were prolonged periods during Snow Goose yolk synthesis when maximum daily temperatures did not rise above freezing (Fig. 3). Soils in the preferred feeding sites of Snow Geese were frozen, and shallow-water sites were covered in ice, making them inaccessible for grubbing and shoot pulling (C. M. Sharp pers. obs.). This reduced the accessibility of high-quality exogenous nutrients to Snow Geese during these periods and appears to have forced them to allocate more endogenous protein to yolk formation on those days. Interestingly, the proportion of endogenous lipids allocated to yolk over the same period did not change, which suggests that females were able to acquire sufficient carbohydrates and fat, but not protein, when unable to feed on belowground biomass. In 2006, there was also a 3-day period of below-freezing temperatures during albumen synthesis, which may have resulted in the increased dependence on endogenous protein for albumen synthesis

in that year (Fig. 2). Hahn et al. (2012) demonstrated rapid turnover in yolk and albumen (6.0 and 3.2 days, respectively) when nutrient sources are changed, which suggests that even a short period of increased reliance on endogenous nutrients could result in detectable change in the isotopic signature of egg components. These results suggest that fluctuation in access to exogenous nutrients caused by weather might have a substantial effect on nutrient allocation during breeding in species that rely heavily on exogenous nutrients.

Canada Geese also experienced freezing conditions during synthesis of yolk (2005) and albumen (2006 and 2008), but their general reliance on endogenous nutrients and use of aboveground biomass minimized the effect of sudden drops in temperature, which demonstrates how the feeding and nutrient allocation strategies of Canada Geese are well suited for conditions typical of early arrival at northern latitudes. This provides valuable insight into the evolution of nutrient allocation strategies and how access to stored nutrients can allow individuals to cope with stochastic environments.

Although our analysis of the effects of temperature on nutrient allocation strategy during albumen synthesis in Snow Geese does not support the arguments above, the results must be interpreted cautiously because there are a number of assumptions and estimates that were used to estimate “albumen production date.” If any values used in estimating “albumen production date” are incorrect, any potential effect of weather could be masked by this unknown error. As a result, our assessment of the effects of temperature on nutrient allocation during albumen synthesis is likely inconclusive. A more comprehensive analysis of weather and its effect on nutrient allocation would undoubtedly help clarify how weather can shape nutrient allocation strategy.

Body size, exogenous nutrients, and nutrient allocation to eggs.—Body size has been proposed as an important factor in explaining where a species falls on the capital–income continuum, with only larger species having the capacity for capital breeding (Meijer and Drent 1999, Johnson 2006, Klaassen et al. 2006, Houston et al. 2007). Given that Canada Geese nesting on Akimiski Island are considerably larger than Lesser Snow Geese (Table 4), our results appear to be consistent with the body-size hypothesis. However, comparison of recent studies examining nutrient allocation to eggs in geese does not support the body-size hypothesis (Table 4). Smaller-bodied Brant (*Branta bernicla*) and Emperor Geese (*Chen canagica*) use a substantially greater proportion of endogenous protein to produce yolk protein than larger Greater Snow Geese on Bylot Island (Table 4). Also, Barnacle Geese (*B. leucopsis*) and Canada Geese (which are 2.5× larger) use similar amounts of endogenous nutrients to form all egg components, but substantially more than Greater Snow Geese (which are 1.5× larger). Finally, Lesser Snow Geese at Cape Churchill use a greater proportion of endogenous nutrients to produce the lipid and albumen portion of their eggs than Lesser Snow Geese on Akimiski Island, even though they are considered the same population (Table 4; Hobson et al. 2011). Although not statistically rigorous, this comparison across species indicates that larger goose species do not necessarily allocate greater amounts of endogenous nutrients to egg production than smaller species (Table 4) and suggests that other proximate factors play an important role in determining nutrient allocation strategies within and among species.

Thomas (1988) proposed that the relative availability of resources (local or distant from breeding grounds), and their quality, directly influenced strategies of nutrient allocation to

reproduction in avian species. Canada Geese and Snow Geese differ substantially in how they forage, especially during the pre-laying period. Snow Geese are characterized as “grubbers,” excavating rich nutrient supplies associated with belowground plant parts for which their bills are well adapted (Bellrose 1976). By contrast, although Canada Geese grub under certain conditions (Abraham and Jefferies 1997, C. M. Sharp pers. obs.), they are grazers that feed primarily on lower-quality aboveground biomass. Thus, Snow Geese are better able to exploit exogenous resources on the breeding grounds than Canada Geese and can subsequently allocate more exogenous nutrients to their eggs, when such nutrients are available.

Arrival times of Snow and Canada geese on the breeding grounds might also influence how exogenous nutrients are allocated to eggs. Canada Geese arrive before suitable nesting habitat is accessible (Newton 1977, Raveling and Lumsden 1977, Raveling 1978) and begin laying once nesting habitat is snow free. By contrast, the roughly two-week-later arrival of Snow Geese at the James Bay lowlands generally occurs when snow melt and ground thaw have progressed and important foraging resources (e.g., belowground plant parts) are more accessible (Prevett et al. 1985). In 2005–2008, Canada Geese were in the later stages of rapid follicle development (RFD) and had begun to lay eggs when the Snow Geese arrived (C. M. Sharp pers. obs.). Thus, arriving later provides Snow Geese with access to feeding habitats (coastal marshes) during RFD that are inaccessible for much of the period of RFD in Canada Geese. As such, the greater availability of exogenous nutrients for Snow Geese contributes to their exploitation of these nutrients for egg formation (Prevett et al. 1979, 1985).

Ganter and Cooke (1996) reasoned that foraging conditions on the breeding grounds help to explain annual variation in clutch size of Snow Geese, suggesting that, in years with favorable conditions, females allocated more exogenous nutrients to egg production. The work of Hobson et al. (2011) indicates that even within a population, nutrient allocation to eggs can vary among colonies, depending on proximate factors such as availability of high-quality forage. Hahn et al. (2011) also noted that variation in forage availability might be responsible for changes in resource use for yolk in some years. The sensitivity of Snow Geese to variation in available exogenous nutrients on the breeding grounds (Figs. 2 and 3) might provide further evidence that access to exogenous nutrients is an important factor in shaping nutrient allocation during egg production. Previous findings combined with the results of the present study present a strong case that access to exogenous nutrients is an important proximate factor driving how nutrients are allocated during egg formation.

High-latitude breeding animals can thrive in unpredictable and sometimes harsh Arctic environments, and different species have adapted to the constraints of breeding at high latitudes in different ways. Canada Geese, for example, arrive before feeding and nesting areas are snow free (Raveling 1978). Access to large endogenous nutrient stores (large body size) enables them to use their stores for self maintenance, investment in eggs, and incubation when access to exogenous nutrients is limited (Afton and Paulus 1992). Early arrival permits a longer total breeding season, which is necessary for longer development periods related to their larger body size. Snow Geese arrive later, just when feeding and nesting areas are becoming suitable and individuals are usually able to acquire exogenous nutrients close to the nesting areas. Smaller-bodied species can breed at high latitudes because they minimize the costs associated with transporting endogenous

stores by using flexible strategies that help them deal with the variability of the Arctic environment. However, larger-bodied species are able to arrive earlier, which enables them to take advantage of exogenous nutrients when they are available but can increase their reliance on endogenous nutrients when environmental conditions are poor.

Variations in diet quality and timing of reproduction have important consequences in shaping overall breeding strategies of high-latitude breeding geese. Although body size does not appear to dictate nutrient allocation to egg production in geese, body size undoubtedly has an influence on overall breeding strategies (e.g., migration, egg production, incubation, and brood rearing) across avian taxa because it determines a species' capacity to store endogenous nutrients (Klaassen et al. 2006). Species can use local nutrients to minimize the need to carry endogenous reserves or to conserve endogenous nutrients for use when exogenous nutrients cannot meet demands. Exogenous nutrients may also be used to fuel one portion of reproductive investment, while using endogenous nutrients to meet other reproductive demands. Although endogenous stores are costly to transport and maintain over long distances and lengthy periods, they provide important capital to be utilized when income alone cannot meet demand. Differences in nutrient allocation strategies within and among species reflect variation in access to endogenous and exogenous nutrients. As a general pattern, overall breeding strategies in high-latitude breeding animals thus represent a balance between access to exogenous resources at the time of breeding and capacity to store and carry endogenous stores.

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LITERATURE CITED

- ABRAHAM, K. F., AND R. L. JEFFERIES. 1997. High goose populations: Causes, impacts, and implications. Pages 7–72 in *Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group* (B. D. J. Batt, Ed.). U.S. Fish and Wildlife Service, Washington, D.C., and Canadian Wildlife Service, Ottawa, Ontario.
- ABRAHAM, K. F., J. O. LEAFLOOR, AND H. G. LUMSDEN. 1999. Establishment and growth of the Lesser Snow Goose, *Chen caerulescens caerulescens*, nesting colony on Akimiski Island, James Bay, Northwest Territories. *Canadian Field-Naturalist* 113:245–250.
- AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care. Pages 62–108 in *Ecology and Management of Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnston, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The costs of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 in *Ecology and Management of Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnston, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459–471.
- BELLROSE, F. C. 1976. *Ducks, Geese, and Swans of North America*. Stackpole Books, Harrisburg, Pennsylvania.
- BLIGH, E. G., AND W. J. DYER. 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemical Physiology* 37:911–917.
- BONNET, X., D. BRADSHAW, AND R. SHINE. 1998. Capital versus income breeding: An ectothermic perspective. *Oikos* 83:333–342.
- CHEREL, Y., K. A. HOBSON, F. BAILLEUL, AND R. GROSCOLAS. 2005. Nutrition, physiology, and stable isotopes: New information from fasting and molting penguins. *Ecology* 86:2881–2888.
- COOPER, J. A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildlife Monographs*, no. 61.
- COOPER, J. A., AND B. D. J. BATT. 1972. Criteria for aging giant Canada Goose embryos. *Journal of Wildlife Management* 36:1267–1270.
- COSTA, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposia of the Zoological Society of London* 66:293–314.
- DIGNARD, N., R. LALUMIÈRE, A. REED, AND M. JULIEN. 1991. Habitats of the northeast coast of James Bay. *Occasional Paper No. 70*. Canadian Wildlife Service, Ottawa, Ontario.
- DRENT, R., AND S. DAAN. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68:225–252.
- DZUBIN, A., AND E. G. COOCH. 1992. *Measurements of Geese: General Field Methods*. California Waterfowl Association, Sacramento.
- GANTER, B., AND F. COOKE. 1996. Pre-incubation feeding activities and energy budgets of Snow Geese: Can food on the breeding grounds influence fecundity? *Oecologia* 106:153–165.
- GATES, R. J., D. F. CAITHAMER, W. E. MORITZ, AND T. C. TACHA. 2001. Bioenergetics and nutrition of Mississippi valley population Canada Geese during winter and migration. *Wildlife Monographs*, no. 146.
- GAUTHIER, G., J. BETY, AND K. A. HOBSON. 2003. Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. *Ecology* 84:3250–3264.
- GLEASON, J. S. 2003. Influence of sympatric Snow Geese (*Chen caerulescens caerulescens*) on reproductive performance, behavior, and food habits of Canada Geese (*Branta canadensis interior*) on Akimiski Island, Nunavut. Ph.D. dissertation, University of Western Ontario, London, Ontario.
- GLOUTNEY, M. L., AND K. A. HOBSON. 1998. Field preservation techniques for the analysis of stable-carbon and nitrogen isotope ratios in eggs. *Journal of Field Ornithology* 69:223–227.
- HAHN, S., B. J. HOYE, H. KORTHALS, AND M. KLAASSEN. 2012. From food to offspring down: Tissue-specific discrimination and turn-over of stable isotopes in herbivorous waterbirds and other avian foraging guilds. *PLoS ONE* 7(2):e30242.
- HAHN, S., M. J. J. E. LOONEN, AND M. KLAASSEN. 2011. The reliance on distant resources for egg formation in High Arctic breeding Barnacle Geese *Branta leucopsis*. *Journal of Avian Biology* 42:159–168.
- HAMANN, J., B. ANDREWS, AND F. COOKE. 1986. The role of follicular atresia in inter- and intra-seasonal clutch size variation in

- Lesser Snow Geese (*Anser caerulescens caerulescens*). *Journal of Animal Ecology* 55:481–489.
- HOBSON, K. A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: Patterns of isotopic fractionation and turnover. *Condor* 97:752–762.
- HOBSON, K. A., R. T. ALISAUSKAS, AND R. G. CLARK. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: Implications for isotopic analyses of diet. *Condor* 95:388–394.
- HOBSON, K. A., C. M. SHARP, R. L. JEFFERIES, R. F. ROCKWELL, AND K. F. ABRAHAM. 2011. Nutrient allocation strategies to eggs by Lesser Snow Geese (*Chen caerulescens*) at a sub-Arctic colony. *Auk* 128:156–165.
- HOUSTON, A. I., P. A. STEPHENS, I. L. BOYD, K. C. HARDING, AND J. M. MCNAMARA. 2007. Capital or income breeding? A theoretical model of female reproductive strategies. *Behavioral Ecology* 18:241–250.
- JAGER, H. I., K. A. ROSE, AND A. VILA-GISP. 2008. Life history correlates and extinction risk of capital-breeding fishes. *Hydrobiologia* 602:15–25.
- JOHNSON, R. A. 2006. Capital and income breeding and the evolution of colony founding strategies in ants. *Insectes Sociaux* 53:316–322.
- JÖNSSON, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66.
- KLAASSEN, M., K. F. ABRAHAM, R. L. JEFFERIES, AND M. VRTISKA. 2006. Factors affecting the site of investment, and the reliance on savings for Arctic breeders: The capital–income dichotomy revisited. *Ardea* 94:371–384.
- LAWSON, S. L. 2006. Comparative reproductive strategies between Long-tailed Ducks and King Eiders at Karrak Lake, Nunavut: Use of energy resources during the nesting season. MSc. thesis, University of Saskatchewan.
- LEAFLOOR, J. O., M. R. J. HILL, D. H. RUSCH, K. F. ABRAHAM, AND R. K. ROSS. 2000. Nesting ecology and gosling survival of Canada Geese on Akimiski Island, Nunavut, Canada. Pages 109–116 in *Towards Conservation of the Diversity of Canada Geese (Branta canadensis)* (K. M. Dickson, Ed.). Occasional Paper No. 103. Canadian Wildlife Service, Ottawa, Ontario.
- LINDSTEDT, S. L., AND M. S. BOYCE. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* 125:873–878.
- LOURDAIS, O., X. BONNET, R. SHINE, D. DENARDO, G. NAULLEAU, AND M. GUILLON. 2002. Capital-breeding and reproductive effort in a variable environment: A longitudinal study of a viviparous snake. *Journal of Animal Ecology* 71:470–479.
- MAINGUY, S. K., AND V. G. THOMAS. 1985. Comparisons of body reserve buildup and use in several groups of Canada Geese. *Canadian Journal of Zoology* 63:1765–1772.
- MEIJER, T., AND R. DRENT. 1999. Re-examination of the capital and income dichotomy in breeding birds. *Ibis* 141:399–414.
- NEWTON, I. 1977. Timing and success of breeding in tundra-nesting geese. Pages 113–126 in *Evolutionary Ecology* (B. Stonehouse and C. M. Perrins, Eds.). Macmillan, London.
- O, P. C., P. M. KOTANEN, AND K. F. ABRAHAM. 2006. Geese and grazing lawns: Responses of the grass *Festuca rubra* to defoliation in a subarctic coastal marsh. *Canadian Journal of Botany* 84:1732–1739.
- OWEN, R. B., JR., AND K. J. REINECKE. 1979. Bioenergetics of breeding dabbling ducks. Pages 71–93 in *Waterfowl and Wetlands—An Integrated Review* (T. A. Bookhour, Ed.). La Crosse Printing, La Crosse, Wisconsin.
- PARNELL, A. C., R. INGER, S. BEARHOP, AND A. L. JACKSON. 2010. Source partitioning using stable isotopes: Coping with too much variation. *PLoS ONE* 5(3):e9672.
- PREVETT, J. P., I. F. MARSHALL, AND V. G. THOMAS. 1979. Fall foods of Lesser Snow Geese in the James Bay region. *Journal of Wildlife Management* 43:736–742.
- PREVETT, J. P., I. F. MARSHALL, AND V. G. THOMAS. 1985. Spring foods of Snow and Canada geese at James Bay. *Journal of Wildlife Management* 49:558–563.
- QUINN, G. P., AND M. J. KEOUGH. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, New York.
- RAVELING, D. G. 1978. The timing of egg laying by northern geese. *Auk* 95:294–303.
- RAVELING, D. G., AND H. G. LUMSDEN. 1977. Nesting ecology of Canada Geese in the Hudson Bay Lowlands of Ontario: Evolution and population regulation. Ontario Ministry of Natural Resources, Fish and Wildlife Research Report No. 98.
- ROBBINS, C. T., L. A. FELICETTI, AND M. SPONHEIMER. 2005. The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* 144:534–540.
- RUBENSTEIN, D. R., AND K. A. HOBSON. 2004. From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecology & Evolution* 19:256–263.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' goose. *Wilson Bulletin* 82:5–13.
- SCHMUTZ, J. A., K. A. HOBSON, AND J. A. MORSE. 2006. An isotopic assessment of protein from diet and endogenous stores: Effects on egg production and incubation behaviour of geese. *Ardea* 94:385–397.
- SHARP, C. M., K. F. ABRAHAM, AND G. BURNES. 2009. Embryo development influences the isotopic signatures of egg components in incubated eggs. *Condor* 111:361–365.
- STATSOFT. 2003. STATISTICA (data analysis software system), version 6. Statsoft, Tulsa, Oklahoma.
- STEARNS, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- STEPHENS, P. A., I. L. BOYD, J. M. MCNAMARA, AND A. I. HOUTON. 2009. Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology* 90:2057–2067.
- THOMAS, V. G. 1988. Body condition, ovarian hierarchies, and their relation to egg formation in anseriform and galliform species. Pages 353–363 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). National Museum of Natural Sciences, University of Ottawa Press, Ottawa.
- WALTERS, S. E., AND D. H. RUSCH. 1997. Accuracy of egg flotation in determining the age of Canada Goose nests. *Wildlife Society Bulletin* 25:854–857.
- WARNER, D. A., X. BONNET, K. A. HOBSON, AND R. SHINE. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *Journal of Animal Ecology* 77:1242–1249.
- WHEATLEY, K. E., C. J. A. BRADSHAW, R. G. HARCOURT, AND M. A. HINDELL. 2008. Feast or famine: Evidence for mixed capital–income breeding strategies in Weddell seals. *Oecologia* 155:11–20.