

Ecological implications of reduced forage quality on growth and survival of sympatric geese

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Summary

1. Allometric constraints associated with digesting leaves require relatively small avian herbivores to consume high-quality forage. How such constraints are overcome during ontogeny when energy and nutrient requirements are relatively high has not been adequately explored.

2. We compared growth trajectories of Canada and lesser snow goose goslings raised on grass-based diets that differed in protein (10%, 14% or 18%) and fibre (30% or 45%) with those of free-living goslings on Akimiski Island, Canada. This common-garden experiment allowed us to test the hypotheses that (i) smaller-bodied geese are more negatively affected by reduced forage quality than larger-bodied geese, and (ii) goslings from subarctic brood-rearing areas have a limited capacity to slow growth in response to reduced forage quality.

3. Canada goose goslings fed low-protein (10%) diets were on average 44% lighter in body mass, had slower growth rates and were delayed >20 days in reaching 90% of asymptotic size compared with Canada goose goslings fed 18% protein. In contrast, snow goose goslings were unable to survive on the low-protein diets, and those fed high- or medium-protein diets grew at a similar rate and achieved similar asymptotic size. Canada and snow goose goslings fed low-protein diets had reduced growth rates of the tarsus and delayed emergence of the 9th primary.

4. Free-ranging Canada goslings on Akimiski Island were similar in mass and structural size to captive-reared goslings fed low-protein diets. In contrast, snow goslings were similar in mass and structural size to the captive-reared goslings fed the high- and medium-protein diets. This suggests that degraded habitats with mostly low-protein forage may be able to support Canada goslings better than snow goslings which require higher-quality forage to survive.

5. Size-related differences in gosling growth and survival in response to diminished diet quality may influence population size when available food reaches a lower threshold in protein content. However, goslings can avoid such density-dependent population regulation if they are able to move their broods and find adequate quality and quantity of forage.

Key-words: arctic geese, *Branta canadensis*, Canada goose, *Chen caerulescens*, forage quality, growth, lesser snow goose, logistic growth curve, survival

Introduction

Body size is thought to limit the quantity and quality of plant food that can be eaten by herbivores (Demment & van Soest 1985), and such constraints may be most difficult to overcome during ontogeny when mass-specific

energy and nutrient requirements are relatively high (Ricklefs 1979, 1996; Klasing 1998; Starck & Ricklefs 1998). Much of the energy in plants is contained in the structural cell wall, and its digestion requires fermentation and a longer retention time in the digestive tract for assimilation (Stevens & Hume Ian 1995). Yet, as body size declines, herbivores must overcome the simultaneous constraints of higher mass-specific metabolic rates and smaller guts. Such allometric constraints predict that smaller herbivores must

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select higher-quality forage to satisfy nutritional requirements compared with larger herbivores (Demment & van Soest 1985), although the implications for these constraints during ontogeny have not been adequately explored.

Avian herbivores are particularly interesting in terms of the proposed allometric constraints because they are relatively small compared with other vertebrate herbivores, do not have large fermentation chambers, and the high energy demands of flight seem incompatible with the ecological limitations associated with eating leaves (Morton 1978; Parra 1978; Dudley & Vermeij 1992). In fact, <3% of extant bird species are herbivorous, most of which are poor flyers, suggesting that these constraints are challenging to circumvent (McWilliams 1999). The true geese (Order Anseriformes, Tribe Anserini) are exceptional avian herbivores in that they are strong flyers, many species have long migrations, and all species eat leaves throughout their life cycle. Moreover, during ontogeny when energy demands are especially high, goslings rely entirely on plants of relatively high quality and quantity to satisfy their nutrient requirements (Owen 1970; Sedinger & Raveling 1984, 1986; Sedinger 1986; Aubin *et al.* 1993; McWilliams 1999). For geese nesting in arctic and subarctic habitats where the growing season is short and forage quality declines rapidly through the season (Hik & Jefferies 1990; Gadallah & Jefferies 1995a; Srivastava & Jefferies 1996; Cadieux, Gauthier & Hughes 2005), strong selection for rapid growth rates of goslings requires that hatching is synchronized with the punctuated availability of relatively high-quality food so that goslings can reach maturity before fall migration (Sedinger & Raveling 1986; Aubin *et al.* 1993; Lesage & Gauthier 1997; Lepage, Gauthier & Reed 1998; Badzinski *et al.* 2002). As growing goslings must consume relatively large quantities of plant material to satisfy their energy and nutrient requirements, fast-growing herbivorous geese in arctic or subarctic ecosystems must be highly sensitive to changes in either the quality or availability of forage during this critical period.

To determine the influence of diet quality, we studied survival and growth of Canada (*Branta canadensis*, Linnaeus 1758) and lesser snow goose goslings (hereafter snow goose, *Chen caerulescens caerulescens*, Linnaeus 1758) from a subarctic nesting area where quality and availability of brood-rearing habitat have been dramatically affected by the overabundant snow goose population, a keystone herbivore in this ecosystem (Kerbes, Kotanen & Jefferies 1990; Jefferies, Jano & Abraham 2006). Long-term field studies at La Pérouse Bay, Manitoba, Canada have shown that overgrazing and grubbing by local nesting and migrant snow geese caused a trophic cascade that resulted in large-scale, long-term reductions in the availability of high-quality, preferred forage plants in coastal saltmarshes (Cargill & Jefferies 1984; Jefferies & Rockwell 2002; Jefferies, Jano & Abraham 2006; Kotanen & Abraham 2013). Changes in forage quality and quantity on high-latitude breeding areas have led to declines in gosling survival (Cooch *et al.* 1991b; Francis *et al.* 1992; Williams

et al. 1993), gosling growth rates (Cooch *et al.* 1991a), adult body size (Cooch *et al.* 1991b; Sedinger, Flint & Lindberg 1995; Winiarski, McWilliams & Rockwell 2012) and fecundity (Cooch *et al.* 1989; Sedinger, Flint & Lindberg 1995). Similar degradation of habitat and depletion of forage plants at Akimiski Island, Nunavut, Canada (Abraham & Jefferies 1997; Gleason 2003; Abraham, Jefferies & Alisaukas 2005) has resulted in dramatic declines in Canada geese (Leafloor *et al.* 1996, 2000; Leafloor, Ankney & Rusch 1998a). Body size and survivorship of goslings declined at La Pérouse Bay and Akimiski Island during growth presumably as a result of limited availability of high-quality forage (Cooch *et al.* 1991b; Francis *et al.* 1992; Williams *et al.* 1993; Leafloor, Ankney & Rusch 1998a; Winiarski, McWilliams & Rockwell 2012). Differences in body size between sympatric Canada geese and lesser snow geese could influence their ability to respond to reductions in forage quality and availability, which in turn might affect gosling growth and survival.

We conducted a common-garden experiment that involved raising Canada and snow goose goslings on grass-based diets that differed in quality but were within the range of plant quality available and eaten by wild geese on arctic and subarctic brood-rearing areas (Tables 1 and 2). Our objectives were to determine how dietary fibre and protein affect survival and growth of sympatric geese that differ in body size. We compared growth trajectories of captive goslings fed ecologically relevant diets with those of free-living goslings on Akimiski Island to test the following hypotheses: (i) effects of diet quality on survival and growth are more prominent for smaller-bodied snow geese than the larger Canada geese, and (ii) goslings from subarctic brood-rearing areas have limited capacity to slow their growth in response to reduced forage quality.

Materials and methods

EGG COLLECTION AND INCUBATION

We collected 100 Canada goose and 100 snow goose eggs (one egg per nest) on the north shore of Akimiski Island, Nunavut (53°11' N, 81°38' W) on 31 May 1995, and transported them in portable incubators by plane to Madison, Wisconsin (43°8' N, 89°20' W) on the day of collection. Thereafter, all eggs were incubated in a poultry incubator at 36.1 ± 0.7 °C (dry bulb temperature, mean ± SE) and adequate humidity (28.9 ± 1.4 °C wet bulb temperature) and were auto-rotated every 4 h. Pipped eggs were transferred to a stationary incubator for hatching (dry bulb: 35.6 ± 0.8 °C; wet bulb: 30.2 ± 1.9 °C) and hatched goslings were allowed to dry for *c.* 10 h before removal. Two eggs of each species were infertile. Of the remaining 98 eggs of each species, 89% of Canada goose eggs and 88% of snow goose eggs hatched. However, 18 of the late-hatching snow goslings died within 4 days of hatch for non-nutritional reasons and were not included in the study. We marked all goslings at hatch with size 1 monel web tags, and each gosling was randomly assigned to a diet group without replacement; all diet groups included goslings with a similar range of hatch dates.

Table 1. Nutrient content of selected forage plants collected in tidal marshes and freshwater habitats at La Pérouse Bay (LP Bay), Manitoba, Yukon–Kuskokwim Delta (Y–K Delta), Alaska, USA and Alaska National Wildlife Refuge (ANWAR), Alaska, USA. Changes in nutrient content of the same forage plants across years are provided when available. All values are mean \pm SE for each species or a range of values published. If multiple values were given through time within a season, we report the peak value

Species	Nitrogen (%)	Protein ¹ (%)	Fibre		Habitat	Location	Year	Source ³
			NDF ² (%)	ADF ² (%)				
Tidal Marsh								
<i>Carex mackenziei</i>	2.2 \pm 0.1	14.0 \pm 0.7	50.4 \pm 0.8	21.1 \pm 0.8	Mudflat	Y–K Delta	1978–1979	2
<i>Carex subspathacea</i>	3.0 \pm 0.4	19.0 \pm 1.6	47.6 \pm 1.6	23.1	Mudflat	Y–K Delta	1978–1979	2
	2.8–3.4	17.5–21.3	–	–	Saltmarsh	LP Bay	1978–1979	1
	2.1 \pm 0.4	13.1 \pm 1.9	–	–	Coastal	LP Bay	1983	3
	3.8 \pm 0.3	23.5 \pm 1.8	–	21.3 \pm 2.6	Saltmarsh	LP Bay	1993	4
<i>Puccinellia phryganodes</i>	2.4 \pm 0.1	15.2 \pm 0.6	49.5 \pm 1.9	25.8 \pm 1.0	Mudflat	Y–K Delta	1978–1979	2
	1.8–2.5	11.3–15.6	–	–	Saltmarsh	LP Bay	1978–1979	1
	2.5–4.3	15.6–26.9	–	–	Saltmarsh	LP Bay	1986–1987	6
	3.1 \pm 0.5	19.6 \pm 3.2	–	23.0 \pm 1.5	Saltmarsh	LP Bay	1993	4
<i>Stellaria humifusa</i>	1.6 \pm 0.1	10.0 \pm 0.6	–	–	Lowlands	LP Bay	1983	3
<i>Triglochin palustris</i>	4.8 \pm 0.3	30.1 \pm 1.7	23.7 \pm 1.2	23.7	Mudflat	Y–K Delta	1978–1979	2
	3.1 \pm 0.2	19.5 \pm 1.5	29.1 \pm 0.8	28.0	Meadow	Y–K Delta	1978–1979	2
Freshwater Marsh								
<i>Carex aquatilis</i> ⁴	3.2 \pm 0.3	20.0 \pm 1.8	–	27.4 \pm 1.9	Freshwater	LP Bay	1993	4
<i>Empetrum nigrum</i>	0.8 \pm 0.1	5.0 \pm 0.4	36.8	29.2	Meadow	Y–K Delta	1978–1979	2
<i>Eriophotum angustifolium</i>	1.9 \pm 0.1	11.8 \pm 0.8	40.0 \pm 1.6	16.1 \pm 1.8	Flooded	ANWAR	1986–1987	5
	2.0 \pm 0.2	12.3 \pm 1.0	44.1 \pm 2.4	17.6 \pm 1.2	Upland	ANWAR	1986–1987	5
<i>Festuca rubra</i>	2.2 \pm 0.4	13.4 \pm 2.7	–	32.3 \pm 2.6	Freshwater	LP Bay	1993	4

¹Protein content was calculated as $6.25 \times$ total nitrogen.

²Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were measured following the methods of Goering & Van Soest (1970) as modified by Undersander, Mertens & Thiex (1993).

³Sources: (1) Cargill & Jefferies (1984); (2) Sedinger & Raveling (1984); (3) Bazely & Jefferies (1985); (4) Gadallah & Jefferies (1995b); (5) Hupp *et al.* (1996); (6) Hik & Jefferies (1990).

⁴Shoots only.

Table 2. Measured composition (% dry mass) of experimental diets fed to captive-reared Canada and lesser snow goose goslings. Diets were a factorial combination of four levels of protein (very high VH, high HP, medium MP and low LP) and two levels of fibre (Low LF and High HF)

Diet		Fibre					Soluble		Energy (kJ g ⁻¹)
Protein	Fibre	Nitrogen	Protein ¹	NDF ²	ADF ²	Lignin	Lipid	Carbohydrate	
Very High	Low	4.2 \pm 0.8 ^a	26.3 \pm 0.5 ^a	28.4 \pm 1.5 ^c	16.3 \pm 0.8 ^b	1.3 \pm 0.1 ^a	1.6 \pm 0.2	43.7	18.8 \pm 0.3 ^a
	High ³	3.4 \pm 0.2 ^b	21.8 \pm 1.3 ^b	36.7 \pm 0.8 ^{bc}	20.8 \pm 0.4 ^{bc}	2.1 \pm 0.1 ^a	1.2 \pm 0.2	40.4	19.1 \pm 0.3 ^a
High	Low	2.9 \pm 0.1 ^c	18.3 \pm 0.7 ^c	32.1 \pm 2.0 ^b	16.1 \pm 1.1 ^b	2.5 \pm 0.3 ^{ab}	2.8 \pm 0.2	46.9	16.7 \pm 0.5 ^{bc}
	High	2.9 \pm 0.1 ^c	18.1 \pm 0.6 ^c	46.3 \pm 3.6 ^{ac}	25.2 \pm 2.1 ^{ac}	2.8 \pm 0.2 ^{ab}	1.5 \pm 0.2	34.1	17.8 \pm 0.6 ^{ab}
Medium	Low	2.3 \pm 0.1 ^{de}	14.6 \pm 0.4 ^d	28.3 \pm 1.2 ^b	13.6 \pm 0.7 ^b	1.8 \pm 0.2 ^a	2.2 \pm 0.2	54.9	16.8 \pm 0.4 ^{bc}
	High	2.1 \pm 0.1 ^d	13.2 \pm 0.5 ^{de}	50.2 \pm 0.3 ^a	26.8 \pm 0.3 ^a	3.1 \pm 0.2 ^b	1.2 \pm 0.1	35.4	16.7 \pm 0.4 ^{bc}
Low	Low	1.7 \pm 0.2 ^{ef}	10.9 \pm 1.4 ^e	30.7 \pm 2.8 ^b	15.7 \pm 1.1 ^b	2.1 \pm 0.3 ^a	2.2 \pm 0.2	56.2	17.1 \pm 0.3 ^{bc}
	High	1.5 \pm 0.1 ^f	9.5 \pm 0.5 ^f	44.3 \pm 2.5 ^{ac}	23.3 \pm 1.8 ^{ac}	2.7 \pm 0.2 ^{ab}	1.3 \pm 0.1	44.9	17.8 \pm 0.3 ^{ab}

Means (\pm SE) in a column with the same letters are not significantly different ($P > 0.05$, Fischer's multiple mean comparison).

¹Protein content was calculated as $6.25 \times$ total nitrogen.

²Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were measured following the methods of Goering & Van Soest (1970) as modified by Undersander, Mertens, and Thiex (1993).

³Given the nutrient composition of the ingredients used to construct diets (Table S1, Supporting information), it was not possible to formulate the very high-protein diet with as high fibre as the other high-fibre diets.

EXPERIMENTAL DIETS

Diets were formulated to simulate the protein and fibre content of natural forage consumed by goslings in arctic and subarctic breeding habitats (Table 1), although the lowest dietary protein

levels were expected to be at or below that required of growing goslings so that we could determine their protein requirements. Diets were comprised of the same five ingredients: beet sugar (*Beta vulgaris altissima*), soya bean (*Glycine max*) meal, orchard grass (*Dactylis glomerata*) hay, oat hulls (*Avena sativa*) and wheat

middling (*Triticum aestivum*, flour by-product; Table S1, Supporting information). The use of orchard grass, oat and wheat ensured that dietary fibre was derived primarily from grasses, as it is for wild goslings (Sedinger 1992). We added a vitamin and mineral premix (1 g premix per 100 g diet) to each diet, that we formulated to satisfy the vitamin and mineral requirements of domestic geese (Summers & Leeson 1985). Addition of minerals ensured that the balance of macronutrients (in this case protein) and fibre, rather than micronutrients, determined the nutritional adequacy of the diets.

Diet mixtures were dried and homogenized and then measured for total protein, neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin, lipid, soluble carbohydrate and energy content (Table 2). Total nitrogen was measured using the Kjeldahl method by the University of Wisconsin Soil and Plant Analysis Lab. Per cent NDF, ADF and lignin were measured following the methods of Goering & Van Soest (1970) as modified by Undersander, Mertens & Thiex (1993). Lipid was extracted using petroleum ether solvent refluxed for 6 h (Dobush, Ankney & Krementz 1985) in a Goldfish extraction apparatus, and soluble carbohydrate was estimated by subtraction (% Soluble Carbohydrate = 100% - % protein - % fibre - % lipid). Total energy density (kJ g⁻¹) was measured by combustion in a Phillipson microbomb calorimeter (Gentry Instruments, Aiken, SC, USA) with a benzoic acid standard.

MAINTENANCE AND DIETS OF GOSLINGS

Goslings were reared communally by diet group for their first 7–8 days in round cardboard enclosures (46 cm tall, 2.5 m diameter) containing 5–10 cm of pine shavings as bedding, a heat lamp, drinking water and appropriate food per treatment group. This communal housing allowed goslings to huddle for thermoregulation, more quickly acclimate to captive conditions and grow large enough to then be housed individually in cages. All goslings were placed in individual galvanized welded-wire cages (46 × 74 × 71 cm, 2.5 cm² mesh, 20 cages per rack) at 7 days of age for the remainder of the study (up to 100 days total). To avoid foot and leg injuries to young goslings, we used smaller mesh (1.2 cm²) floor inserts with PVC-coated wire on the floor of each cage until goslings were about 5 weeks old. Enclosures and cage racks were housed indoors and maintained at ambient temperature (c. 22 °C) with a 12-h light:12-h dark photoperiod. Food, water, oyster shell grit and sand were provided *ad libitum*.

During the early growth phase (0–21 days), goslings were fed one of six diets that included a factorial combination of three levels of protein (very high VHP c. 24%; high HP c. 18%; and low LP c. 10%) and two levels of neutral detergent fibre (NDF) content (high HF c. 45% and low LF c. 30%), but all diets were similar in overall energy content (16.7–19.1 kJ g⁻¹; Table 2). We specifically formulated diets to be representative of selected foods of wild goslings (Table 1), and we expected the higher level of dietary fibre to increase processing time and potentially limit food intake of goslings. Protein content ranged above and below expected protein requirements (c. 18%) of growing goslings based on studies of domestic waterfowl (National Research Council 1984; Sedinger 1992) and was within the range of wild foods (Table 1).

The factorial combination of these dietary fibre and protein levels (Table 2) allowed us to determine the level at which protein deficiency caused a reduction in growth rates, and fibre content further reduced diet quality. After 3 weeks, we found that >18% protein was more than adequate for gosling growth and as we

found no apparent or statistical differences between growth rates for goslings in these groups, we combined VHP and HP dietary protein levels and reduced half of all the birds to the medium-protein diet (MP), while maintaining the dietary fibre levels for all diet groups. These two protein reductions at 21 days of age resulted in the following six diet groups [*N* = number of birds/group, see Tables 4, S2 and S3 (Supporting information) for Canada and snow geese, respectively] during the late growth phase (22–100 days): HP/HF (high protein/high fibre), HP/LF (high protein/low fibre), MP/HF (medium protein/high fibre), MP/LF (medium protein/low fibre), LP/HF (low protein/high fibre) and LP/LF (low protein/low fibre; see Table 2 for nutrient composition of these six diets).

MEASUREMENTS OF GOSLINGS

Beginning 1 or 2 days after hatch, we weighed goslings every 2–3 days with an electronic balance (±0.1 g) to 21 days and thereafter with a Pesola spring scale (±1 g) or larger electronic balance (±1 g). Following the methods of Dzubin & Cooch (1992), we measured culmen, diagonal tarsus length and ninth primary length with digital calipers (±0.1 mm) every 2–4 days throughout development. Age of goslings when ninth primary erupted was estimated as the mid-point in time between the age when the ninth primary was first detected and the age when previously measured (always 2–4 days prior). Asymptotic size of ninth primary was defined as the length of the feather when the feather shaft cleared. When ninth primaries exceeded the length of calipers, we measured with a ruler to the nearest 1 mm. Gosling mortality was recorded daily and the experiment ended when surviving goslings were 80–102 days of age, and all except those fed the poorest quality diets had completed growth.

SURVIVAL

To estimate survival functions for Canada and snow goose goslings for each of the diet groups, we used the Kaplan–Meier product-limit method (Kaplan & Meier 1958; Lee 1992) in PROC LIFETEST (SAS/STAT[®] software 9.3; SAS Institute Inc. 2011). Goslings that died at <4 days of age or for non-nutritional reasons were censored from the analysis (Lee 1992). To test for differences in survival functions between diets and between species on the same diets, we used the Mantel–Haenszel log-rank test for equality across treatment groups because a greater proportion of mortality occurred for young goslings (<15 days old) (Mantel & Haenszel 2004). We calculated proportional hazard ratios using PROC PHREG for all diets relative to the best quality diet: high protein and low fibre (HP/LF). Potential effects of hatch date on survival were minimized through randomization in this analysis because goslings hatching at different times were equally distributed among diet groups. In addition, a previous study of captive Canada geese suggested that hatch dates did not affect growth rates when diet quality remained constant, and food was provided *ad libitum* (Leafloor, Ankney & Rusch 1998b).

ESTIMATING GROWTH PARAMETERS FOR INDIVIDUAL GOSLINGS

We initially analysed growth of culmen, diagonal tarsus and body mass for individual birds that survived more than 60 days with the reparameterized version of the Richard's process-error

method which uses a 4th parameter, m , that controls the shape of the growth curve (Richards 1959; White 1980; Brisbin 1986a,b; Brisbin *et al.* 1987) providing a means to select the most appropriate model [logistic: $m > 2$; Gompertz: $m \approx 1$ (Richards 1959; Ricklefs 1983)]. For our growth data on captive Canada and snow goslings, the shape parameter, m , was >2 for all structural measurements, indicating that the equation reduces to the simpler logistic equation. Further, the calculated pseudo R^2 of the Richard's model was similar to that for the logistic model with only three of the four parameters. Thus, based on the principle of parsimony, we used the logistic growth model for all subsequent analyses.

We used a least squares nonlinear regression procedure (PROC NLIN, Marquardt method; SAS Institute Inc. 2011) to fit the following logistic growth model (Ricklefs 1983) to measurements of mass, culmen, diagonal tarsus and ninth primary length for individual birds that survived more than 60 days:

$$W(t) = \frac{A}{(1 + be^{-kt})}$$

where W is the structural measurement (in g for mass and mm for culmen, tarsus or ninth primary), A is the asymptote, k is the growth rate constant, and t is age in days. Parameter b was calculated as $(A - W_{\text{initial}})/W_{\text{initial}}$, where W_{initial} is the initial measurement after hatch.

The logistic growth analysis was complicated for tarsus because many of the goslings fed low-protein diets had not yet reached asymptotic size when the study was completed, although they were on average within 10% of the asymptotic tarsus length of goslings fed medium and high dietary protein. As a result, the logistic model did not adequately converge to an asymptote or the asymptote was overestimated for goslings fed these low-quality diets. To force models to converge, we assumed the asymptotic tarsus length of these goslings was the mean asymptotic tarsus length for male and female goslings fed high or medium dietary protein.

The logistic growth analysis was also complicated for ninth primary because diet affected the age at emergence of primary feathers (range was 19–36 days of age for Canada geese, 15–34 days of age for snow geese). Consequently, we subtracted the age of emergence from each measurement age to shift the curve towards the origin and fit the logistic growth model for only the period of ninth primary growth from emergence to asymptotic size.

STATISTICAL ANALYSES: EFFECTS OF DIET ON GROWTH OF GOSLINGS

The product of the logistic growth modelling was a set of parameter estimates (i.e. A , k and b) for each individual that were then used to test for effects of diet quality on growth of male and female Canada and snow goose goslings. For this analysis, we combined goslings of a given gender and species that were fed the VHP or HP diets because we expected protein levels $>18\%$ to be more than sufficient for growing goslings (National Research Council 1984) and because we did not detect consistent differences in the parameter estimates for goslings raised on these higher-protein diets ($P > 0.05$ for 84% of all comparisons). Thus, the statistical analyses that tested for the effects of diet quality on growth parameters included six diets that were a factorial combination of protein (HP, MP, LP) and fibre (HF, LF; see Table 2 for diet composition).

We used a factorial analysis of variance (ANOVA, PROC GLM; SAS Institute Inc. 2011) to examine the effects of gender (SEX), diet group (DIET) and their interaction (SEX \times DIET) on the parameter estimates from the logistic growth analyses of structural size and body mass of goslings for each species. When significant differences were detected for a given parameter, we used Fisher's protected least squares difference (FPLSD) (Carmer & Swanson 1973) to examine the influence of protein content (PROTEIN), fibre content (FIBRE) and their interaction. We also used a two-way ANOVA to examine the effect of diet group (DIET) on growth rates (k) across the two species (SPECIES) and their interaction (SPECIES \times DIET). We accepted statistical significance at $P < 0.05$ for all tests.

COMPARISONS WITH WILD GOSLINGS

Wild goslings on Akimiski Island, Nunavut were web-tagged at hatching using standard methods (see Leafloor *et al.* 2000 for details) and recaptured *c.* 5–8 weeks later. Growth curves generated for Canada and snow goose goslings on the experimental diets were then compared graphically to the measurements of wild goslings on Akimiski Island in the same year.

Results

EFFECTS OF DIET QUALITY ON SURVIVAL

Comparison across diets for each species

Kaplan–Meier log-rank survival probabilities for Canada goose goslings <21 days of age (Fig. 1a) did not differ across diet treatment groups (log-rank $\chi^2 = 2.74$, d.f. = 5, $P = 0.74$; Fig. 1a); however, gosling survival was marginally influenced by decreasing protein content of the diets (log-rank $\chi^2 = 11.85$, d.f. = 5, $P = 0.037$, Fig. 1c). For snow goose goslings, significant reductions in survival were apparent with decreasing diet quality (i.e. low protein), especially during early growth (log-rank $\chi^2 = 28.34$, d.f. = 5, $P < 0.0001$; Fig. 1b) as well as during growth up to 80 days (log-rank $\chi^2 = 24.64$, d.f. = 5, $P = 0.0002$; Fig. 1d).

Proportional hazard ratios for Canada and Snow goose goslings were calculated for each of the diet groups relative to the high-protein and low-fibre (HP/LF) diet: the highest quality diet. We found that Canada goslings had comparable hazard ratios for the high- or low-protein diets ($P > 0.05$, Hazard ratio = 0.71–1.2; Table 3). Snow goslings, however, fed the low-protein, high-fibre diets (LP/HF) had 4 times higher mortality than goslings fed the high-protein, low-fibre diet (HP/LF) ($\chi^2 = 9.29$, $P = 0.002$, Hazard ratio = 4.03; Table 3) and 2 times higher mortality when fed the low protein, low fibre (LP/LF) diet ($\chi^2 = 2.586$, $P = 0.11$, Hazard ratio = 2.05; Table 3).

Comparison between species for each diet

When we compared the two species on the same diets, we found that survival probabilities were similar between Canada and snow goslings on all of the high- and med-

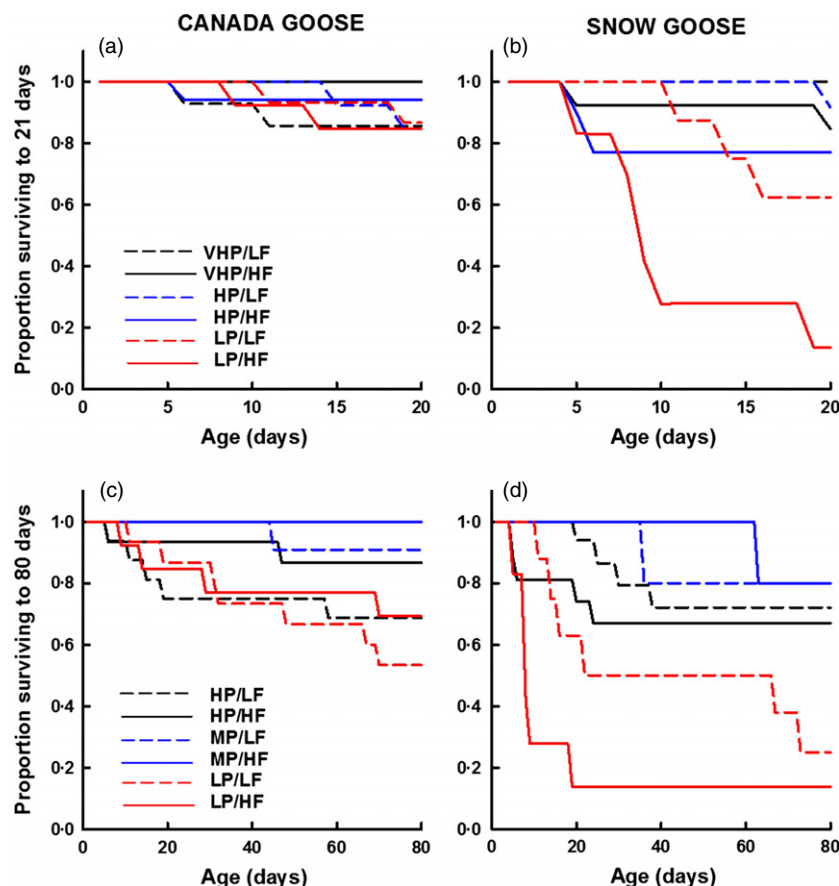


Fig. 1. Survival probability of captive-reared Canada and snow goose goslings to 21 days old (a and b) and to 80 days old (c and d). Goslings were fed one of six experimental diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF).

ium-protein diets. Snow goslings fed the lowest quality diet (LP/HF) had significantly lower survival than Canada goslings fed this same diet during early growth (to 21 days log-rank $\chi^2 = 11.79$, d.f. = 1, $P = 0.0006$; Fig. 1a, b) as well as after 21 days to adult size (up to 80 days log-rank $\chi^2 = 9.91$, d.f. = 1, $P = 0.0016$; Fig. 1c,d).

EFFECTS OF DIET QUALITY ON GOSLING GROWTH

For goslings that survived more than 60 days, logistic growth curves for body mass, culmen length and diagonal tarsus length (mm) are shown in Fig. 2 for Canada goslings and Fig. 3 for snow goslings and the associated full suite of parameter estimates are in Tables S2 and S3 (Supporting information), respectively. Males were heavier and larger than females, and Canada goslings were heavier and larger than snow goslings. Diet effects were most evident when goslings were fed the lowest protein (10%) and these diet effects were usually more evident in snow geese.

For Canada goose goslings, asymptotic body mass differed between diets ($F_{5,55} = 7.94$, $P < 0.0001$), between males and females ($F_{1,55} = 47.42$, $P < 0.0001$), and there was a significant interaction (DIET \times SEX $F_{5,55} = 2.71$, $P = 0.03$; Fig. 2a,b). Final body mass of Canada goslings fed the low-protein diets was 38% lower for females and 14% lower for males compared with those fed the high- or medium-protein diets (Table S2, Supporting information). For snow goose goslings, asymptotic body mass

Table 3. Proportional hazard ratios for captive-reared Canada goose ($n = 85$) and lesser snow goose ($n = 54$) fed diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF). Hazard ratios were generated for goslings >80 days old relative to the high-protein, low-fibre (HP/LF) diet

Diet		χ^2	P	Hazard ratio
Protein	Fibre			
Canada Goose				
High	Low	–	–	–
	High	0.341	0.56	0.81
Medium	Low	0.435	0.51	0.77
	High	0.899	0.34	0.71
Low	Low	0.263	0.61	1.2
	High	0.001	0.97	0.99
Snow Goose				
High	Low	–	–	–
	High	0.190	0.66	1.18
Medium	Low	0.011	0.92	0.95
	High	0.044	0.83	0.9
Low	Low	2.586	0.11	2.05
	High	9.290	0.002	4.03

was consistently higher for males for each diet (SEX $F_{1,20} = 14.97$, $P = 0.0001$); however, low survival of goslings fed the low-protein diets made it difficult to detect differences in asymptotic body mass across diet treatment groups (DIET $F_{4,20} = 2.04$, $P = 0.127$; DIET \times SEX

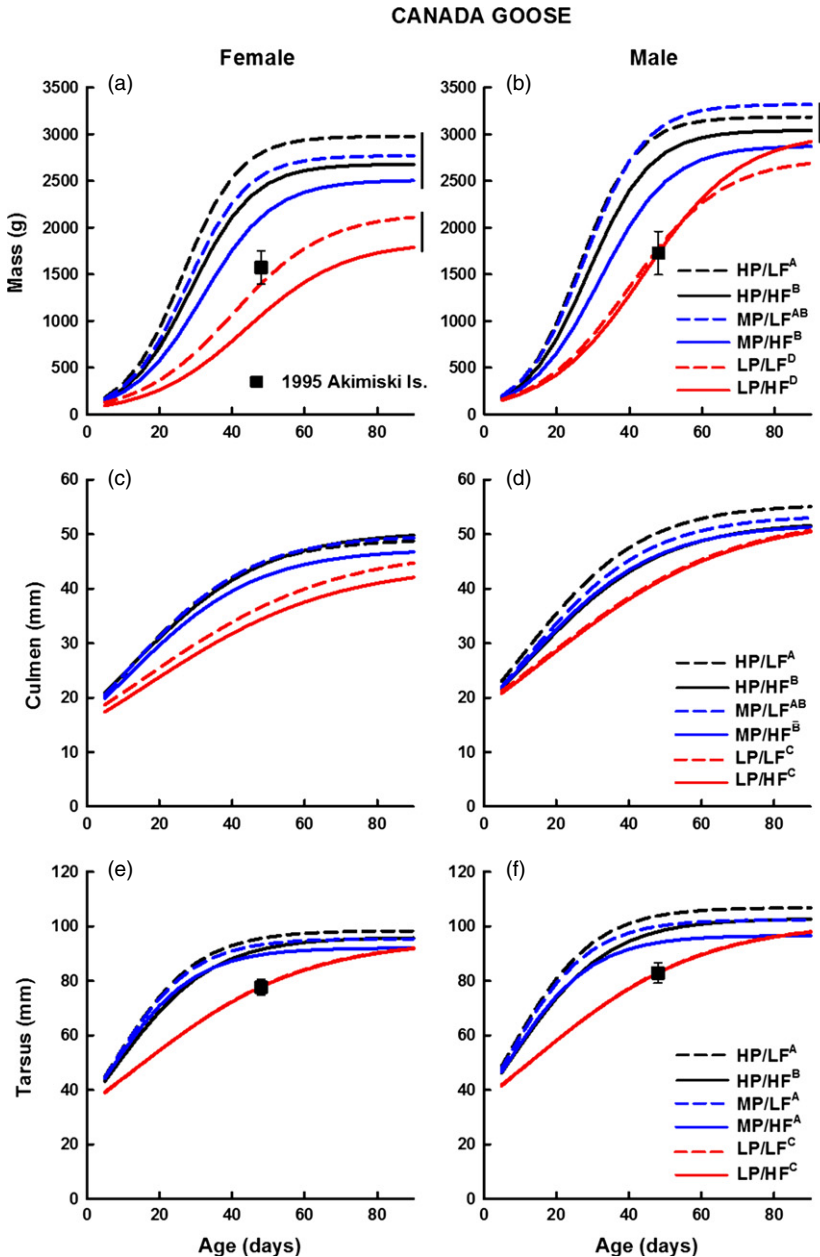


Fig. 2. Growth curves (lines) for mass (g), culmen length (mm) and diagonal tarsus length (mm) fit to the logistic model for female and male Canada goose goslings. Goslings were fed one of six experimental diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF). For each gender, differences between diets in asymptotic mass are denoted by non-overlapping vertical bars. Diets in the legend that share the same letter were not significantly different in growth rate (k) of mass and tarsus length, genders combined. Rectangles are mean (\pm SE) body mass (g) and diagonal tarsus length of wild goslings from Akimiski Island banded in 1995 that were web-tagged at hatch and then recaptured at on average 48 days of age. Data for culmen length were not available in 1995.

$F_{4,20} = 0.74$, $P = 0.58$; Fig. 3a,b; Table S3, Supporting information).

For both Canada and snow goose goslings, growth rates (k) of body mass were significantly lower for goslings fed low-protein diets relative to those fed high- or medium-protein levels (DIET Canada $F_{5,55} = 47.90$, $P < 0.001$; snow $F_{4,20} = 13.10$, $P < 0.0001$), but were similar across genders (SEX Canada $F_{1,55} = 1.70$, $P = 0.5$; snow $F_{1,20} = 1.90$, $P < 0.18$; Table S2 and S3, Supporting information).

For both Canada and snow goose goslings, final culmen length was larger in males than females (SEX Canada $F_{1,55} = 30.94$, $P < 0.0001$; snow $F_{1,20} = 9.69$, $P = 0.006$), but did not differ across the diet groups (DIET Canada $F_{5,55} = 1.14$, $P = 0.35$, Fig. 2c,d; snow $F_{4,20} = 1.66$, $P = 0.20$, Fig. 3c,d). However, growth rates (k) of the

culmen were significantly lower for Canada goslings fed low-protein diets ($F_{5,55} = 21.81$, $P < 0.0001$; Table S2, Supporting information), and the same trend was evident for snow goslings ($F_{4,20} = 2.65$, $P = 0.064$, Table S3, Supporting information). In addition, Canada and snow goslings fed low-protein diets took >28 days and >42 days longer, respectively, to reach 90% of asymptotic culmen length ($T_{90\%}$, Canada $F_{5,55} = 17.75$, $P < 0.0001$; snow $F_{4,20} = 3.83$, $P = 0.015$; Table 4) than goslings fed the high-protein diets.

Similar to other structural measures, growth rates of the diagonal tarsus were significantly lower for goslings fed low-protein diets (Canada $F_{5,55} = 53.79$, $P < 0.0001$, Fig. 2e,f; snow $F_{4,20} = 7.51$, $P = 0.004$, Fig. 3e,f). In addition, it took >38 days and >39 days longer for the tarsus to reach $T_{90\%}$ for Canada ($F_{5,55} = 47.16$, $P < 0.0001$;

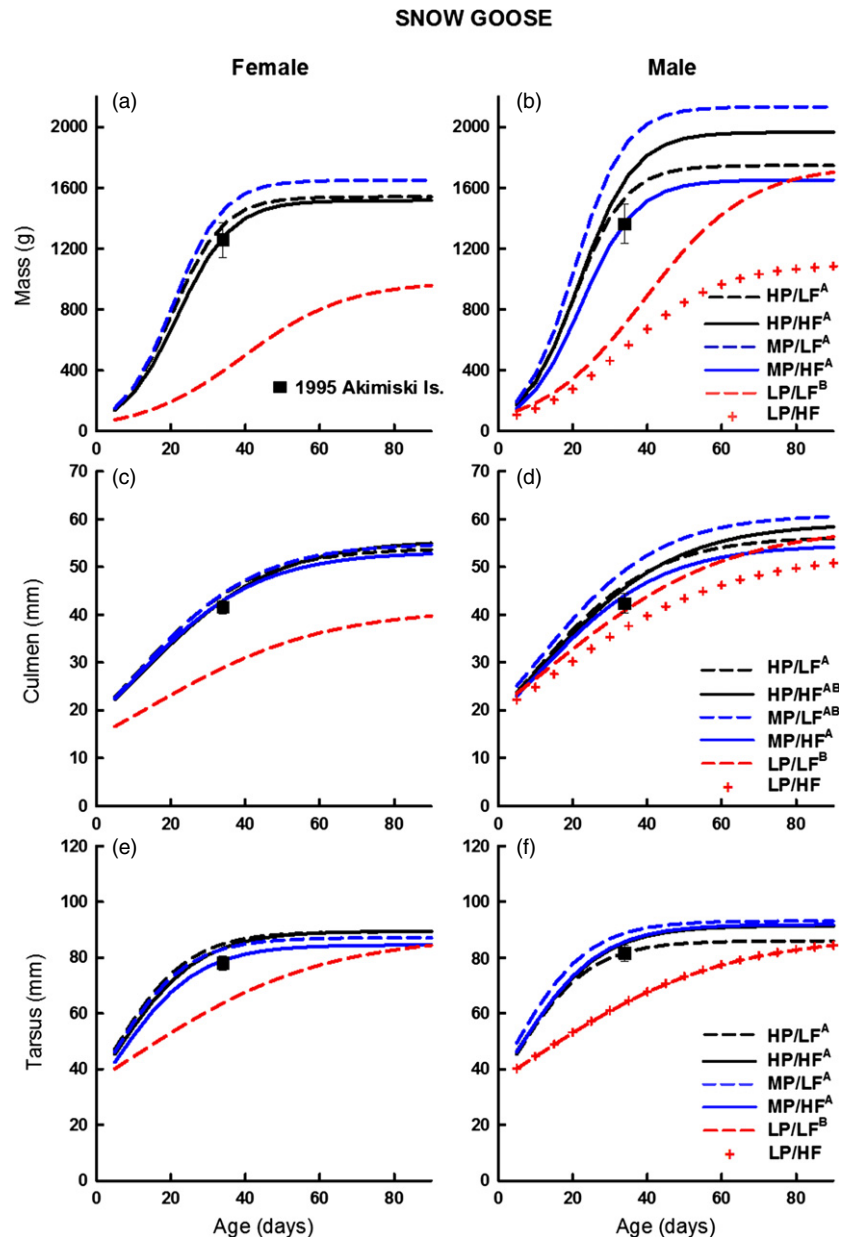


Fig. 3. Growth curves for mass (g), culmen length (mm) and diagonal tarsus length (mm) fit to the logistic model for female and male lesser snow goose goslings. Goslings were fed one of six experimental diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF). Only one Snow gosling fed the LP/HF diet survived (+). Diets in the legend that share the same letter were not significantly different in growth rate (k), genders combined. Rectangles denote the mean (\pm SE) mass, culmen length or tarsus length of wild goslings from Akimiski Island in 1995 that were web-tagged at hatch and then recaptured at on average 34 days of age.

Table 4) and snow goose ($F_{4,20} = 23.32$, $P < 0.0001$; Table 4) goslings, respectively.

EFFECTS OF DIET QUALITY ON GROWTH AND EMERGENCE OF 9TH PRIMARY

For both Canada and snow goslings, asymptotic length of the 9th primary and its growth rate (k) did not differ by DIET and SEX, nor their interactions (all $P > 0.05$, Table 5, Fig. 4), although asymptotic length of the primary feather was 9–14% shorter for birds on the low-protein diets. The age of emergence of the 9th primary for Canada goslings was significantly affected by DIET (Canada $F_{5,51} = 58.19$, $P < 0.0001$) with primary feathers emerging 16 days later for birds fed the low-protein, high-fibre (LP/HF) diets (Table 5). For snow goslings,

emergence of the ninth primary was also affected by DIET ($F_{4,12} = 31.76$, $P < 0.0001$). The 9th primary emerged 16 or 21 days later for goslings fed the LP/LF or LP/HF diet ($n = 1$ and 3, respectively) compared with goslings fed the HP/LF diets (Table 5). For both Canada and snow goose goslings, age of 9th primary emergence was significantly affected by dietary protein (Canada $F_{2,51} = 179.60$, $P < 0.0001$; snow $F_2 = 47.59$, $P < 0.001$, Table 5) but not dietary fibre (Canada $F_{1,51} = 0.16$, $P = 0.69$; snow $F_{1,12} = 1.32$, $P = 0.27$, Table 4).

The growth rate constant (k) for 9th primary was not significantly affected by diet for both Canada (DIET $F_{5,51} = 2.30$, $P = 0.058$, SEX $F_{1,51} = 3.06$, $P = 0.09$, DIET \times SEX $F_{5,51} = 0.67$, $P = 0.65$, Table 5, Fig. 4a) and snow goose goslings (DIET $F_{5,12} = 1.03$, $P = 0.44$, SEX $F_{1,12} = 0.68$, $P = 0.42$, DIET \times SEX $F_{4,12} = 0.07$,

Table 4. Age in days (mean \pm SE) to reach 90% (T_{90}) of asymptotic mass, culmen, and diagonal tarsus length for captive-reared Canada and snow goose goslings fed one of six diets that were a factorial combination of protein (3 levels: High HP, Medium MP, and Low LP) and fibre (2 levels: Low LF and High HF)

Diet Protein	Fibre	N	Mass (days)	Culmen (days)	Tarsus (days)
Canada Goose					
High	Low	10	43.9 \pm 1.6 ^d	47.2 \pm 1.7 ^b	32.7 \pm 1.2 ^b
	High	13	47.7 \pm 1.2 ^d	53.1 \pm 2.0 ^b	37.6 \pm 1.7 ^b
Medium	Low	10	45.8 \pm 1.1 ^d	48.9 \pm 1.8 ^b	31.2 \pm 1.0 ^b
	High	15	53.2 \pm 1.1 ^c	51.0 \pm 2.1 ^b	32.3 \pm 1.5 ^b
Low	Low	9	68.2 \pm 2.4 ^b	74.0 \pm 4.4 ^a	64.5 \pm 2.7 ^a
	High	10	74.7 \pm 4.3 ^a	74.8 \pm 4.9 ^a	66.8 \pm 4.8 ^a
Snow Goose					
High	Low	10	35.3 \pm 1.2 ^b	45.7 \pm 2.9 ^b	26.9 \pm 1.9 ^b
	High	8	38.4 \pm 1.7 ^b	52.1 \pm 2.3 ^b	30.8 \pm 2.9 ^b
Medium	Low	4	35.9 \pm 3.3 ^b	47.9 \pm 5.7 ^b	26.3 \pm 2.4 ^b
	High	5	38.4 \pm 2.2 ^b	47.2 \pm 2.6 ^b	29.4 \pm 1.8 ^b
Low	Low	3	69.6 \pm 3.3 ^a	69.2 \pm 11.4 ^a	65.4 \pm 1.8 ^a
	High	1	63.0	66.8	65.0

Means within a column with the same letter were not significantly different (ANOVA, Fisher's Protected LSD multiple mean comparison).

$P = 0.99$ Table 5, Fig. 4b). Inspection of the residuals showed that growth of the ninth primary was linear between 10% and 90% of asymptotic length, so we estimated daily growth rates of ninth primary for each individual during this linear phase of growth. For Canada goslings, growth rates of the ninth primary averaged 6.8 mm day⁻¹ (range: 6.6–7.0 mm day⁻¹). For snow goslings, growth rates of the ninth primary averaged 6.4 mm day⁻¹ (range: 5.8–6.8 mm day⁻¹).

Table 5. Mean (\pm SE) parameter estimates for 9th primary feather from a logistic growth model for captive-reared Canada and lesser snow goose goslings fed grass-based diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF). Logistic growth model of the form $W = A/(1 + be^{-kt})$, where A is the asymptotic mass for both sexes combined (not significantly different), k is the growth rate constant, and b is the limit [$b = (A - \text{initial mass})/\text{initial mass}$]. Curves begin at the age of emergence of the 9th primary ($T_{\text{Emergence}}$, days) and end at the age when primary length is completed ($T_{\text{Asymptote}}$, days). Differences between diets were evident for T_{EMERGE} and $T_{\text{ASYMPTOTE}}$; values within a column with the same letter were not significantly different (ANOVA, Fisher's protected LSD multiple mean comparison)

Protein	Fibre	N	Asymptote (A) (mm)	k	b	Pseudo R^2	$T_{\text{Emergence}}$ (days)	$T_{\text{Asymptote}}$ (days)
Canada Goose								
High	Low	10	281 \pm 7	0.143 \pm 0.006	40.81 \pm 6.97	0.990–0.999	19 \pm 1 ^b	71 \pm 2 ^b
	High	13	273 \pm 5	0.160 \pm 0.006	84.79 \pm 24.18	0.980–0.999	20 \pm 1 ^b	70 \pm 2 ^b
Medium	Low	9	274 \pm 4	0.154 \pm 0.005	54.78 \pm 10.27	0.992–0.998	20 \pm 1 ^b	71 \pm 1 ^b
	High	15	269 \pm 6	0.149 \pm 0.004	58.60 \pm 8.03	0.989–0.999	20 \pm 1 ^b	71 \pm 1 ^b
Low	Low	7	255 \pm 7	0.154 \pm 0.004	25.85 \pm 2.25	0.996–0.998	36 \pm 2 ^a	81 \pm 1 ^a
	High	8	268 \pm 4	0.135 \pm 0.005	16.79 \pm 3.14	0.991–0.999	36 \pm 1 ^a	80 \pm 1 ^a
Snow Goose								
High	Low	8	252 \pm 7	0.166 \pm 0.008	49.54 \pm 8.93	0.985–0.998	13 \pm 1 ^b	63 \pm 1 ^b
	High	5	247 \pm 7	0.152 \pm 0.011	26.82 \pm 7.10	0.995–0.999	16 \pm 1 ^b	62 \pm 1 ^b
Medium	Low	3	248 \pm 18	0.150 \pm 0.008	28.41 \pm 3.03	0.974–0.997	15 \pm 1 ^b	61 \pm 4 ^b
	High	4	236 \pm 11	0.180 \pm 0.009	56.07 \pm 8.67	0.990–0.995	15 \pm 1 ^b	61 \pm 4 ^b
Low	Low	2	215 \pm 5	0.147 \pm 0.006	14.31 \pm 6.26	0.997–0.999	34 \pm 4 ^a	72 \pm 6 ^a
	High	1	230	0.162	18.17	0.997–0.997	29	65

EFFECTS OF DIET QUALITY ON GROWTH RATE BETWEEN SPECIES

Growth rate constants (k) for body mass were significantly higher for snow goslings than Canada goslings for all high and medium-protein diets, but did not differ for goslings on the low-protein diets (SPECIES \times DIET, $F_{5,86} = 3.17$, $P = 0.011$). No significant differences in growth rates of culmen or diagonal tarsus were found between snow and Canada goslings for any diet (all $P > 0.05$). Diet quality affected growth rates of primary feathers in different ways for Canada compared with snow goslings (SPECIES \times DIET $F_{5,74} = 2.87$, $P = 0.02$), with snow goslings having a slightly higher growth rate constant than Canada goslings when fed the HP/LF ($P = 0.0074$) and MP/HF ($P = 0.0026$) diets. In general, daily growth rates of primary feathers over the linear portion of the curve were similar between species and across diets (6.4–6.8 mm day⁻¹), and the main effect of reduced diet quality was the delay in primary feather emergence and time to reach $T_{90\%}$ for both Canada and snow geese.

COMPARISON BETWEEN CAPTIVE AND FREE-LIVING GOSLINGS

Free-living Canada goslings were on average 48 days of age (range 46–50 days) and were similar in mass and size to captive goslings of similar age that were fed the low-protein diets (female 1573 \pm 178 g, male 1729 \pm 233 g; Fig. 2). In contrast, snow goslings at about 34 days (range 32–36 days) were similar in mass and size to captive goslings of similar age that were fed the medium- or higher-protein diets (female 1258 \pm 115 g; male

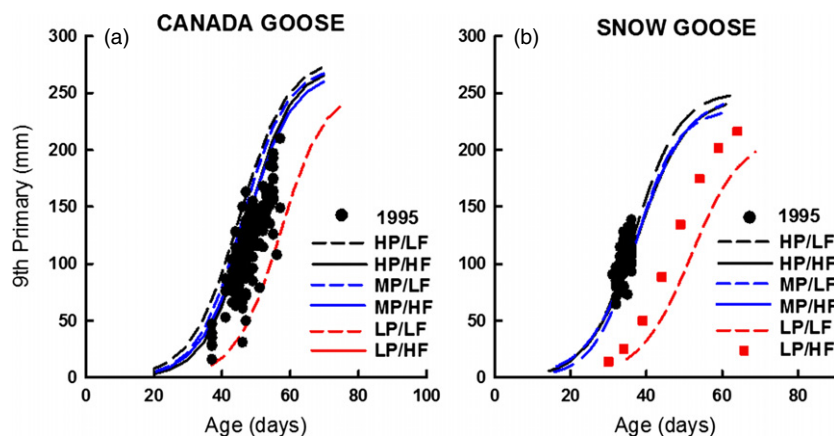


Fig. 4. Growth curves for 9th primary fit to the logistic model for captive-reared Canada and snow goose goslings. Goslings were fed one of six experimental diets that were a factorial combination of protein (3 levels: high HP, medium MP and low LP) and fibre (2 levels: low LF and high HF). Note that only one snow gosling fed the LP/HF diet survived. No significant effects of diet or gender were found for the asymptote or growth rate (k) constant (all $P > 0.05$), although age of emergence ($T_{\text{Emergence}}$) and age when reaching final length ($T_{\text{Asymptote}}$) were significantly different between diets (Table 4). Rectangles denote the 9th primary length of wild goslings from Akimiski Island in 1995 that were web-tagged at hatch and then recaptured when 46–50 days old for Canada gosling and 32–36 days old for snow goslings.

1363 ± 128 g; Fig. 3). This pattern was consistent for body mass and all structural measurements (Figs 2 and 3), as well as for ninth primary length (Fig. 4).

Discussion

INTERSPECIFIC DIFFERENCES IN RESPONSE TO DIET QUALITY

Structural size and growth rates (k) for both Canada and snow goose goslings were significantly affected by diet quality, although how diet quality affected size and growth rates differed between the species (Tables S2 and S3, Supporting information; Figs 2 and 3). The larger Canada goslings had similar survival across all diet groups, but slower growth rates as dietary protein declined. For Canada goslings that survived >60 days, goslings were lighter in mass and smaller in size as dietary protein level decreased from high (>18%) to medium (14%) and to low (10%). The smaller snow goose goslings, on the other hand, maintained high growth rates and reached similar asymptotic size when fed either the high- (18%) or medium-(14%) protein diets, but reduced growth rates and final size of goslings were significantly lower for goslings fed the low-protein diet (10%). Moreover, snow goslings fed the low-protein diets had lower survival and were 4–6 times more likely to die than those on higher-protein diets (Table 3). Thus, the smaller-bodied snow goose appeared to be more negatively affected by reduced protein levels during growth than the larger-bodied Canada goose, which is consistent with our first hypothesis. Contrary to our expectations, however, higher levels of dietary fibre did not consistently affect growth rates and survival of goslings of either species.

PHENOTYPIC FLEXIBILITY IN GROWTH

Snow goslings fed the high- or medium-protein diets grew at a relatively fixed rate and achieved similar asymptotic size, whereas the Canada goslings were able to reduce their growth rate and size in response to the same reduction in dietary protein. For both Canada and snow goose goslings, however, maturation was delayed when dietary protein was inadequate. The relatively fixed growth rate exhibited by snow goose goslings on both diets above 14% protein is consistent with the hypothesis that smaller goslings may have limited capacity to respond to lower forage quality below some threshold. In contrast, the degree of phenotypic flexibility in growth rate and size demonstrated by Canada goose goslings in response to decreased diet quality suggests that larger species may have an advantage, especially when mitigating the constraints imposed by small body size. Phenotypic flexibility in growth in response to diet quality is common in altricial as well as other precocial species of birds (Shrew & Ricklefs 1988). For example, altricial white-fronted bee eaters (*Merops bullockoides*), European starlings (*Sturnus vulgaris*), song sparrows (*Melospiza melodia*) and zebra finches (*Peophila guttata*) as well as precocial chickens (*Gallus gallus* f. dom.) and Japanese quail (*Coturnix coturnix japonica*) slow growth, delay fledging or attainment of adult size and retard feather growth in response to reduced food intake and diet quality (McRoberts 1965; Boag 1987; Shrew & Ricklefs 1988; Emlen *et al.* 1991; Searcy, Peters & Nowicki 2004). Less common are species such as snow geese in our study that grow at a relatively fixed rate regardless of diet quality (Shrew & Ricklefs 1988). For example, growth rate of Leach's storm petrel (*Oceanodroma leucorhoa*) did not change with reduced diet quality (Ricklefs 1987), although this ability to grow

normally despite variation in diet quality may be the product of its relatively slow growth rate, nutrient requirements and large fat reserves (Ricklefs & Schew 1994). The relatively rapid growth rate of snow geese and its limited capacity to retard growth in response to reduced diet quality likely explains the high mortality of snow goose goslings fed the inadequate dietary protein. The yet untested mechanistic explanation for these interspecific differences in phenotypic flexibility in growth in response to declining forage quality is that snow geese continue to allocate resources to growth at the expense of self-maintenance and survival. In contrast, Canada geese may reduce resource allocation to growth, attempt to satisfy the minimal costs of self-maintenance, and as a result, more often survive.

Geese are known to have some of the fastest growth rates reported for a precocial species, and as high as some altricial species of similar size (Ricklefs 1973; Sedinger 1986; Aubin *et al.* 1993). Snow geese had consistently higher growth rates ($k = 0.134\text{--}0.148$) than Canada geese ($k = 0.103\text{--}0.128$) when fed the same high- and medium-protein diets, but growth rates were similar between species when fed the low-protein diets (Canada: $k = 0.075\text{--}0.079$; Snow: $k = 0.072\text{--}0.077$). Maximum growth rate for lesser snow goslings on HP diets was comparable to that for free-living lesser snow goslings in the arctic (e.g. McConnell River, Northwest Territories, Canada, $k = 0.151$ (Aubin, Dunn & MacInnes 1986), suggesting that the diet of free-living goslings must have been quite high quality given the additional costs of thermoregulation and foraging by wild geese. Cackling goose (*Branta canadensis minima*, $k = 0.074$) on the Yukon-Kuskokwim Delta, Alaska, USA (Sedinger 1986), and the large-bodied greater snow goose (*Chen caerulescens atlantica*, $k = 0.09$) on Bylot Island, Canada (Lesage & Gauthier 1997), had growth rates equivalent to our captive-reared goslings fed the low-protein diets. Lindholm, Gauthier & Desrochers (1994) found a much higher growth rate for greater snow geese ($k = 0.168$) when captive-reared goslings were fed native grasses on Bylot Island supplemented with pellet food.

The web-tagged, free-living Canada and snow goslings banded on Akimiski Island in 1995 were similar in mass and size to our captive goslings fed certain ecologically relevant diets. Specifically, body mass and size of free-living snow goslings most resembled that of the captive birds fed the high- or medium-protein diets (Fig. 3), whereas free-living Canada goslings were more similar in size to captive goslings fed the low-protein diets (Fig. 2). These apparent differences between species captured in comparable habitats support the notion that Canada geese are more flexible in their growth responses than snow goslings. Although our comparison of growth rates for free-living as well as captive goslings must be cautiously interpreted, they demonstrate (i) extensive intraspecific variation in growth rates due to diet quality and (ii) growth rates of captive-reared goslings were usually

higher than that of free-living goslings likely in part because the latter inevitably incur additional energy and nutrient costs compared with captive goslings.

FORAGE QUALITY IN RELATION TO GOSLING REQUIREMENTS

Based on the significantly reduced survival and slower growth rates for both Canada and snow goslings fed low-protein diets, we infer that goslings require on average at least 10–14% dietary protein. Reduced survival and slower growth was especially evident for snow goslings fed the 10% protein diet, which suggests that their protein requirements are at least 14% and higher than those of Canada goslings. These estimated protein requirements are in general agreement with earlier studies on domestic geese where Allen (1983) and Stevenson (1985) found that crude protein requirements were 16–20% from 0 to 4 weeks of age, but declined to 14% thereafter. Other waterfowl species, such as ducks, have been shown to require >16% dietary protein to reach maximum growth rates (Holm & Scott 1954; Scott *et al.* 1959; Lightbody & Ankney 1984), whereas some gallinaceous species require >24% dietary protein (Nestler, Bailey & McClure 1942). Incidentally, protein content of available forage is generally above 10%, and preferred species such as grasses are >14% protein or higher (Table 1). For herbivorous geese, it is no surprise that protein content of forage is usually considered the most limiting nutrient for growing goslings (Kerbes, Kotanen & Jefferies 1990; Gadallah & Jefferies 1995a,b; Lesage & Gauthier 1997; Cadieux, Gauthier & Hughes 2005).

Forage quality for herbivores is also related to dietary fibre because it affects food intake rate and digestibility (Demment & van Soest 1985; Illius & Gordon 1993) and thus the amount of acquired nutrients. In our study, dietary fibre of experimental diets ranged from 28% to 50% NDF (Table 2), which is well within the range of those found in wild forage species (Table 1). For all structural measures, we consistently found significant effects of protein content on survival and growth rates; however, we did not find consistent effects of fibre on survival, growth rates, structural size and body mass, or timing of growth for Canada and snow goose goslings, with two exceptions. Canada goslings fed low- or medium-protein diets with high fibre (LP/HF or MP/HF) took on average 6–8 days longer to reach 90% of asymptotic body mass than goslings fed the low-fibre diets with the same amount of protein (Table 4). Perhaps the larger Canada goose goslings were able to adequately compensate for most changes in dietary fibre partially because of phenotypic flexibility in gut size which can accommodate large changes in food intake while maintaining relatively constant digestibility (Karasov & McWilliams 2005; McWilliams & Karasov 2005; van Gils *et al.* 2006, 2008). For the goslings in this study, McWilliams & Leafloor (2005) found that both Canada and snow goslings fed the high-fibre diets had lar-

ger gizzard mass and longer small intestine length, but only the Canada geese increased food intake when fed high-fibre diets. The very large-bodied Bewick's swan (*Cygnus columbianus bewickii*) also exhibited considerable phenotypic flexibility in gut length in response to changes in forage quality (van Gils *et al.* 2008). Interestingly, changes in gut length were associated with increased food intake in these Bewick's swans (van Gils *et al.* 2008) just as in Canada geese. Thus, at least for these few species of avian herbivores that have been studied, larger body size seems associated with greater phenotypic flexibility in gut size and an enhanced ability to compensate for reduced forage quality. We propose that digestive constraints associated with consuming poor-quality diets (low protein or high fibre) limited food intake of snow goslings, whereas the larger Canada goslings had not yet reached these limits. Such a result is consistent with the hypothesis that animals of smaller body size generally select diets of lower fibre content and a smaller proportion of their energy requirements is satisfied by energy yield from fibre fermentation (Demment & van Soest 1985; Illius & Gordon 1993).

REDUCED DIET QUALITY DELAYS GROWTH OF BODY PARTS

High nutrient demand during growth for Canada and snow goose goslings was especially apparent at two points during growth based on survival curves (Fig. 1c,d) and growth of body mass and structural size (Figs 2 and 3) and primary feathers (Fig. 4): (i) between 10 and 20 days when protein allocation shifts from growth of the legs and digestive organs to growth of breast muscle and other tissues in preparation for migration (Cooch *et al.* 1993; Lesage & Gauthier 1997; Badzinski *et al.* 2002), and (ii) at about 30 days old when the ninth primary feathers have emerged and are rapidly growing. Geese invest energy into body parts needed to obtain food such as the growing legs to find food or escape predators as well as develop digestive organs to process food efficiently (Sedinger & Raveling 1984; Sedinger 1986; Lindholm, Gauthier & Desrochers 1994; Lesage & Gauthier 1997; Badzinski *et al.* 2002). We found such a pattern for Canada and snow goslings where body parts associated with locomotion (tarsus) and food acquisition (culmen) grew at a faster rate early in development (Figs 2 and 3), and the growth rate of these structures was relatively insensitive to diet quality except when dietary protein was deficient (Table 4).

The most apparent delay in structural growth was observed with the delayed emergence of flight feathers for birds fed low-protein diets (*c.* 16 days for Canada and *c.* 14 days for snow geese). Interestingly, the delay in emergence did not alter the growth rate once feathers had emerged (*c.* 6.4–6.8 mm day⁻¹). Concomitantly, we observed a secondary increase in mortality at or near the day of flight feather emergence for both species, especially

for goslings on the low-protein diets (Table 5, Fig. 1). This suggests that the added protein burden of growing primary feathers for goslings fed low dietary protein resulted in reduced survival and a *c.* 2 week delay in completion of growth (Tables 4 and 5). There is a benefit if goslings are devoting nutrients to growing more proteinaceous tissue to attain greater structural size while delaying flight capabilities. However, this delay can have serious consequences for geese constrained by a short growing season in the arctic (Owen 1970; Cooke, Findlay & Rockwell 1984; Sedinger, Flint & Lindberg 1995).

Goslings that eat low-quality forage could avoid taking more time to attain larger size and simply fledge at a smaller body size, although such a growth strategy would result in smaller adult size because there is little evidence of compensatory growth or catch-up growth in geese after the first summer (Cooch *et al.* 1991b; Hector & Nakagawa 2012). Smaller-sized adult geese have reduced fitness because of well-documented body size effects on fecundity (Cooch *et al.* 1991b; Francis *et al.* 1992; Sedinger 1992; Sedinger, Flint & Lindberg 1995; Leafloor *et al.* 2000; Alisauskas *et al.* 2011). Thus, the reduced asymptotic size of Canada and snow geese on certain diets likely has consequences for lifetime reproductive success of these geese, and underscores the importance of adequate forage quality and quantity during early growth (Lindholm, Gauthier & Desrochers 1994; Gadallah & Jefferies 1995a; Sedinger, Flint & Lindberg 1995; Leafloor, Ankney & Rusch 1998a, b).

ECOLOGICAL IMPLICATIONS OF REDUCED FORAGE QUALITY

The consequences of major changes in habitat quality near breeding colonies in the Hudson Bay lowlands can be evaluated based on these captive studies. As the snow goose population continues to grow due to reduced winter mortality and high-quality habitats on wintering and migration stopover sites (Alisauskas *et al.* 2011), the quantity and quality of available forage on breeding areas will continue to decline (Jefferies, Rockwell & Abraham 2004). How goslings respond to these changes in forage availability on the brood-rearing areas will determine the long-term consequences of the over-abundant snow goose population to sympatric populations of Canada geese in lower Hudson Bay and James Bay. On Akimiski Island, long-term data have shown that Canada gosling body size was smallest in years when hatching was late relative to the peak in forage availability and when local abundance of breeding adults was high. In addition, breeding bird abundance and nest density for 1995 were about average for Canada geese when compared to the same data from 1993 to 2010 (R. Brook, unpubl. data).

Our results suggest that the more flexible growth strategy of Canada goose goslings will enable them to tolerate reductions in forage quality, whereas snow goose goslings will not survive in areas with low-quality forage. It

appears that the smaller body size of snow geese limits their capacity to tolerate low-quality forage relative to Canada goose goslings and this drives them to disperse to better quality habitat as long as it is available (Cooch *et al.* 1991b; Sedinger & Flint 1991; Gadallah & Jefferies 1995b; Jefferies, Jano & Abraham 2006; Winiarski, McWilliams & Rockwell 2012). The reduced growth and survival of snow geese in response to decreased forage quality provides a mechanism for density-dependent regulation of the snow goose population, although this appears not to be occurring because the snow goose population in lower Hudson Bay continues to expand into new areas (Koons, Rockwell & Aubry 2014). Snow geese likely avoid such density-dependent population regulation by moving their broods' sometimes great distances to find adequate quality and quantity of forage in surrounding habitats (R. F. Rockwell, pers. comm.).

In general, larger body size confers some advantages for herbivores in that smaller herbivores must select higher-quality forage to satisfy nutritional requirements compared with larger herbivores (Demment & van Soest 1985). We have shown for two species of high-latitude breeding avian herbivores that larger size was also associated with greater flexibility in growth in response to forage quality, which in turn enhanced growth and survival during ontogeny. These size-related differences in growth strategy (fast and less flexible growth vs. slow and more flexible growth) for these two species of avian herbivores indicate a sensitive, but species-specific, response to changes in forage quality and quantity caused by abundance of the geese themselves or by climate change.

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References

- Abraham, K. & Jefferies, R. (1997) High goose populations: causes, impacts and implications. *Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group* (ed. B.D.J. Batt), *Arctic Goose Joint Venture Special Publication*, pp. 7–72. US Fish and Wildlife Service, Washington, DC, and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Abraham, K.F., Jefferies, R.L. & Alisauskas, R.T. (2005) The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology*, **11**, 841–855.
- Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L. *et al.* (2011) Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. *Wildlife Monographs*, **179**, 1–42.
- Allen, N. (1983) Nutrition of growing geese (feeding requirements). *Revue Avicole*, **93**, 97–98.
- Aubin, A.E., Dunn, E.H. & MacInnes, C.D. (1986) Growth of lesser snow geese on arctic breeding grounds. *The Condor*, **88**, 365–370.
- Aubin, A.E., Dzubin, A., Dunn, E.H. & MacInnes, C.D. (1993) Effects of summer feeding area on gosling growth in snow geese. *Ornis Scandinavica*, **24**, 255–260.
- Badzinski, S.S., Ankney, C.D., Leafloor, J.O. & Abraham, K.F. (2002) Growth and development of pre-fledging Canada Geese and Lesser Snow Geese: ecological adaptation or physiological constraint? *The Auk*, **119**, 221–227.
- Bazely, D.R. & Jefferies, R.L. (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *Journal of Applied Ecology*, **22**, 693–703.
- Boag, P.T. (1987) Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). *Auk*, **104**, 155–166.
- Brisbin, I.L. (1986a) PCB intake and the growth of waterfowl: multivariate analyses based on a reparameterized Richards sigmoid model. *Growth*, **50**, 1.
- Brisbin, I.L. (1986b) Sigmoid growth analyses of wood ducks: the effects of sex, dietary protein and cadmium on parameters of the Richards model. *Growth, Development, and Aging*, **50**, 41.
- Brisbin, I.L. Jr, Collins, C.T., White, G.C. & McCallum, D.A. (1987) A new paradigm for the analysis and interpretation of growth data: the shape of things to come. *The Auk*, **104**, 552–554.
- Cadioux, M.-C., Gauthier, G. & Hughes, R.J. (2005) Feeding ecology of Canada Geese (*Branta canadensis interior*) in sub-arctic inland tundra during brood-rearing. *The Auk*, **122**, 144–157.
- Cargill, S.M. & Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669–686.
- Carmer, S.G. & Swanson, M.R. (1973) An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *Journal of the American Statistical Association*, **68**, 66–74.
- Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. (1989) Long-term decline in fecundity in a Snow Goose population: evidence for density dependence? *Journal of Animal Ecology*, **58**, 711–726.
- Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F. (1991a) Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology*, **72**, 503–512.
- Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. (1991b) Long-term decline in body size in a Snow Goose population: evidence of environmental degradation? *Journal of Animal Ecology*, **60**, 483–496.
- Cooch, E., Jefferies, R., Rockwell, R. & Cooke, F. (1993) Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia*, **93**, 128–138.
- Cooke, F., Findlay, C.S. & Rockwell, R.F. (1984) Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *The Auk*, **101**, 451–458.
- Demment, M.W. & van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, **125**, 641–672.
- Dobush, G.R., Ankney, C.D. & Kremetz, D.G. (1985) The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. *Canadian Journal of Zoology*, **63**, 1917–1920.
- Dudley, R. & Vermeij, G.J. (1992) Do the power requirements of flapping flight constrain folivory in flying animals? *Functional Ecology*, **6**, 101–104.
- Dzubin, A. & Cooch, E.G. (1992) *Measurements of Geese: General Field Methods*. California Waterfowl Association, Sacramento, California, USA.
- Emlen, S.T., Wrege, P.H., Demong, N.J. & Hegner, R.E. (1991) Flexible growth rates in nestling white-fronted bee-eaters: a possible adaptation to short-term food shortage. *Condor*, **93**, 591–597.
- Francis, C.M., Richards, M.H., Cooke, F. & Rockwell, R.F. (1992) Long-term changes in survival rates of lesser snow geese. *Ecology*, **73**, 1346–1362.
- Gadallah, F.L. & Jefferies, R.L. (1995a) Comparison of the nutrient contents of the principal forage plants utilized by Lesser Snow Geese on summer breeding grounds. *Journal of Applied Ecology*, **32**, 263–275.
- Gadallah, F.L. & Jefferies, R.L. (1995b) Forage quality in brood rearing areas of the Lesser Snow Goose and the growth of captive goslings. *Journal of Applied Ecology*, **32**, 276–287.

- van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C. (2006) Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biology*, **4**, e376.
- van Gils, J.A., Beekman, J.H., Coehoorn, P., Corporaal, E., Dekkers, T., Klaassen, M. *et al.* (2008) Longer guts and higher food quality increase energy intake in migratory swans. *Journal of Animal Ecology*, **77**, 1234–1241.
- Gleason, J. (2003) *Influence of Sympatric Lesser Snow Geese (Chen Caerulescens Caerulescens) on Reproductive Performance, Behavior, and Food Habits of Canada Geese (Branta Canadensis Interior) on Akimiski Island, Nunavut*, pp. 186. University of Western Ontario, London, Ontario, Canada.
- Goering, H. K. & Van Soest, P. J. (1970) *Forage Fiber Analysis*. USDA Agricultural Research Service, Handbook number 379. US Department of Agriculture, Superintendent of Documents, US Government Printing Office, Washington, DC.
- Hector, K.L. & Nakagawa, S. (2012) Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, **81**, 583–593.
- Hik, D.S. & Jefferies, R.L. (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. *Journal of Ecology*, **78**, 180–195.
- Holm, E.R. & Scott, M. (1954) *Studies on the Nutrition of Wild Waterfowl*. New York Conservation Department, New York, NY.
- Hupp, J.W., White, R.G., Sedinger, J.S. & Robertson, D.G. (1996) Forage digestibility and intake by lesser snow geese: effects of dominance and resource heterogeneity. *Oecologia*, **108**, 232–240.
- Illius, A.W. & Gordon, I.J. (1993) Diet selection in mammalian herbivores: constraints and tactics. *An Interdisciplinary Approach to Foraging Behavior*, Vol. **157**, pp. 181. Blackwell Scientific Publishing, Boston, Massachusetts, USA.
- Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, **94**, 234–242.
- Jefferies, R.L. & Rockwell, R.F. (2002) Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, **5**, 7–16.
- Jefferies, R.L., Rockwell, R.F. & Abraham, K.F. (2004) Agricultural food subsidies, migratory connectivity and large-scale disturbance in Arctic coastal systems: a case study. *Integrative and Comparative Biology*, **44**, 130–139.
- Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, **53**, 457–481.
- Karasov, W. & McWilliams, S. (2005) Digestive constraints in mammalian and avian ecology. *Physiological and ecological adaptations to feeding in vertebrates* (eds J.M. Starck, T. Wang), pp. 87–112. Science Publishers, Inc., Enfield, New Hampshire.
- Kerbes, R.H., Kotanen, P.M. & Jefferies, R.L. (1990) Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology*, **27**, 242–258.
- Klasing, K.C. (1998) *Comparative Avian Nutrition*. CAB International, New York.
- Koons, D.N., Rockwell, R.F. & Aubry, L.M. (2014) Effects of exploitation on an overabundant species: the lesser snow goose predicament. *Journal of Animal Ecology*, **83**, 365–374.
- Kotanen, P.M. & Abraham, K.F. (2013) Decadal changes in vegetation of a subarctic salt marsh used by lesser snow and Canada geese. *Plant Ecology*, **214**, 409–422.
- Leafloor, J.O., Ankney, C.D. & Rusch, D.H. (1998a) Environmental effects on body size of Canada Geese. *The Auk*, **115**, 26–33.
- Leafloor, J.O., Ankney, C.D. & Rusch, D.H. (1998b) Environmental effects on body size of Canada Geese. *The Auk*, **115**, 26–33.
- Leafloor, J.O., Rusch, D.H., Smith, A.E. & Wood, J.C. (1996) Hunting vulnerability of local and migrant Canada geese: a comment. *The Journal of Wildlife Management*, **60**, 452–457.
- Leafloor, J., Hill, M., Rusch, D., Abraham, K. & Ross, R. (2000) Nesting ecology and gosling survival of Canada geese on Akimiski Island, Nunavut. *Towards conservation of the diversity of Canada geese* (ed K.M. Dickson), pp. 109–116. Canadian Wildlife Service Occasional Papers No. 103 Ottawa.
- Lee, E.T. (1992) *Statistical Methods for Survival Data Analysis*. John Wiley & Sons Inc., New York.
- Lepage, D., Gauthier, G. & Reed, A. (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia*, **114**, 226–235.
- Lesage, L. & Gauthier, G. (1997) Growth and organ development in greater snow goose goslings. *The Auk*, **114**, 229–241.
- Lightbody, J.P. & Ankney, C.D. (1984) Seasonal influence on the strategies of growth and development of Canvasback and Lesser Scaup ducklings. *The Auk*, **101**, 121–133.
- Lindholm, A., Gauthier, G. & Desrochers, A. (1994) Effects of hatch date and food supply on gosling growth in Arctic-nesting Greater Snow Geese. *The Condor*, **96**, 898–908.
- Mantel, N. & Haenszel, W. (1959) Statistical Aspects of the Analysis of Data From Retrospective Studies of Disease. *Journal of the National Cancer Institute*, **22**, 719–748.
- McRoberts, M.R. (1965) Growth retardation of day-old chickens and physiological effects at maturity. *Journal of Nutrition*, **87**, 31–40.
- McWilliams, S.R. (1999) Digestive strategies of avian herbivores. *Proceedings of the 22nd International Ornithological Congress* (eds N.J. Adams & R.H. Slotow), pp. 2198–2207. BirdLife South Africa, Johannesburg, South Africa.
- McWilliams, S.R. & Karasov, W.H. (2005) Migration takes guts. *Birds of two Worlds: the ecology and evolution of migration* (eds R.R. Greenberg & P. P. Marra), pp. 67–78. Smithsonian Institution Press, Washington, D.C.
- McWilliams, S. & Leafloor, J. (2005) Effects of elevated CO₂ on keystone herbivores in modern arctic ecosystems. *A history of atmospheric CO₂ and its effects on plants, animals, and ecosystems* (eds I.T. Baldwin, M.M. Caldwell, G. Heldmaier, R.B. Jackson, O.L. Lange, H.A. Mooney, E.D. Schulze, U. Sommer, J.R. Ehleringer, M. Denise Dearing & T.E. Cerling), pp. 369–393. Springer-Verlag, New York, NY.
- Morton, E. (1978) Avian arboreal folivores: why not. *The Ecology of Arboreal Folivores* (ed. G. Montgomery), pp. 123–130. Smithsonian Institution Press, Washington, District of Columbia, USA.
- National Research Council. (1984) *Nutrient Requirements of Poultry: Nutritional Data for the United States and Canada Feeds*. National Academies Press, Washington, District of Columbia, USA.
- Nestler, R.B., Bailey, W.W. & McClure, H.E. (1942) Protein requirements of bobwhite quail chicks for survival, growth, and efficiency of feed utilization. *The Journal of Wildlife Management*, **6**, 185–193.
- Owen, R.B. (1970) The bioenergetics of captive blue-winged teal under controlled and outdoor conditions. *Condor*, **72**, 153–163.
- Parra, R. (1978) Comparison of foregut and hindgut fermentation in herbivores. *The Ecology of Arboreal Folivores* (ed. G.G. Montgomery). Smithsonian Institution Press, Washington, District of Columbia, USA.
- Richards, F. (1959) A flexible growth function for empirical use. *Journal of Experimental Botany*, **10**, 290–301.
- Ricklefs, R.E. (1973) Patterns of growth in birds II. Growth rate and model of development. *Ibis*, **115**, 177–201.
- Ricklefs, R.E. (1979) Patterns of growth in birds. V. a comparative study of development in the starling, common tern, and Japanese quail. *The Auk*, **96**, 10–30.
- Ricklefs, R.E. (1983) Avian postnatal development. *Avian Biology*, **7**, 1–83.
- Ricklefs, R.E. (1987) Response of adult Leach's storm-petrels to increased food demand at the nest. *The Auk*, **104**, 750–756.
- Ricklefs, R.E. (1996) Avian energetics, ecology, and evolution. *Avian Energetics and Nutritional Ecology* (ed. C. Carey). Chapman & Hall, New York.
- Ricklefs, R. & Schew, W. (1994) Foraging stochasticity and lipid accumulation by nestling petrels. *Functional Ecology*, **8**, 159–170.
- SAS Institute Inc. (2011) *SAS/STAT 9.3 User's Guide*. SAS Institute, Cary, North Carolina, USA.
- Scott, M.L., Hill, F.W., Parsons, E.H., Bruckner, J.H. & Dougherty, E. (1959) Studies on duck nutrition. *Poultry Science*, **38**, 497–507.
- Searcy, W.A., Peters, S. & Nowicki, S. (2004) Effects of early nutrition on growth rate and adult size of song sparrows *Melospiza melodia*. *Journal of Avian Biology*, **35**, 269–279.
- Sedinger, J.S. (1986) Growth and development of Canada goose goslings. *The Condor*, **88**, 169–180.
- Sedinger, J.S. (1992) Ecology of pre fledging waterfowl. *Ecology and Management of Breeding Waterfowl* (eds B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu), pp. 109–127. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Sedinger, J.S. & Flint, P.L. (1991) Growth rate is negatively correlated with hatch date in black brant. *Ecology*, **72**, 496–502.
- Sedinger, J.S., Flint, P.L. & Lindberg, M.S. (1995) Environmental influence on life-history traits: growth, survival, and fecundity in black brant (*Branta bernicla*). *Ecology*, **76**, 2404–2414.

- Sedinger, J.S. & Raveling, D.G. (1984) Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. *The Auk*, **101**, 295–306.
- Sedinger, J.S. & Raveling, D.G. (1986) Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. *Journal of Animal Ecology*, **55**, 1083–1102.
- Shrew, W.A. & Ricklefs, R.E. (1988) Developmental plasticity. *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum* (eds J.M. Starck & R.E. Ricklefs), pp. 288–304. Oxford University Press, Oxford, UK.
- Srivastava, D.S. & Jefferies, R.L. (1996) A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology*, **84**, 31–42.
- Starck, J.M. & Ricklefs, R.E. (1998) *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*. Oxford University Press, Oxford, UK.
- Stevens, C.E. & Hume Ian, D. (1995) *Comparative Physiology of the Vertebrate Digestive System*. Cambridge University Press, Cambridge, UK.
- Stevenson, M.H. (1985) Effects of diets of varying energy concentrations on the growth and carcass composition of geese. *British Poultry Science*, **26**, 493–504.
- Summers, J.D. & Leeson, S. (1985) *Poultry Nutrition Handbook*. Department of Animal and Poultry Science, Ontario Agricultural Science, Guelph, Ontario, Canada.
- Undersander, D., Mertens, D.R. & Thiex, N. (1993) *Forage Analysis Procedures*. National Forage Testing Association, Omaha, Nebraska, USA.
- White, G.C. (1980) Estimation and comparison of parameters in stochastic growth models for barn owls. *Growth*, **44**, 97–111.
- Williams, T.D., Cooch, E.G., Jefferies, R.L. & Cooke, F. (1993) Environmental degradation, food limitation and reproductive output: juvenile survival in Lesser Snow Geese. *Journal of Animal Ecology*, **62**, 766–777.
- Winiarski, K.J., McWilliams, S.R. & Rockwell, R.F. (2012) Rapid environmental degradation in a subarctic ecosystem influences resource use of a keystone avian herbivore. *Journal of Animal Ecology*, **81**, 1132–1142.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Nutritional composition of dietary ingredients (% dry mass, crude protein and fiber) and percent composition of ingredients in diets fed to captive-reared Canada and snow goose goslings.

Table S2. Mean (\pm SE) fitted parameters for mass (g), culmen length (mm) and diagonal tarsal length (mm) generated by the logistic growth model of captive-reared Canada goose goslings fed grass-based diets consisting of a factorial combination of protein (3 levels, High HP, Medium MP, and Low LP) and fiber (2 levels, High HF and Low LF).

Table S3. Mean (\pm SE) fitted parameters for mass (g), culmen length (mm) and diagonal tarsal length (mm) generated by the logistic growth model of captive-reared Lesser Snow goose goslings fed grass-based diets consisting of a factorial combination of protein (3 levels, High HP, Medium MP, and Low LP) and fiber (2 levels, Low LF and High HF).