



## FEEDING ECOLOGY OF CANADA GEESE (*BRANTA CANADENSIS INTERIOR*) IN SUB-ARCTIC INLAND TUNDRA DURING BROOD-REARING

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**ABSTRACT.**—The diet of adult Canada Geese (*Branta canadensis interior*) and their goslings was determined during the brood-rearing season in a freshwater tundra habitat using esophageal contents from 25 adult females, 27 adult males, and 59 goslings. Habitat use by geese and the availability and quality of aboveground biomass in wet sedge meadows and around ponds in lichen-heath tundra were also evaluated throughout the summer. During the first four weeks of brood-rearing, adult Canada Geese ate primarily graminoids (>65%), especially leaves of the short form of *Carex aquatilis* and *Eriophorum* spp., which had the highest nitrogen concentration (2.5–3.5%). Although graminoids were also important for goslings, they consumed a greater variety of other plant species (68%) than adults, especially in the first two weeks, possibly because of their inexperience. Late in the brood-rearing period, as the nitrogen concentration of graminoid plants declined, adults shifted to a diet composed mainly of berries (>40%, mostly *Empetrum nigrum*). At that time, goslings consumed fewer berries (24%) and maintained a higher proportion of nitrogen-rich plants in their diet (53% leaves, mostly graminoids) than adults, presumably to complete their growth. Plant species consumed by geese over the summer indicated a preference for high-quality plants (i.e. those with a high nitrogen concentration). Consequently, wet sedge meadow, the habitat that offered plant species of highest quality, was the habitat most heavily used throughout the summer, particularly around peak hatch. Goose grazing had no effect on seasonal production of aboveground biomass of graminoids, probably because of the relatively low density of the goose population. Received 23 June 2003, accepted 28 August 2004.

**Key words:** berries, *Branta canadensis interior*, brood-rearing, Canada Goose, diet, graminoids, Nunavik, Polemond River.

### Écologie alimentaire de *Branta canadensis interior* pendant la période d'élevage des jeunes dans un milieu d'eau douce sub-arctique

**RÉSUMÉ.**—Le régime alimentaire des adultes et des juvéniles de la Bernache du Canada (*Branta canadensis interior*) a été déterminé pendant la période d'élevage des jeunes, dans un milieu d'eau douce, à partir de contenus d'œsophage (25 femelles adultes, 27 mâles adultes et 59 juvéniles). L'utilisation de l'habitat ainsi que la disponibilité et la qualité de la biomasse végétale des prairies humides de *Carex* et des bords d'étang situés dans des arbustiaies lichéniques ont aussi été évaluées pendant l'été. Pour les quatre premières semaines de la période d'élevage, les adultes de la Bernache du Canada ont consommé davantage des plantes graminoides (>65%),

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surtout des feuilles de *Carex aquatilis* de petite taille et d'*Eriophorum* spp., dont les concentrations en azote étaient les plus élevées (2,5–3,5%). Malgré que les graminoides soient également importants pour les oisons, ces derniers ont consommé une plus grande variété d'autres espèces de plantes (68%) que les adultes, particulièrement durant les deux premières semaines, possiblement en raison de leur inexpérience. Plus tard durant la période d'élevage, lorsque la concentration en azote des plantes graminoides diminuait, les adultes se sont tournés vers un régime principalement composé de fruits (>40%, surtout d'*Empetrum nigrum*). Pour leur part, les oisons n'ont pas consommé autant de fruits (24%) et ils ont maintenu une plus grande proportion de plantes riches en azote dans leur régime alimentaire (53% de feuilles, principalement de graminoides) comparativement aux adultes, vraisemblablement afin de compléter leur croissance. Les espèces de plantes consommées par les bernaches au cours de l'été démontrent une préférence pour les plantes de meilleure qualité, i.e. celles ayant une concentration en azote élevée. Ainsi, la prairie humide de *Carex*, l'habitat offrant les espèces de plantes de plus haute qualité, a été le plus utilisé au courant de l'été, particulièrement autour du pic d'éclosion. Finalement, le broutement des bernaches n'a eu aucun effet sur la production saisonnière de la biomasse aérienne des plantes graminoides, probablement en raison de la densité relativement faible de la population de bernaches.

THE DIGESTIVE PHYSIOLOGY of herbivorous waterfowl, such as geese, imposes constraints on their feeding ecology (Sedinger 1997). Because they retain ingested food for a short time (generally <2 h; Mattocks 1971), geese break down very little of the plant cell wall (Buchsbaum et al. 1986; Sedinger et al. 1989, 1995b). To compensate for that low retention rate, which greatly limits the proportion of food nutrients they absorb, geese must feed on high-quality plants for long periods (40–80% of the day, depending on season; Sedinger and Bollinger 1987, Gauthier et al. 1988, Jefferies et al. 1994, Gawlik and Slack 1996) to ingest enough food to meet their nutritional requirements.

Constraints are particularly severe during summer for growing goslings and breeding females. In tundra regions, the growing season of plants is short (<105 days; Jefferies et al. 1994), and newly hatched goslings have less than two months to increase their body mass by >20× (Aubin et al. 1986, Sedinger 1986, Lesage and Gauthier 1997). Adult females invest a large amount of endogenous reserves in reproduction (≤50% of their body mass), and they must rebuild those reserves before fall migration (Ankney and MacInnes 1978, Ankney 1982, Gates et al. 1998). Therefore, requirements for specific nutrients should differ between adults and young: goslings should require more nitrogen to maximize their growth, whereas adult females should require more energy-rich food

(soluble carbohydrates or fat) to replenish their body reserves. Those different requirements are apparently still evident in fall, when immature geese, having yet to complete their growth, have been found foraging in habitats where plants have higher nitrogen content than those used by adults (Raveling and Zezulak 1991).

To meet their nutritional demands, goslings and adult females require large amounts of high-quality food during summer (Thomas and Prevett 1982, Gadallah and Jefferies 1995, Sedinger 1997). Geese are known for their ability to select food plants according to nutrient content, especially nitrogen (Owen 1972, Gauthier and Bédard 1990, Fox 1993, Kristiansen et al. 1998, Therkildsen and Madsen 1999). Grazing by geese can also affect availability and quality of forage plants (Kerbes et al. 1990, Gauthier et al. 1995), both of which can vary seasonally. Quality and availability of food plants are key factors affecting gosling growth rate and survival during the first year of life (Owen and Black 1989, Sedinger et al. 1995a, Leafloor et al. 1998).

Canada Geese (*Branta canadensis*) breed in many sub-Arctic regions. Although their summer diet has been studied in salt marshes (Sedinger and Raveling 1984, 1986), little is known of their feeding habits in inland tundra, especially during the brood-rearing season. Yet tundra is the habitat most often used by Arctic-nesting Canada Geese in North America (Bellrose 1980, Owen 1980). We studied the

summer foraging ecology of Canada Geese (*B. c. interior*) breeding in the inland tundra of the Ungava Peninsula, Québec. Our objectives were to (1) determine and compare the diet (species and plant parts) of adult and young Canada Geese during the brood-rearing season and (2) evaluate whether seasonal changes in quality (nitrogen concentration) and abundance of some food plants available to geese could explain differences in diet and habitat use.

#### METHODS

**Study area.**—Field work was conducted 60 km south of Povungnituk, on the northeastern coast of Hudson Bay, Nunavik, Québec, Canada (59°31'N, 77°36'W). The 33-km<sup>2</sup> study area—a fairly flat tundra region located ~10 km inland from the coast, along the Polemond River—was characterized by lichen-heath tundra (65%), lakes (22%), wet sedge meadows (11%), and ponds and streams (2%). Lichen-heath tundra was dominated by lichens and by *Betula glandulosa*, *Vaccinium vitis-idaea*, and *Empetrum nigrum*; wet sedge meadows were mostly covered by mosses and by *Carex aquatilis* and *Eriophorum angustifolium*; margins of most ponds located in patches of lichen-heath tundra were dominated by *C. aquatilis*, *C. saxatilis*, and *C. chordorrhiza*; *E. angustifolium*, *C. rariflora*, and *C. aquatilis* covered much of the wet meadow along stream edges, whereas *Salix lanata* was dominant along lakeshores. By the end of summer, most ponds and streams and a few small lakes had dried up. In 2001, snow cover was gone by the third week of May. From mid-May to early August, air temperature and rainfall were measured at 0800 and 2000 hours EST using a minimum–maximum thermometer and a pluviometer. In 2001, average minimum and maximum temperatures were 7.0°C and 14.9°C, respectively, and the region received 104 mm of rain.

Canada Geese from the Atlantic Population breed throughout Northern Québec; the highest concentrations are found near the coasts of northern Hudson Bay and southern and western Ungava Bay (Kaczynski and Chamberlain 1968, Malecki and Trost 1990). The study area was located in the area of highest nesting density. Breeding geese generally arrive on the study area before 20 May (our arrival date), and peak hatch occurs in the third week of June (R. J. Hughes unpubl. data). Geese raise their

broods within a few kilometers from where they nest, and goslings fledge at ~63 days of age (Bellrose 1980). In addition, large numbers of nonbreeding (*B. c. interior*) and temperate-breeding (mostly *B. c. maxima*) Canada Geese migrate to the area for their wing molt (W. F. Harvey and J. Rodrigue unpubl. data).

**Diet.**—We studied the diet of geese during the first 45 days of brood-rearing, which we divided into three equal periods according to gosling age (0–15 days, 16–30 days, and 31–45 days). Between peak hatch (24 June; R. J. Hughes unpubl. data) and 8 August 2001, we collected 57 adults and 61 goslings by shooting. We attempted to collect equal numbers of adults and young of each sex in each of the three periods. All adults collected were accompanied by young; when possible, one gosling per brood was collected along with one of its parents. We sexed all birds by cloacal examination and removed the contents of the esophagus and proventriculus (hereafter referred to as esophageal content) within 2 h after death. The esophageal content was sorted by plant species and plant parts, oven-dried to constant mass at 45°C for 24–36 h, and weighed to the nearest 0.01 g.

A total of 54 vascular plant species was found in the esophagi (Cadieux 2002). They were grouped into the following eight categories: *Carex* spp., *Eriophorum* spp., Gramineae, *Vaccinium* spp., other Ericaceae, *Empetrum nigrum*, *Equisetum* spp., and other taxa (i.e. all items that were rare in the diet). Plant tissues were further separated into berries, flowering parts, leaves, and other parts. Data are presented as aggregate percentage of dry mass of each food item category or plant part (Swanson et al. 1974) for adult females, adult males, and goslings (we ignored sex of goslings) at each period during brood-rearing.

**Aboveground biomass and plant quality.**—On 26 May, before any significant goose grazing had occurred, we erected eight seasonal exclosures in as many wet sedge meadows known to be used by geese in previous years, and eight others along pond margins in lichen-heath tundra. Those two habitats were selected because they were believed to be the most important for brood-rearing geese. Exclosures were 1 × 1 m and were made of chicken wire (1-inch mesh) 60 cm high. From 26 May to 4 August, we visited exclosures every 14 days (six sampling dates). Each exclosure was divided into a grid of

one hundred  $10 \times 10$  cm squares. At each sampling date, two randomly chosen pieces of turf were taken inside the enclosure (ungrazed) and pooled. We avoided removing samples adjacent to those previously sampled. Two more random samples were taken a few meters outside each enclosure (grazed) in a  $1 \times 1$  m area on the same dates. All samples were brought back to camp where they were kept cool and processed within three days following sampling.

On the second sampling date, we relocated one enclosure in wet sedge meadows because the plant community did not match that found in other enclosures. That enclosure was excluded from the analyses for the first sampling date. Also, one enclosure along a pond margin was excluded from all analyses because it remained flooded throughout the summer and no vegetation grew.

We cut all vegetation present on the pieces of turf at the lower limit of chlorophyllous (i.e. green) tissues. We retained only live vascular plants, and sorted them into four categories: *Carex* spp., *Eriophorum* spp., Gramineae, and dicotyledons. We also counted the number of shoots of each category. Plants were oven-dried to constant mass at  $45^\circ\text{C}$  for 24–36 h and weighed to the nearest 0.01 g. We report dry biomass and include only graminoids, because dicotyledonous species (mostly *Potentilla palustris*, *Salix* spp., and *Hippurus tetraphylla*) accounted for only 8% of total biomass sampled and were found in very small amounts in esophagi.

We measured total nitrogen concentration of *Eriophorum* spp., *Carex* spp., and Gramineae from material collected for biomass estimates (i.e. leaves and flowering parts combined), because we anticipated that those items should be most important in the diet. We did not measure plant fiber, because it varies much less, seasonally and among species, than nitrogen in Arctic graminoids (Sedinger and Raveling 1984, Manseau and Gauthier 1993). *Carex* spp. were divided into two subcategories, because of a difference in growth form of the sedges (mainly *C. aquatilis*) between the two habitats: “tall *Carex*” (~50 cm high) were found along pond margins, whereas “short *Carex*” (~15 cm high) were found in wet sedge meadows. To obtain sufficient material for nitrogen analyses at each sampling date, we pooled samples from more than one enclosure (or grazed site). Because of insufficient material, nitrogen of *Eriophorum* spp. was determined only in samples

from wet sedge meadows. Because of pooling, sample sizes varied depending on plant type, grazing treatment (grazed or ungrazed), habitat, and sampling date. Nitrogen concentration was determined with the automated Kjeldahl method in a Flow Injection Analyser (Lachat Quikchem 4000, Namur, Belgium; AOAC 1984) using 0.5-g samples. Results are expressed on a dry-mass basis.

*Habitat use.*—To estimate intensity of use by geese of the habitats where we sampled plant biomass, we marked a  $1 \times 20$  m transect near each enclosure. On the date that enclosures were set up, all feces present in the transect were removed. At each sampling date thereafter, we counted and removed all feces from the transect. No distinction was made between droppings from adults or goslings.

*Plant availability in three habitats.*—In July 2001, we sampled vegetation in three habitats (wet sedge meadows, lichen-heath tundra, and stream edges) used by geese. Pond margins in lichen-heath tundra were not sampled, because they resembled vegetation found along stream edges and were little used by geese (see below). To facilitate identification, we conducted sampling after the flowering peak of most plant species. We visually estimated the percentages of ground covered by bare rocks and soil, permanent water bodies, *B. glandulosa* shrubs, and vascular and nonvascular plants (mosses and lichens), using ten randomly located  $20 \times 20$  m quadrats in both lichen-heath tundra and wet sedge meadows. Three  $1 \times 1$  m subquadrats randomly placed inside each  $20 \times 20$  m quadrat were used to identify and determine the percentages of ground covered by individual species of vascular plants, mosses, and lichens. For streams, 10 randomly chosen  $5 \times 10$  m quadrats (including the stream itself oriented along the long axis of the quadrat) were used to conduct similar sampling. Data were subsequently pooled into the same eight plant categories used for the diet to obtain an index of food plant availability for geese in our study area.

*Statistical analyses.*—We compared goose diet among the three brood-rearing periods and age–sex classes (adult males, adult females, and goslings) using a two-way MANOVA on the aggregate percentage data of our eight food categories to evaluate overall effects. Because variances were heterogeneous and residuals were not normally distributed, we performed



the MANOVA on arcsine-transformed data. We examined individual effects using two-way ANOVAs on rank-transformed data for the main effects and the aligned rank transformation (ART) to test for interaction terms (Salter and Fawcett 1993). Comparisons between means were made using contrast statements in SAS (SAS Institute 1999).

We used a three-way ANOVA for repeated measures (repeated factor: sampling date) and an autoregressive dependence of first order (AR1) (Littel et al. 2000) to test the effects of date, habitat, and grazing treatment (grazed or ungrazed) on the log-transformed data of aboveground biomass and arcsine-transformed data of shoot density. We performed a three-way ANOVA with sampling date, grazing treatment, and plant category as factors to test their effects on the nitrogen concentration of food plants. We applied a square-root transformation to goose feces data and we performed an ANOVA for repeated measures (repeated factor: sampling date) with an AR1 dependence to test the effects of sampling date and habitat on feces density, an index of intensity of habitat use by geese. All comparisons between means following ANOVA were carried out with LSMEANS statements, unless otherwise noted. Significance for all statistical analyses was set at  $P = 0.05$ .

## RESULTS

**Diet.**—Among the 118 geese collected, 7 had no esophageal content and thus were excluded from diet analysis. We determined goose diet using 25 adult females, 27 adult males, and 59 goslings (males and females combined).

The similar diets of adult males and females generally differed from the diet of goslings, but the differences changed over time (MANOVA, interaction period  $\times$  agesex: Wilks'  $\lambda = 0.53$ ,  $F = 2.08$ ,  $df = 4$  and 102,  $P = 0.001$ ; Table 1). Adult geese ate primarily graminoid species (especially *Carex*) for the first 30 days of brood-rearing (>65% of the diet), whereas goslings ate less *Carex* during the first 15 days after hatch (interaction period  $\times$  agesex,  $F = 3.24$ ,  $df = 4$  and 102,  $P = 0.015$ ). The flowering parts of *C. aquatilis* were found in six esophagi. Of those, only two had flowers from the tall form; overall, the tall form accounted for 30% of the *C. aquatilis* consumed by the geese. Young goslings had a more diverse diet and consumed a greater

proportion of "other taxa" than adults (41% vs. <5%, respectively;  $F = 7.57$ ,  $df = 4$  and 102,  $P < 0.001$ ; Table 1).

Horsetails (mostly *Equisetum arvense*) were present in the diet throughout brood-rearing but in small proportion (<10%; Table 1). On average, about 20% of geese collected during each period had consumed some *Equisetum*. *Vaccinium* spp. were also present in small-to-moderate quantities in the diet throughout the summer. In contrast, other Ericaceae (mostly *Andromeda polifolia*) were mainly eaten early in the summer (Table 1; period,  $F = 4.71$ ,  $df = 2$  and 102,  $P = 0.011$ ). *Empetrum nigrum*, which was not eaten in early summer, became the most common food item in late summer for adult females (43%) but not for adult males and goslings (19% and 6%, respectively; interaction period  $\times$  agesex,  $F = 7.68$ ,  $df = 4$  and 102,  $P < 0.001$ ). Finally, we found insects in three goslings' esophagi, but insects accounted for <0.2% of all food items consumed by goslings.

Plant parts eaten tended to differ between adult males and females and goslings, and also changed during the summer (MANOVA, agesex: Wilks'  $\lambda = 0.87$ ,  $F = 1.85$ ,  $df = 2$  and 102,  $P = 0.070$ ; period: Wilks'  $\lambda = 0.65$ ,  $F = 5.96$ ,  $df = 2$  and 102,  $P < 0.001$ ; Table 1). Adults and goslings predominantly ate leaves, especially during the first two periods (>58% of all food items; Table 1). Although the quantity of leaves consumed (mostly *Carex* spp.) declined in late summer ( $F = 7.86$ ,  $df = 2$  and 102,  $P < 0.001$ ), leaves were still present in the esophagi of 98% of geese collected during the last period. During the first period, geese also ate more flowering parts, mainly *A. polifolia* (Ericaceae), than during the other two periods ( $F = 3.48$ ,  $df = 2$  and 102,  $P = 0.035$ ; Table 1). The decrease of flowering parts in the diet throughout brood-rearing was associated with a gradual shift to flowering parts of both sedges and grasses. Similarly, the seasonal decline in the amount of most Ericaceous species consumed (other than *Vaccinium*) was mainly attributable to the disappearance of their flowering parts from the diet.

At the end of the study period, adults concentrated their foraging on berries, unlike goslings (Table 1; interaction period  $\times$  agesex,  $F = 3.35$ ,  $df = 4$  and 102,  $P = 0.013$ ). Whereas females consumed mainly *E. nigrum* berries (42%), males consumed berries of *E. nigrum* berries (19%), *Rubus chamaemorus* berries (9%), and unripe

TABLE 1. Esophageal contents (aggregate percentage of dry mass) of adult Canada Geese (male and female) and their goslings during the brood-rearing season (24 June to 8 August 2001) near the Polemond River, Nunavik, Québec. Values with different letters within a row differ significantly (contrast based on an ANOVA on rank-transformed data,  $P < 0.05$ ). Only letters for comparisons that were significant are shown. Lowercase letters are for comparisons made between periods within the same age-sex and uppercase letters are for comparisons made between age-sex within the same period.

Food item	Adult female			Adult male			Gosling		
	24 June– 9 July (8) <sup>a</sup>	10–24 July (7)	25 July– 8 August (10)	24 June– 9 July (6)	10–24 July (11)	25 July– 8 August (10)	24 June– 9 July (20)	10–24 July (18)	25 July– 8 August (21)
	Species								
<i>Carex</i> spp. <sup>b</sup>	38.7 aA	42.7 a	8.6 b	44.9 aA	60.4 a	22.1 b	16.5 B	31.3	27.6
<i>Eriophorum</i> spp. <sup>c</sup>	36.4	20.3	3.9	11.8	25.4	19.4	7.8	27.8	12.4
Gramineae <sup>d</sup>	7.2	21.4	17.5	8.3	12.0	2.6	7.6	13.9	20.3
<i>Vaccinium</i> spp. <sup>e</sup>	0.5	8.1	6.0	14.6	0.0	12.8	9.1	12.9	22.9
Other Ericaceae <sup>f</sup>	13.2 a	2.6 b	0.4 b	13.0 a	0.0 b	0.6 b	9.6 a	0.2 b	0.1 b
<i>Empetrum nigrum</i>	0.0 a	0.0 a	43.4 bA	0.0 a	0.0 a	19.4 bB	0.0	0.0	5.6 B
<i>Equisetum</i> spp. <sup>g</sup>	0.0	1.6	8.3	2.8	1.7	0.0	8.3	4.4	3.4
Other taxa <sup>h</sup>	3.9 A	3.3	11.9	4.6 aA	0.5 a	23.2 b	41.1 aB	9.6 b	7.8 b
				Plant parts					
Berries	0.5 a	10.4 a	46.5 bA	2.9 a	0.0 a	40.7 bAB	2.3 a	11.9 a	23.5 bB
Flowering parts	32.4 a	26.4 b	11.2 b	32.5 a	4.8 b	11.0 b	25.2 a	10.9 b	11.4 b
Leaves	67.1 a	61.3 a	33.8 b	61.8 a	93.1 a	38.1 b	58.8 a	66.7 a	53.3 b
Other parts <sup>i</sup>	0.0 A	1.9 A	8.5 A	2.9 A	2.1 A	10.2 A	13.7 B	10.6 B	11.8 B

<sup>a</sup> Numbers in parentheses represent sample sizes.  
<sup>b</sup> *Carex aquatilis*, *C. atrofusca*, *C. bigelowii*, *C. capillaris*, *C. chondrorhiza*, *C. misandra*, *C. rariflora*, *C. saxatilis*, *C. williamsii*, and *Carex* spp.  
<sup>c</sup> *Eriophorum angustifolium*, *E. scheuchzeri*, and *Eriophorum* spp.  
<sup>d</sup> *Agrostis borealis*, *Arctagrostis latifolia* ssp. *latifolia*, *Calamagrostis canadensis*, *C. deschampsoides*, *C. lapponica*, *Duportia fisheri*, *Festuca rubra*, *Phippsia algida*, *Poa arctica*, and grass species.  
<sup>e</sup> *Vaccinium uliginosum* and *V. vitis-idaea*.  
<sup>f</sup> *Andromeda polifolia*, *Arctostaphylos alpina*, *Cassiope tetragona*, and *Ledum decumbens*.  
<sup>g</sup> *Equisetum arvense* and *E. variegatum*.  
<sup>h</sup> 25 vascular plant species (families: Betulaceae, Caryophyllaceae, Compositae, other Cyperaceae, Haloragaceae, Juncaceae, Leguminosae, Liliaceae, Polygonaceae, Ranunculaceae, Rosaceae, Salicaceae, Scrophulariaceae; for the complete list of species, see appendix B in Cadieux 2002), mosses, lichens and insects (*Diptera* spp.).  
<sup>i</sup> Stems, roots, seeds, and whole plants.

berries of *Vaccinium* spp. (10%). In contrast, gosling diet continued to be dominated by leaves (53%) in late summer, with berries accounting for only 24% of food consumed (*Vaccinium* spp. [9%], *V. uliginosum* [5%], *E. nigrum* [5%], and *V. vitis-idaea* [4%]).

**Biomass of available food plants.**—Total aboveground live biomass of graminoids increased steadily during the summer (date,  $F = 46.2$ ,  $df = 5$  and 154,  $P < 0.001$ ), with the period of most intense growth occurring from mid-June to late July (Fig. 1). Total aboveground biomass of graminoids did not differ between habitats ( $F = 2.77$ ,  $df = 1$  and 154,  $P = 0.11$ ) and was not influenced by grazing ( $F = 0.07$ ,  $df = 1$  and 154,  $P = 0.80$ ; all interactions,  $P > 0.34$ ). Biomass at the end of summer (last two periods) averaged  $97.6 \pm 11.3 \text{ g m}^{-2}$  in grazed plots, compared with  $93.8 \pm 13.5 \text{ g m}^{-2}$  in ungrazed plots. Goose grazing did not affect the biomass of any plant species category (all species,  $P > 0.23$ ).

Some differences between habitats were found at the species level. Aboveground biomass of *Carex* spp. was consistently higher along pond margins in lichen-heath tundra than in wet sedge meadows ( $F = 23.0$ ,  $df = 1$  and 154,  $P < 0.001$ ; Fig. 1) and accounted for 87% and 40% of all graminoid plants in each habitat, respectively. That difference occurred because tall *Carex* dominated along pond margins, whereas the short form dominated in wet sedge meadows (shoot density was similar in wet sedge meadows [ $1,465 \pm 164 \text{ shoots m}^{-2}$ ] and along pond margins [ $1,413 \pm 146 \text{ shoots m}^{-2}$ ];  $F = 0.69$ ,  $df = 1$  and 154,  $P = 0.414$ ). Biomass of *Eriophorum* around ponds remained constant throughout the summer but increased steadily in wet sedge meadows (interaction sampling date  $\times$  habitat:  $F = 3.94$ ,  $df = 5$  and 154,  $P = 0.002$ ; Fig. 1). *Eriophorum* accounted for ~40% of the total biomass in wet sedge meadows, compared with only 4% in pond margins (shoot density:  $3,223 \pm 285 \text{ shoots m}^{-2}$  for wet

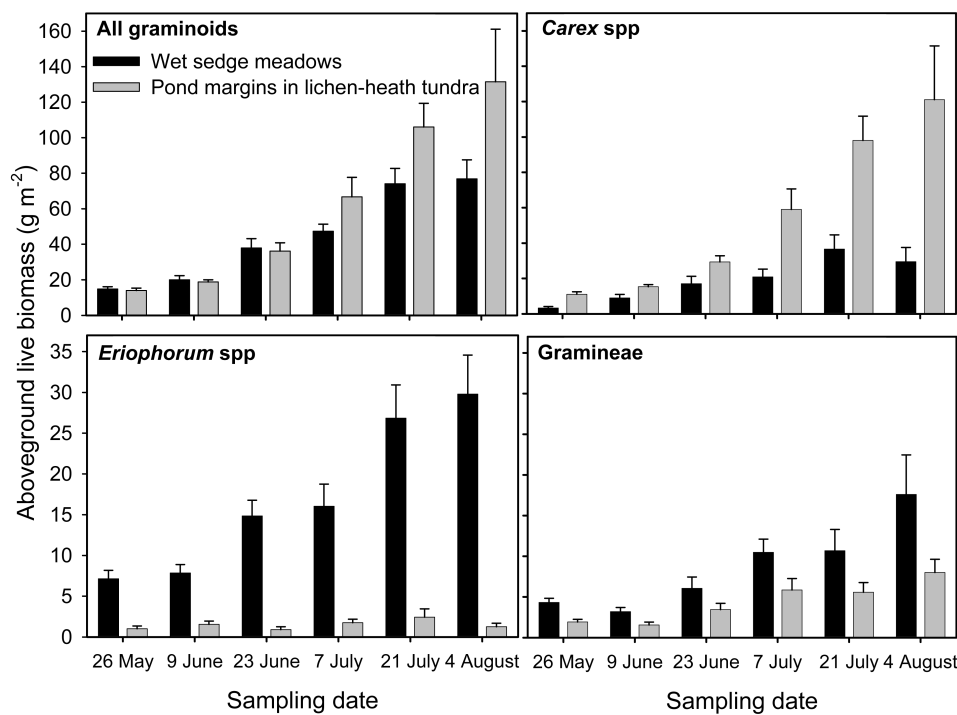


FIG. 1. Seasonal trend in aboveground live biomass (mean  $\pm$  SE) of all graminoids, *Carex* spp., *Eriophorum* spp., and Gramineae in wet sedge meadows and along pond margins in lichen-heath tundra. Values for grazed and ungrazed sites are pooled because they were not significantly different. Sample sizes at each date: wet sedge meadows:  $n = 16$ , except 26 May where  $n = 14$ ; pond margins in lichen-heath tundra:  $n = 14$ .

sedge meadows vs.  $148 \pm 25$  shoots  $\text{m}^{-2}$  for pond edges;  $F = 79.1$ ,  $\text{df} = 1$  and  $154$ ,  $P < 0.001$ ). Aboveground biomass of Gramineae also differed between habitats ( $F = 8.18$ ,  $\text{df} = 1$  and  $154$ ,  $P = 0.008$ ; Fig. 1). In contrast to *Carex*, wet sedge meadows supported a higher grass biomass (20% of all graminoid plants) compared to pond margins (9%), and also a higher shoot density ( $1,202 \pm 103$  vs.  $288 \pm 37$  shoot  $\text{m}^{-2}$ , respectively;  $F = 23.8$ ,  $\text{df} = 1$  and  $154$ ,  $P < 0.001$ ).

**Quality of food plants.**—Peak nitrogen concentration of all plant species was reached around 9 June, two weeks before peak hatch of goslings, and declined thereafter (sampling date:  $F = 74.8$ ,  $\text{df} = 5$  and  $101$ ,  $P < 0.001$ ; Fig. 2). At the peak, *Eriophorum*, Gramineae and short *Carex* had a higher nitrogen concentration (3.5–3.7%) than tall *Carex* spp. (2.8%). Seasonal decline in nitrogen of short *Carex* was delayed, compared with other plants (interaction plant type  $\times$  sampling date:  $F = 2.55$ ,  $\text{df} = 15$  and  $101$ ,  $P = 0.003$ ); thus, short *Carex* showed the highest nitrogen level in mid-summer. Nitrogen concentration of Gramineae displayed the steepest seasonal decline. Thus, that group had the lowest nitrogen level—1.5%, a value comparable to that of tall *Carex*—on the

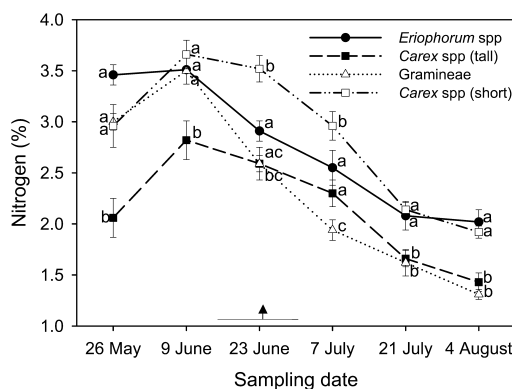


FIG. 2. Seasonal trend in nitrogen concentration (mean  $\pm$  SE) of tall and short *Carex* spp., *Eriophorum* spp., and Gramineae available to geese during the summer. Sample sizes for each sampling period were 3, 3, 6, 7, 10, and 10, respectively, for *Eriophorum* spp.; 4, 6, 7, 8, 9, and 8 for tall *Carex* spp.; 2, 1, 4, 7, 7, and 9 for Gramineae; and 2, 4, 7, 8, 9, and 7 for short *Carex* spp. Arrow and horizontal line at bottom indicate peak hatch and range. Means with the same letter are not significantly different within a sampling date (LSMEANS,  $P > 0.05$ ).

last sampling date, 4 August. Throughout the summer, nitrogen concentration did not differ between grazed and ungrazed sites ( $F = 2.94$ ,  $\text{df} = 1$  and  $101$ ,  $P = 0.09$ ).

**Habitat use.**—The seasonal pattern of habitat use by geese, based on feces density, differed between the two habitats where exclosures were set up (interaction:  $F = 7.67$ ,  $\text{df} = 4$  and  $64$ ,  $P < 0.001$ ; Fig. 3). Use of pond margins in lichen-heath tundra did not change throughout summer and was very low (overall mean feces density:  $0.05 \pm 0.01$  feces  $\text{m}^{-2}$  per two weeks). In contrast, use of wet sedge meadows was much higher (overall mean:  $0.37 \pm 0.07$  feces  $\text{m}^{-2}$  per two weeks), with a clear peak on 23 June, which coincided with peak hatch of goslings in 2001.

**Plant availability in three habitats.**—Overall plant species composition differed among habitats. Vascular plant cover was higher in wet sedge meadows and stream edges than in lichen-heath tundra (67% and 63% vs. 49% of plant cover, respectively; Table 2). The largest differences were found for *Carex* spp. and *Eriophorum* spp., because, collectively, graminoid species covered >40% of wet sedge meadows, but only 5% of lichen-heath tundra. In contrast, Ericaceae (including *Vaccinium* spp.) and *Empetrum* had greater coverage in lichen-heath tundra than in the other two habitats (22% vs. <2%, respectively), as did lichens, mosses, and litter.

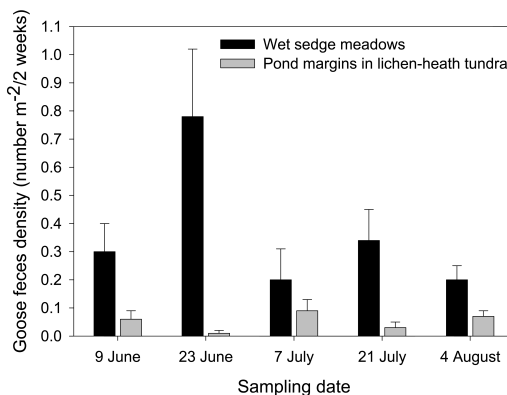


FIG. 3. Goose feces density (mean  $\pm$  SE) in wet sedge meadows and around pond margins in lichen-heath tundra during summer. Sample sizes at each date: wet sedge meadows,  $n = 8$  except 9 June where  $n = 7$ ; pond margins in lichen-heath tundra,  $n = 7$ .



TABLE 2. Average percentage ( $\pm$  SE) of groundcover of available plant species in the three principal habitats used by geese near the Polemond River, Nunavik, Québec. We used the same plant categories as those used for diet (Table 1).

Species <sup>a</sup>	Cover (%)		
	Wet sedge meadows	Lichen-heath tundra	Stream edges
<i>Carex</i> spp.	27.5 (1.9)	4.2 (1.1)	28.6 (5.1)
<i>Eriophorum</i> spp.	12.3 (3.6)	0.1 (0.1)	8.5 (2.3)
Gramineae	5.6 (2.9)	0.6 (0.3)	5.1 (3.1)
<i>Vaccinium</i> spp.	0.0 (0.0)	7.7 (1.5)	0.4 (0.2)
Other Ericaceae	0.8 (0.5)	7.8 (1.8)	0.7 (0.5)
<i>Empetrum nigrum</i>	0.1 (0.1)	6.5 (2.1)	0.5 (0.4)
<i>Equisetum</i> spp.	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Other vascular plants	20.4 (2.8)	22.7 (3.1)	19.6 (4.4)
Lichens, mosses, litter	17.5 (5.3)	33.9 (3.2)	5.2 (1.8)
Nonvegetated areas <sup>b</sup>	15.8 (4.1)	16.6 (3.3)	31.4 (4.2)

<sup>a</sup> For details on plant species, see footnotes to Table 1.  
<sup>b</sup> Bare rocks, soil, and permanent water bodies.

DISCUSSION

*Diet in relation to age and sex.*—Although we found many similarities in the diets of adults and goslings, there were some notable differences, especially during the first two weeks after hatch, despite the fact that most goslings were collected at the same time and place as adults. In temperate marshes, Buchsbaum (1985) found that the diets of male and female Canada Geese were similar, but less diverse than those of their goslings. He suggested that either (1) different nutritional requirements of goslings as compared with their parents or (2) their inexperience in selecting appropriate food plants could explain the differences. The latter explanation is consistent with our observations that the gosling diet became progressively more similar, as goslings aged, to that of adults, and that the number of plant taxa in their diet decreased markedly after two weeks. Young goslings may sample a greater array of food plants to learn which plant species and parts have the highest quality (Giroux and Bédard 1988).

In the early phase of their development, goslings require a great deal of protein to build muscle mass and other protein-rich organs, which makes nitrogen one of the most limiting nutrients for growing goslings (Gadallah and Jefferies 1995). Even though goslings may select plants with the highest nitrogen concentrations (Manseau and Gauthier 1993), Thomas and Prevett (1980) suggested that goslings

would benefit further by supplementing their diet with invertebrates. Gadallah and Jefferies (1995) observed that insects were present in high numbers in willow and tall freshwater sedge (habitats similar to those of our study area) and that Lesser Snow Geese (*Chen caerulescens caerulescens*) consumed them opportunistically. In ducklings, invertebrates represent a considerable proportion of the diet and are an essential source of nitrogen for their growth (Sedinger 1992). Nitrogen content of insects is much higher than in plants, even in the Arctic (~8% vs. ~3%, respectively; Klasing 1998). Yet soft-bodied insects were a negligible constituent of the goslings' diet (see also Sedinger and Raveling 1984), though they may be under-represented in esophageal contents because they are likely digested very quickly (Swanson and Bartonek 1970).

Many migrant bird species demonstrate seasonal shifts in diet toward food with a high energy:protein ratio during premigratory periods (Bairlein and Gwinner 1994). Sedinger and Raveling (1984) and Sedinger and Bollinger (1987) observed that Cackling Geese (*B. hutchinsii minima*) ingested less of their preferred food, arrowgrass (*Triglochin palustris*), and more seeds of *Carex* and berries of *E. nigrum* in late summer. Fruits and seeds are rich in soluble carbohydrates (e.g. sucrose and starch), compared with other plant parts (Robbins 1993, Bairlein and Gwinner 1994), and they provide birds with the energy required for premigratory fat deposition

(Thomas and Prevett 1982, Sedinger and Raveling 1984, Hupp and Robertson 1998). We also observed a diet shift toward berries when they started to ripen in late July, but the shift was more pronounced in adults (and especially in females) than in goslings. Because of their high investment in reproduction, female geese may lose  $\leq 50\%$  of their body mass during nesting (Raveling 1979, Ankney 1982, Gates et al. 1998). During prenesting and nesting, males increase time spent in vigilance at the expense of feeding, and thus also lose fat (Gauthier and Tardif 1991, Choinière and Gauthier 1995). Nevertheless, females probably have a greater need than males to replenish endogenous reserves lost during nesting, and that could explain the trend of a higher proportion of energy-rich food in their diet toward the end of brood-rearing.

Although goslings also increased the proportion of berries in their diet later in the summer, that dietary shift was much less pronounced than in adults, because  $>50\%$  of their diet was still composed of leaves. At that time, goslings were still growing rapidly (Badzinski et al. 2002) and had to balance their high nitrogen requirements with their energy needs. In goslings of Lesser Snow Geese and Greater Snow Geese (*C. c. atlantica*), priority is given to growth of muscle tissues until fledging, and premigratory fat accumulation is delayed until afterward (Wypkema and Ankney 1979, Lesage and Gauthier 1997). Delaying deposition of fat reserves while building proteinaceous tissue could help goslings attain greater structural size, which may have important fitness consequences (Cooke et al. 1984, Owen and Black 1989, Sedinger et al. 1995a). Selection of plants with the highest nitrogen concentration, such as graminoids, should thus be more critical for goslings than for parents in late summer (Buchsbaum 1985).

A food plant of interest found in the diet throughout the summer was *Equisetum* spp. Horsetails have previously been reported as spring and fall food for Snow and Canada geese staging along James and Hudson bays (Thomas and Prevett 1982, Craven 1984). Thomas and Prevett (1982) evaluated the nitrogen concentration of *Equisetum fluviatile* at 2.4 to 3.8%; thus, *Equisetum* spp. could provide growing goslings with a high-quality food during summer. Although Equisetaceae were absent from the vegetation plots we sampled, they occurred

at several locations within the study area. Their constant presence in small quantities in esophagi suggests that geese consumed them whenever they were encountered, but that they were probably not sufficiently abundant for geese to focus their foraging activity on them.

*Diet in response to seasonal variation in food quality.*—Throughout the summer, leaves of graminoid species were the most common part of the diet, a finding also reported in studies of other Arctic-breeding species (Eisenhauer and Kirkpatrick 1977, Giroux et al. 1984, Sedinger and Raveling 1984, Laing and Raveling 1993, Manseau and Gauthier 1993, Gadallah and Jefferies 1995). Until late July, both goslings and adults consumed more sedges (*Carex* and *Eriophorum*) than grasses, and most of the *Carex* eaten was of the short form. Thus, geese consumed the two graminoid species (short *Carex* and *Eriophorum*) with the highest nitrogen levels throughout the summer. Other studies have demonstrated the ability of geese to select plant species and parts with the highest nitrogen and lowest fiber contents (Sedinger and Raveling 1984, Manseau and Gauthier 1993, Fox et al. 1998).

Seasonal decline in nitrogen concentration of the aboveground biomass of Arctic graminoids has been shown in other studies (Sedinger and Raveling 1986, Manseau and Gauthier 1993, Gadallah and Jefferies 1995). Nitrogen reaches its highest level shortly after snowmelt, which usually coincides with or precedes peak hatch of goslings (Sedinger and Raveling 1986, Manseau and Gauthier 1993, Lepage et al. 1998, present study). Thus, as aboveground biomass increases during summer, both adults and young are confronted with a food source of declining quality. Even though graminoid availability was highest at the end of summer, the high fiber content of those plants may be another reason why geese, especially adults, switch to berries. However, goslings may be obliged to continue consuming more graminoids than adults later into the summer to complete their growth, despite the declining nitrogen concentration of graminoids. Because the hatching period occurs after the peak in plant protein concentration, early-hatched goslings may have a distinct advantage over their late-hatched counterparts.

*Food availability, habitat use, and effect of grazing.*—At our study site, wet sedge meadows, stream edges, and pond margins

provided geese with a higher availability of graminoid plants than did lichen-heath tundra. However, in late summer, geese probably spent more time foraging in the latter habitat because they could find high densities of *Vaccinium* and *Empetrum* berries. Negligible use of pond margins in lichen-heath tundra, as compared with wet sedge meadows, was unexpected, given that both habitats had a similar graminoid biomass and the ponds offered goslings refuges from predators (Hughes et al. 1994, Duclos 2002). However, we noted a considerable difference in plant composition between the two habitats: wet sedge meadows were dominated by *Eriophorum* and short *Carex*, the plants of highest quality, whereas pond margins were dominated by tall *Carex*, with little *Eriophorum*. Because tall graminoid swards not only have a low nitrogen concentration but also a high fiber content (Riddington et al. 1997, Hassall et al. 2001), the low use of pond margins could reflect the poor quality of the food found there. Other studies have also reported that ponds surrounded by tall vegetation were avoided by geese (Giroux et al. 1984, Laing and Raveling 1993). Therefore, despite its low availability in terms of biomass, geese apparently preferred to forage on short *Carex* because of its high nitrogen concentration.

Increased nitrogen concentration is a common response of plants to grazing (Ydenberg and Prins 1981, Cargill and Jefferies 1984, Gauthier et al. 1995), because new leaves have higher nitrogen concentration than older leaves (Ydenberg and Prins 1981). However, the lack of difference in nitrogen concentration between grazed and ungrazed sites is not surprising, considering the light grazing pressure we observed. Indeed, our exclosures provided no evidence of a reduction in standing crop caused by goose grazing, in contrast to the situation prevailing at many other Arctic sites used by geese. At La Pérouse Bay, Lesser Snow Geese consumed  $\geq 80\%$  of the net aboveground primary production of salt marshes (Cargill and Jefferies 1984), whereas Greater Snow Geese on Bylot Island removed 30–90% in freshwater meadows (Gauthier et al. 1995). Population density in our study area appears to be relatively low (25 parental geese and 27 goslings  $\text{km}^{-2}$  in 2001; R. J. Hughes unpubl. data) compared with that reported at La Pérouse Bay (116 parental geese and 145 goslings  $\text{km}^{-2}$ ; density estimated

from data of Ganter 1994 and Cooke et al. 1995) and on Bylot Island (34 parental geese and 54 goslings  $\text{km}^{-2}$ ; Reed et al. 1998). The fact that Snow Geese are colonial breeders, whereas Canada Geese are dispersed nesters, may explain those differences in densities. Another factor that may attenuate the effect of grazing by Canada Geese is that they mostly eat plant parts that do not affect the survival of plants (Buchsbaum 1985), such as leaves and fruits, unlike Snow Geese, which feed by grubbing and shoot pulling (Prevett et al. 1985).

In conclusion, inland tundra habitats at the Polemond River offer high-quality forage plants to brood-rearing geese, especially short *Carex* spp. and *Eriophorum* spp. in wet sedge meadows and *Empetrum* berries in lichen-heath tundra at the end of summer. High forage quality and biomass apparently enable Canada Geese to rear their young in the same area where they nest. That may benefit goslings, because they are not forced to undertake the long movements to brood-rearing areas observed in some goose populations (Cooch et al. 1993, Mainguy 2003), thus minimizing energy expenditure and potential exposure to predators. The minimal effect of grazing may also contribute to the short distances moved by brood-rearing geese at our study site. Indeed, broods rarely move  $>3.5$  km from their nest site during the first seven weeks of brood-rearing (data from 306 marked broods in 1997–1999; R. J. Hughes unpubl. data). Hence, our results suggest that the density of Canada Geese at the Polemond River is presently below the local carrying capacity.

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