

FEEDING ECOLOGY OF GREATER SNOW GOOSE GOSLINGS IN MESIC TUNDRA ON BYLOT ISLAND, NUNAVUT, CANADA

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Abstract. Although mesic tundra is a habitat commonly used by arctic-nesting geese, their feeding ecology in this habitat is little known compared to wetlands. Our objectives were to determine the diet and food selection of Greater Snow Goose (*Chen caerulescens atlantica*) goslings in relation to the nutritional quality of plants growing in mesic tundra habitats on Bylot Island, Nunavut, Canada. We used two different but complementary approaches: examination of esophageal contents of sacrificed wild goslings, and direct observation of the feeding activity of captive, human-imprinted goslings. The latter method was innovative and provided a reliable description of the diet, with results comparable to those obtained from wild goslings. Although mesic habitats have a more diverse floristic composition than wetlands and sparse graminoid cover, Gramineae were preferentially selected and dominated the diet (~50%). The rest of the diet consisted mainly of members of the Juncaceae, Polygonaceae, and Leguminosae families. The diet of very young goslings was diverse, but as they aged and gained efficiency, they concentrated on a few taxa. Goslings ate mostly leaves (~80%), but flowers (~20%) were also important. Food selection was influenced by nitrogen and total phenolic compounds content of plants, but the ratio of phenolic compounds to nitrogen in plant organs was most determinative of food choice. Neutral detergent fiber content of plants did not influence plant selection. Both plant nutritional quality and availability determined gosling diet across different mesic habitats and growing goslings appeared to maximize their intake of metabolizable proteins.

Key words: diet, food quality, food selection, Greater Snow Goose, mesic tundra.

Ecología de la Alimentación en los Polluelos de *Chen caerulescens atlantica* en la Tundra Húmeda en la Isla Bylot; Nunavut; Canadá

Resumen. Aunque la tundra húmeda es un ambiente usado comúnmente por los gansos que nidifican en el ártico, la ecología alimentaria en este ambiente es poco conocida en comparación con la de los humedales. Nuestros objetivos fueron determinar la dieta y la selección de alimentos de los polluelos de *Chen caerulescens atlantica* en relación con la calidad nutricional de las plantas que crecen en los ambientes húmedos de la tundra en la Isla Bylot, Nunavut, Canadá. Usamos dos enfoques diferentes pero complementarios: exámenes del contenido del esófago de polluelos silvestres sacrificados y observación directa de la actividad de alimentación de polluelos cautivos que se vieron sujetos a impronta por parte de humanos. El último método fue innovador y brindó una descripción confiable de la dieta, con resultados comparables a aquellos obtenidos para polluelos silvestres. Aunque los ambientes húmedos poseen una composición florística más diversa que los humedales y que la cobertura rala de pastos, las gramíneas fueron seleccionadas con preferencia y dominaron la dieta (~50%). El resto de la dieta estuvo constituida principalmente por elementos de las familias Juncaceae, Polygonaceae y Leguminosae. La dieta de los polluelos más jóvenes fue diversa, pero a medida que envejecieron y se tornaron más eficientes, se concentraron en unos pocos taxones. Los polluelos comieron principalmente hojas (~80%), pero las flores (~20%) también fueron importantes. La selección de los alimentos estuvo influenciada por el contenido de nitrógeno y de compuestos fenólicos totales en las plantas, pero el cociente entre compuestos fenólicos y nitrógeno en los órganos de las plantas determinó en gran medida la selección de los alimentos. El contenido de fibras neutras de detergente de las plantas no influyó la selección de las plantas. Tanto la calidad nutricional de las plantas como su disponibilidad determinaron la dieta de los polluelos a través de los diferentes ambientes húmedos y los polluelos en crecimiento parecieron maximizar el consumo de proteínas metabolizables.

INTRODUCTION

Herbivorous animals have access to an abundant food source. However, plants have relatively low nutritional value compared to animal tissues (Batzli et al. 1980, Klasing 1998), and plant quality can vary considerably spatially (across habitat types) and temporally (across seasons). Therefore, most herbivores show preferences for specific habitats based on food quality (Langvatn and Hanley 1993, Wilmshurst et al. 2000, Ruckstuhl and Neuhaus 2002). Nonetheless, factors such as food depletion or movements between high-quality patches may force animals to feed in less preferred or suboptimal habitats at times (Whitham 1980, Hansson 1997). In some situations, high population density may lead to overgrazing or even destruction of preferred feeding habitats, forcing animals to move to alternative feeding habitats, often of lower quality. A prominent example of this is the population increase of the Lesser Snow Goose (*Chen caerulescens caerulescens*) on the west coast of Hudson Bay, Canada. Geese have exceeded the carrying capacity of their breeding habitats (Jefferies et al. 2004, Abraham et al. 2005), resulting in severe degradation of their preferred feeding habitat, coastal salt marsh (Kerbes et al. 1990, Iacobelli and Jefferies 1991, Jano et al. 1998). Overgrazed salt marshes do not regenerate and geese are forced to move into suboptimal feeding habitats (Gadallah and Jefferies 1995a).

Although many other goose populations have also increased considerably in recent decades (Madsen et al. 1999, Fox et al. 2005), most have not yet exceeded the carrying capacity of their breeding habitats. For instance, the Greater Snow Goose (*Chen caerulescens atlantica*) population has increased more than ten-fold since the early 1970s (Menu et al. 2002, Gauthier et al. 2005), but Massé et al. (2001) estimated that the food requirement of the population in the mid-1990s corresponded to only 46% of the carrying capacity of wetlands at the Bylot Island breeding colony. Grazing levels were nonetheless sufficient to reduce the standing crop and productivity of graminoids (Gauthier et al. 1995, 2004). Geese are sensitive to slight variations in quality and quantity of their food plants because they digest little of the cell wall (Buchsbaum et al. 1986, Sedinger et al. 1989, 1995). Goslings are even

more sensitive due to the high nutrient requirements imposed by growth. Indeed, Lepage et al. (1998) showed that food depletion in wetland habitats can negatively affect gosling growth.

Because arctic-nesting geese prefer to feed in wetlands during brood-rearing, their feeding ecology has been well studied in these habitats (Sedinger and Raveling 1984, Manseau and Gauthier 1993, Gadallah and Jefferies 1995a, Person et al. 1998, Cadieux et al. 2005). However, in the high Arctic, wetlands often cover only a small portion of the landscape (<10% on Bylot Island; Massé et al. 2001), and a significant amount of feeding occurs in upland mesic sites (Gauthier 1993, Hughes et al. 1994, Duclos 2002, Reed et al. 2002). Use of mesic tundra by geese may occur for several reasons, including seasonal decline of food quality in wetlands, food depletion in heavily grazed wetlands, or during movements between wetland patches (Gauthier et al. 1995, Cadieux et al. 2005, Mainguy et al. 2006a).

In contrast to wetland habitats, which are often dominated by a few graminoid species (Cargill and Jefferies 1984, Gauthier et al. 1996, Person et al. 1998), mesic tundra has more diversified plant communities typically dominated by shrubs and a variety of forbs and graminoids (Muc and Bliss 1977, Bergeron 1988, Duclos 2002). Many forbs contain significant amounts of secondary metabolites such as phenolic compounds, which may negatively affect the palatability of plants to geese (Buchsbaum et al. 1984, Gauthier and Bédard 1990, Gauthier and Hughes 1995). Goose feeding ecology in mesic tundra, which is poorly known, has become a pressing issue, as geese have expanded into these habitats due to population increases (Reed et al. 2002). Therefore, our objectives were to determine the diet and food selection of Greater Snow Goose goslings in mesic tundra habitats, and to determine which nutritional attributes of plants growing in those habitats might be influencing selection. We used two approaches to determine the diet: 1) direct observations of the feeding activity of captive goslings in natural habitats, and 2) collection of wild goslings and analysis of their esophageal contents. The former method was innovative and allowed us to examine variations in diet and food selection across habitats and over the season under controlled conditions.

METHODS

STUDY AREA

Fieldwork was carried out in 2002 and 2003 in a 50 km² glacial valley on south Bylot Island, Sirmilik National Park, Nunavut, Canada (73°N, 80°W), site of the largest nesting colony of Greater Snow Geese (Reed et al. 2002). The valley is characterized by wet meadows dominated by graminoids such as *Dupontia fisheri* (Fisher's tundra grass), *Eriophorum* spp. (cotton-grass), and *Carex aquatilis* (water sedge; nomenclature of vascular plants follows Porsild and Cody [1980]) and by mesic tundra in better drained sites, sometimes referred to as uplands (Hughes et al. 1994). Duclos (2002) recognized four main plant communities in mesic and xeric tundra: heath tundra, mesic meadows, dwarf-shrub tundra, and *Salix*-legume tundra. These communities are characterized by dwarf shrubs (*Salix arctica* [arctic willow] and *Cassiope tetragona* [white heather]), forbs (*Stellaria longipes* [long-stalked starwort], *Oxytropis maydelliana* [yellow oxytrope], and *Polygonum viviparum* [alpine bistort]), and some graminoids (*Arctagrostis latifolia* [polar grass], *Poa arctica* [arctic blue grass] and *Luzula nivalis* [arctic wood-rush]; Duclos 2002). Although geese prefer wetlands, a significant amount of feeding occurs in mesic habitats (Gauthier 1993, Hughes et al. 1994, Duclos 2002, Mainguy et al. 2006b).

DIET OF CAPTIVE GOSLINGS

On 4 July 2003, we captured 25 newly hatched goslings (one per nest) and imprinted them on humans. From the 21 surviving goslings, we randomly selected 16 and divided them into four groups (broods), marking all goslings with individually color-coded bands. The diet of goslings was determined by direct observation of birds from a short distance, which allowed us to use a controlled experimental design. We carried out experiments in three different plant communities (hereafter called habitats) following the classification of Duclos (2002): heath tundra, mesic meadows, and *Salix*-legume tundra. Heath tundra is common at low altitude on north-facing slopes; moss and lichen cover is extensive and the ericaceous species *Cassiope tetragona* is the dominant vascular plant (Duclos 2002). Mesic meadows are found on terraces (60–160 m asl) and are dominated by cryptogams and graminoids. *Salix*-legume tundra

is typical of south-facing slopes and principal plants are arctic willow and legumes such as *Astragalus alpinus* (alpine milk-vetch) and *Oxytropis maydelliana*. These habitats are used by wild geese for feeding, and accounted for 6%, 53%, and 11%, respectively, of all mesic tundra found in the study area (Duclos 2002).

For each habitat, we selected four sites (four replicates; one per brood) based on their similarity to the plant communities described by Duclos (2002), the presence of a relatively large and homogeneous habitat patch suitable for our experiments (~200 m²), and the distance from our base camp to minimize distance traveled with goslings. Experiments were conducted five times at approximately weekly intervals from 9 July to 17 August (age of goslings: 5 to 44 days; three habitats × five weeks × four sites, except the last week when only two habitats were sampled; total $n = 56$ experiments). For each experiment, we selected and fenced off with chicken wire a different plot (6 × 1.5 m) within each 200 m² site on each occasion, and subdivided it into three equal subplots. Prior to each experiment, we visually estimated the cover of all plant species present in the three subplots to the nearest 5% (or nearest 1% for cover percentages below 5%). A brood of four goslings was then introduced to the first subplot and we closely watched each gosling one at a time for a 5-min feeding bout. The goslings were observed in a random order. Goslings were then transferred to the other subplots and the same observations were repeated. We thus accumulated 1 hr of observations per plot (four goslings × 15 min each). During observations, we recorded each peck, determined if it was successful or not, i.e., if a food item was ingested, and identified the plant part and species eaten. This was possible because the pecking rate of foraging goslings varies from 25 to 65 pecks min⁻¹ (Manseau and Gauthier 1993). It took four to seven days to conduct 12 experiments (three habitats × four sites) and the interval between each experimental period lasted one to nine days. During periods without experiments, young goslings were kept in an enclosure outside and allowed to graze plants but were also provided with duck pellets. As they grew older (>25 days), they were allowed to graze freely on the tundra during the day but were brought back into a large enclosure at night.

We validated the accuracy of our observations by killing 13 captive goslings immediately after their last feeding trials (eight in *Salix*-legume tundra and five in mesic meadows) and removing their esophageal contents for comparison with what was observed to have been eaten (number of successful pecks recorded). Goslings rested for >10 min before we started the feeding trial and they were sacrificed after completing 10 min of continuous feeding. Esophageal contents were analyzed as in wild goslings (see below).

DIET OF WILD GOSLINGS

We collected a total of 67 goslings (22 from 26 to 31 July 2002 and 45 from 15 July to 13 August 2003) throughout the brood-rearing period (approximate ages: 9 to 38 days according to mean hatching date of the colony; one gosling per brood), after watching them feed for some time to ensure that food was present in their foregut. The GPS coordinates of all collecting sites were recorded and esophagi were removed within a few hours of death. Esophageal contents were sorted by plant species (whenever possible) and plant parts, then dried and weighed. We also counted individual plant fragments, which were easily recognized in the esophagus where no grinding occurs, and we assumed that each fragment corresponded to one peck. Species were identified under a stereomicroscope by comparing distinctive morphological characters of the fragments to a reference plant collection. To determine food availability, we revisited all sites where goslings had been collected (for goslings collected in 2002, the sites were revisited in 2003 on similar dates). Three 50 × 50 cm quadrats were randomly positioned in the path taken by goslings during the last 5–10 min of feeding before they were collected. We determined the percentage cover of all plant species present in each quadrat with the same method used in the feeding plots of captive goslings.

PLANT NUTRITIONAL QUALITY

We sampled some of the plants available to goslings to determine their nutritional attributes. In 2002, we sampled eight plant species at eight different sites between 28 July and 4 August. These plants were *Alopecurus alpinus* (alpine foxtail), *Astragalus alpinus*, *Dryas integrifolia* (mountain avens), *Luzula confusa*

(northern wood-rush), *Salix arctica*, *Salix reticulata* (net-veined willow), *Saxifraga oppositifolia* (purple saxifrage), and *Stellaria longipes*. Plant parts (leaves and flowers) were sampled independently. Seed heads were included in “flowers.” In 2003, five plant species were sampled on 24 July at three different sites. These species were *Arctagrostis latifolia*, *Luzula nivalis*, *Oxyria digyna* (mountain sorrel), *Oxytropis maydelliana*, and *Polygonum viviparum*. Species were selected based on their presumed importance in the diet of goslings (Duclos 2002) and were representative of various plant families. Samples were dried to constant weight at 45°C a few hours after collection and brought back to the laboratory for analysis. We determined total nitrogen content, neutral detergent fiber (hereafter referred to simply as fiber), and total phenolic compounds in tissues following the methods described in Gauthier and Hughes (1995).

STATISTICAL ANALYSES

The sampling unit used in the analysis of captive gosling data was the brood of four goslings. Because of the large number of plant species consumed and the difficulty of analyzing each plant species independently, consumed items were grouped into categories: 10 categories of plant species grouped by family and four categories of plant parts grouped independently of species. *Stellaria longipes* and *Cassiope tetragona* were treated individually because consumption of other species in their respective families was negligible. The final diet was expressed as aggregate proportion (Swanson et al. 1974) of successful pecks (sum of successful pecks of the brood in a specific plant category divided by sum of successful pecks in all categories). Dependent variables in the statistical analysis were the aggregate proportion of successful pecks in each plant category. Because data were not normally distributed, we could not use multivariate analysis of variance (MANOVA). We instead used a logit model with mixed effects, where habitat and the period of the summer were fixed factors and the brood was a random factor. The dependence structure among measurements taken on the same brood was accounted for by a compound symmetric link using the Glimmix macro (Wolfinger and O'Connell 1993) in SAS version 8 (SAS Institute 1999). Finally, we examined seasonal

variation in the overall proportion of successful pecks (sum of successful pecks divided by the total number of pecks recorded for all plant categories) using factorial analysis of variance (ANOVA) with habitat and period of the summer as fixed factors and the brood as a block. In all analyses, interactions between habitat and period were considered but are only reported when they were found to be significant.

We evaluated food selection of captive goslings with the selection ratio (W_i) of Manly et al. (2002). We compared food use to its availability in each plot with $W_i = \Sigma \mu_{ij} / \Sigma \pi_{ij}$ for $j = 1$ to n replicates of the experimental units (brood of four goslings), where μ_{ij} is the proportion of item i consumed by brood j and π_{ij} is the proportion of item i available to brood j . Sites where a given item i was not present were not included in the calculation of W_i . We assessed if W_i were significantly different from 1 using the Bonferroni confidence intervals ($W_i \pm z_{\alpha/(2L)} \times \text{SE}[W_i]$) of Manly et al. (2002), but we applied the procedure sequentially, as described by Sokal and Rohlf (1995). For the smallest SE (W_i), sequential Bonferroni's α is $1 - (1 - \alpha)^{1/L}$, where L is the number of categories; for the second-smallest SE (W_i), $\alpha = 1 - (1 - \alpha)^{1/(L-1)}$; for the third-smallest, $\alpha = 1 - (1 - \alpha)^{1/(L-2)}$, and so on. Two W_i values were considered significantly different when their respective confidence intervals did not overlap.

We validated the observation technique used with captive goslings by comparing the proportion of plant fragments found in the esophagus with the proportion calculated from successful pecks observed in individual goslings with a paired t -test, using the same plant categories as above.

For wild goslings, the sampling unit was each gosling and the diet was expressed as aggregate proportion of dry mass. Food items were grouped into the same categories used for captive goslings. We used the same statistical approach as with captive goslings (logit model using the Glimmix macro in SAS) to test the effect of the period of the summer. We did not examine the effect of habitat because goslings were collected opportunistically and could have fed in more than one habitat prior to collection. We calculated food selection ratios (W_i) as for captive goslings. Selection ratios were also calculated on global diets (all periods and

habitats combined) for both captive and wild goslings and we used Pearson correlation coefficients to compare these two datasets.

We used nested ANOVAs to determine if plants selected by goslings (W_i in overall diet > 1) differed in nutritional quality (percent nitrogen, percent fiber, percent phenolic compounds, and ratio of percent phenolic compounds to percent nitrogen) from those avoided ($W_i < 1$). Plant species were nested into the selected or avoided factor. Means are reported with standard errors (SE).

RESULTS

DIET AND FOOD SELECTION OF CAPTIVE GOSLINGS

Variation among habitats. We recorded grazing on 34 vascular plant species during 3220 min of feeding observations. Overall, Gramineae was the most important plant taxon consumed (~50%; especially *Arctagrostis latifolia*), followed by Juncaceae (*Luzula nivalis* and *L. confusa*, ~20%) and Leguminosae (*Oxytropis maydelliana* and *Astragalus alpinus*, ~15%). However, the proportions of various plant taxa consumed by goslings varied among habitats (Table 1). In heath tundra, goslings consumed mostly species in the Juncaceae and Gramineae families, along with species in the Polygonaceae (mostly *Oxyria digyna*), even though these plants were not abundant (Table 1). Members of the Gramineae and Polygonaceae were highly selected by goslings, as well as species within the Leguminosae and *Stellaria longipes* (Caryophyllaceae). *Cassiope tetragona*, mosses, and *Salix* spp. were the most available plant taxa in that habitat, but they were rarely eaten. In mesic meadows, goslings consumed mainly grasses despite their relatively low availability (Table 1). Mosses and *Salix* spp. were again the most abundant plants in this habitat, but both groups were strongly avoided by the goslings. In the *Salix*-legume tundra, goslings consumed mostly members of the Leguminosae, with species in Gramineae and Juncaceae the next-most consumed forage plants (Table 1). These three taxa, along with *Stellaria longipes* and species in the Polygonaceae (mostly *Polygonum viviparum*), were all selected by goslings, whereas *Salix* spp. and mosses, the most abundant plants in this habitat, were again strongly avoided. In all three habitats, leaves were by

TABLE 1. Food items consumed (based on aggregate proportion of successful pecks) by captive Greater Snow Goose goslings along with availability (percent cover) and selectivity coefficients (W_i ; Manly et al. 2002) of major plant taxa in three different mesic habitats on Bylot Island, Nunavut, Canada. A $W_i > 1$ indicates a food item selected and $W_i < 1$ a food item avoided by goslings (* = $P < 0.05$). Values with the same letter within a column are not significantly different ($P > 0.05$). The F -statistic tests for differences in consumption of items among habitats. The number of replicates of the experimental unit (brood of four goslings) is given besides the habitat names.

Food item	Heath tundra ($n = 16$)			Mesic meadow ($n = 20$)			Salix-legume tundra ($n = 20$)			$F_{2,39}$
	Consumed (%)	Available (%)	W_i	Consumed (%)	Available (%)	W_i	Consumed (%)	Available (%)	W_i	
Plant taxa										
Gramineae ^a	28.9	1.5	16.8* a	79.4	11.1	6.3* a	28.0	3.2	7.7* a	20.3*
Juncaceae ^b	35.7	4.6	6.4* a	4.9	4.1	1.1 b	19.8	3.3	5.8* a	7.4*
Leguminosae ^c	2.8	0.2	13.5* a	0.0	0.0	na	39.3	10.8	3.5* a	na ^j
Polygonaceae ^d	13.1	1.2	12.1* a	0.1	0.2	0.7 cd	1.4	0.6	3.5 a	16.2*
<i>Stellaria longipes</i>	5.1	0.7	8.8* a	2.2	0.8	3.1* ab	3.0	0.9	3.9* a	5.9*
Cruciferae ^e	3.5	0.9	4.6 ab	1.3	0.9	1.8 bc	1.3	0.6	2.4 ab	4.6*
<i>Salix</i> spp. ^f	2.7	8.2	0.5* bc	0.3	18.1	<0.1* c	0.6	37.4	<0.1* c	4.2*
<i>Cassiope tetragona</i>	2.3	24.5	0.1* c	0.1	1.6	0.1* de	<0.1	0.1	0.1* bc	na ^j
Mosses	4.6	23.0	0.2* c	9.0	46.2	0.4* cd	3.2	15.8	0.3* b	1.3 ^k
Others ^g	1.2	35.1		2.5	17.0		3.4	27.4		2.2 ^j
Plant part										
Leaves	89.7	na		84.7	na		89.3	na		6.1 ^k
Flowers ^h	4.3	na		3.8	na		6.4	na		1.6
Stems	1.1	na		1.2	na		0.9	na		<0.1
Other parts ⁱ	4.9	na		10.3	na		3.4	na		1.3 ^k

^a *Arctagrostis latifolia*, *Poa arctica*, *Alopecurus alpinus*, *Hierochloa alpina*, and *Festuca brachyphylla* (species always listed from most to least fed upon by captive goslings).

^b *Luzula confusa* and *L. nivalis*.

^c *Astragalus alpinus* and *Oxytropis maydelliana*.

^d *Oxyria digyna* and *Polygonum viviparum*.

^e *Cardamine bellidifolia*, *Eutrema edwardsii*, and *Draba* spp.

^f *Salix arctica*, *S. herbacea*, and *S. reticulata*.

^g Other items consumed included insects, lichens, *Pedicularis* sp., *Dryas integrifolia*, *Saxifraga oppositifolia*, *Papaver radicatum*, *Ranunculus* sp., soil, *Cerastium alpinum*, *Potentilla* sp., gravel, *Saxifraga tricuspidata*, *S. hieracifolia*, *S. tenuis*, *Melandrium* sp., *Saxifraga nivalis*, *S. cernua*, *S. foliolosa*, *S. rivularis*, and mushrooms.

^h “Flowers” category includes some fruits and seeds.

ⁱ Other parts consumed included moss sporophyte capsules, insects, lichens, buds, roots, gravel, soil, and mushrooms.

^j For statistical analysis, the “others” category also included *Cassiope tetragona* and Leguminosae because these taxa were not represented in all habitats during all periods of the summer (the description of each period is presented in Table 2).

^k There was a significant interaction between the factors habitat and period for these taxa and parts; for mosses and other parts, the habitat effect was significant in periods 1, 2, and 3, and for leaves, it was significant in period 1.

far the dominant plant part consumed (>84%). Among flowers, those of Gramineae and Leguminosae were consumed most frequently.

Seasonal variation. In early summer, captive goslings fed on a wide variety of taxa, but they rapidly concentrated their feeding on a few plant species (Table 2). Grasses increased continuously in the diet until they comprised 61% of successful pecks in late summer, and were highly selected in all periods but the earliest. Rushes and legumes followed opposite seasonal trends: the former was most important midsummer (periods 2, 3, and 4), whereas the latter was most consumed during the earliest and latest periods. However, as we have no data for the last period in the heath tundra habitat, where legumes are uncommon, members of this family may be overrepresented in the diet for period 5. Although the proportion of members of the Polygonaceae in the diet did not vary significantly over time, this family was selected by goslings in all periods but the latest. Many plant taxa that were well represented in the diet of young goslings (mosses, *Salix* spp., *Cassiope tetragona*, and *Stellaria longipes*) had become almost absent from the diet by midsummer. The high consumption of mosses during the earliest period was limited to the mesic meadow habitat, but it declined dramatically by the second period (interaction of habitat*period, $F_{7,39} = 9.2$, $P < 0.001$).

Captive goslings did not succeed in ingesting plant fragments with every peck that we observed. However, their feeding efficiency improved throughout the summer in all habitats and the percentage of pecks that resulted in successful ingestion increased from a mean of 78% in the first period (5–8 days old) to $\geq 90\%$ by the fourth period (28–32 days old; $F_{4,42} = 12.3$, $P < 0.001$; Fig. 1).

Leaves were the most important plant part consumed by goslings, increasing from 56% in early summer to >90% from mid to late summer. This increase was most prominent in the mesic meadow habitat between the first and second period, due to the high rate of moss consumption in this habitat initially (interaction of habitat*period, $F_{7,39} = 5.9$, $P < 0.001$). Flowers and a diversity of other parts, such as sporophyte capsules of mosses, buds, roots, and mushrooms (Table 2), were initially important items in the diet but their importance decreased steadily over time and they had almost com-

pletely disappeared from the diet by late summer. The consumption of plant stems was always negligible.

Validation of the observation technique. We initially assumed that each successful peck would correspond to one plant fragment in the esophagus. However, we found that the number of observed pecks was 19% higher than the number of fragments found in the esophagus of the same gosling. Nevertheless, paired comparisons showed no significant difference between the two methods for any food items when the diet was expressed in proportions (for plant taxa, all $t < 1.4$ and all $P > 0.19$; for plant parts, all $t < 1.7$ and all $P > 0.12$, $df = 12$).

DIET AND FOOD SELECTION OF WILD GOSLINGS

The diet of wild goslings consisted of at least 31 vascular plant species, of which 26 were also eaten by captive goslings; five new species were found in the esophagi of wild goslings but collectively they accounted for <7% of the diet. The most important food items in the esophagi of wild goslings were grasses (>50% of global diet; mostly *Arctagrostis latifolia*), followed by species in the Polygonaceae (Table 3). Juncaceae, Cruciferae, and *Equisetum* sp. (horsetail) were also relatively important (>5% in most periods). All of the above species (except rushes) and Saxifragaceae were significantly selected ($W_i > 1$) by goslings in most periods of the summer, whereas *Salix* spp. were always avoided ($W_i < 1$). Insects were detected but they were a negligible fraction of the diet (<1%; Table 3), as in captive goslings. There was good correlation between captive and wild goslings in overall selection ratios (W_i) among the eight plant families found in the diet of both groups ($r = 0.74$, $df = 7$, $P = 0.04$). Leaves were the dominant plant part eaten by wild goslings (70% of the global diet) although flowers were also important (23%). Flowers consumed most frequently were those of Polygonaceae, Juncaceae, and Cruciferae.

Seasonal variation in the diet of wild goslings was more difficult to assess than that of captive goslings because none were collected in early summer (period 1) and only a few birds were collected in late summer (period 5). Only species within the Polygonaceae and Leguminosae varied significantly in the diet during the summer, with the former decreasing steadily in

TABLE 2. Food items consumed (“Cons.”; based on aggregate proportion of successful pecks) by captive Greater Snow Goose goslings along with availability (“Avail.”; percent cover) and selectivity coefficients (W_i ; Manly et al. 2002) of major plant taxa in five periods of the brood-rearing season on Bylot Island, Nunavut, Canada. A $W_i > 1$ indicates a food item selected and $W_i < 1$ a food item avoided by goslings ($* = P < 0.05$). Values with the same letter within a column are not significantly different ($P > 0.05$). The F -statistic tests for differences in consumption of items among periods of the summer. The number of replicates of the experimental unit (brood of four goslings) is given besides the dates of each period.

Food item	1 9–12 July ($n = 12$)			2 16–22 July ($n = 12$)			3 23–29 July ($n = 12$)			4 1–5 August ($n = 12$)			5 14–17 August ($n = 8$)		
	Cons. (%)	Avail. (%)	W_i	Cons. (%)	Avail. (%)	W_i	Cons. (%)	Avail. (%)	W_i	Cons. (%)	Avail. (%)	W_i	Cons. (%)	Avail. (%)	W_i
Plant taxa															
Gramineae ^a	10.7	8.1	1.7 bed	37.1	4.7	7.0* a	54.2	3.8	13.4* a	58.3	6.3	8.2* a	61.0	4.9	12.2* a
Juncaceae ^b	5.6	5.4	1.0 bed	23.7	4.9	4.9 ab	25.3	3.4	8.0* ab	20.8	3.7	5.8 a	4.7	2.3	1.9 ab
Leguminosae ^c	19.3	3.9	3.6 abcd	8.9	5.7	2.5 abc	8.3	2.9	2.2 bc	11.6	2.2	4.4 ab	30.7	4.4	6.5 ab
Polygonaceae ^d	10.7	0.9	1.4* a	5.8	0.9	6.8* a	3.1	0.6	6.8 ab	3.5	0.5	7.9* a	0.1	0.2	0.4 b
<i>Stellaria longipes</i>	8.0	1.0	7.6* ab	4.7	0.8	5.7* a	2.0	0.8	2.7 ab	2.0	0.8	2.6 a	2.2	0.5	3.7 ab
Cruciferae ^e	3.7	1.0	4.0 abc	2.7	0.8	3.5 ab	1.5	0.8	2.1 c	1.8	0.9	2.4 ab	0.5	0.5	0.9 b
<i>Salix</i> spp. ^f	5.2	23.5	0.2* d	1.4	23.2	0.1* c	0.5	20.8	<0.1* c	0.2	18.0	<0.1* b	0.1	23.3	<0.1* b
<i>Cassiope tetragona</i>	2.6	10.1	0.3* cd	1.4	9.6	0.1* c	0.3	9.0	<0.1* bc	0.2	10.0	<0.1* b	0.0	0.1	na ^j
Mosses	27.2	25.7	1.2 bed	9.0	25.3	0.4* bc	3.2	32.9	0.1* bc	0.9	27.2	<0.1* b	0.3	33.3	<0.1* b
Others ^g	6.8	20.3		5.2	24.2		1.6	25.1		0.7	30.4		0.4	30.5	1.7 ⁱ
Plant part															
Leaves	56.0	na		80.8	na		91.9	na		95.4	na		97.6	na	45.6**
Flowers ^h	15.4	na		7.0	na		3.2	na		2.5	na		1.2	na	13.5*
Stems	0.4	na		0.9	na		1.6	na		1.2	na		0.8	na	1.6
Other parts ⁱ	28.2	na		11.4	na		3.3	na		0.9	na		0.4	na	31.4**

^a *Arctagrostis latifolia*, *Poa arctica*, *Alopecurus alpinus*, *Hierochloa alpina*, and *Festuca brachyphylla* (species always listed from most to least fed upon by captive goslings).
^b *Luzula confusa* and *L. nivalis*.
^c *Astragalus alpinus* and *Oxytropis maydelliana*.
^d *Oxyria digyna* and *Polygonum viviparum*.
^e *Cardamine bellidifolia*, *Eutrema edwardsii*, and *Draba* spp.
^f *Salix arctica*, *S. herbacea*, and *S. reticulata*.
^g Other items consumed included insects, lichens, *Pedicularis* sp., *Dryas integrifolia*, *Saxifraga oppositifolia*, *Papaver radiculatum*, *Ranunculus* sp., soil, *Cerastium alpinum*, *Potentilla* sp., gravel, *Saxifraga tricuspidata*, *S. hieracifolia*, *S. tenuis*, *Melandrium* sp., *Saxifraga nivalis*, *S. cernua*, *S. foliolosa*, *S. rivularis*, and mushrooms.
^h “Flowers” category includes some fruits and seeds.
ⁱ Other parts consumed included moss sporophyte capsules, insects, lichens, buds, roots, gravel, soil, and mushrooms.
^j For statistical analysis, the “others” category also included *Cassiope tetragona* and Leguminosae because these taxa were not represented in all habitats in all periods.
^k Even though there was a significant interaction between the factors habitat and period for these variables, the period effect was significant in each habitat when tested separately.

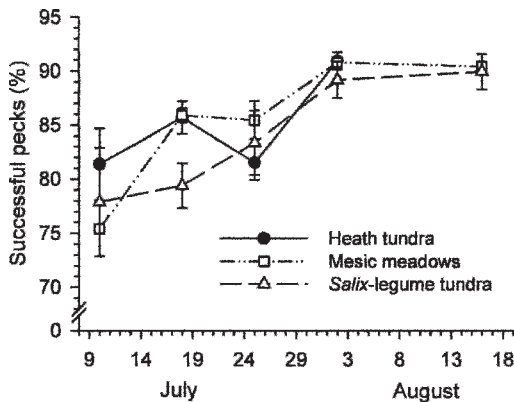


FIGURE 1. Seasonal variation in the percentage of successful pecks (resulting in the ingestion of one food item) by captive Greater Snow Goose goslings foraging in three mesic tundra habitats on Bylot Island, Nunavut, Canada (LS means \pm SE).

importance over time and the latter increasing in late summer (Table 3). The consumption of flowers was highest midsummer and the consumption of stems rose slightly in late summer (Table 3).

PLANT NUTRITIONAL QUALITY

Plants selected by goslings ($W_i > 1$) differed in nutritional attributes from those that were avoided ($W_i < 1$; Fig. 2). Selected plants had a higher nitrogen content ($2.4\% \pm 0.1\%$ vs. $1.4\% \pm 0.1\%$, $F_{1,18} = 11.5$, $P = 0.003$), and lower amounts of phenolic compounds ($10\% \pm 1\%$ vs. $16\% \pm 1\%$, $F_{1,31} = 5.8$, $P = 0.02$), giving a much lower ratio of phenolic compounds to nitrogen (4.1 ± 0.3 vs. 12.2 ± 1.3 , $F_{1,17} = 37.6$, $P < 0.001$) in selected vs. avoided plants. Fiber content did not differ between selected and avoided plant species ($34\% \pm 2\%$ vs. $33\% \pm 4\%$, $F_{1,17} = 0.1$, $P = 0.71$). Selection ratios of individual plants were most highly correlated with the ratio of phenolic compounds to nitrogen ($r = 0.63$, $df = 18$, $P = 0.004$).

DISCUSSION

VARIATION IN DIET AMONG HABITATS

Even though mesic tundra consists of diverse plant communities (Duclos 2002), we found that goslings concentrated their feeding on four key plant families (Gramineae, Juncaceae, Polygonaceae, and Leguminosae), which collectively accounted for more than 80% of the plants eaten in mesic tundra. In arctic wetlands,

goslings typically feed on a few species of grasses and sedges, which are also usually the dominant plants in those habitats (Sedinger and Raveling 1984, Manseau and Gauthier 1993, Gadallah and Jefferies 1995b, Cadieux et al. 2005). We found that grasses (mostly *Arctagrostis latifolia*) were also the most important food item consumed in mesic tundra, even though shrubs were dominant in these habitats and graminoids were relatively uncommon ($\leq 11\%$ of plant cover). In contrast, species in the Cyperaceae were absent from the diet in mesic tundra because plants in this family were scarce in these habitats on Bylot Island ($< 1\%$ of plant cover; Duclos 2002).

The variation in goslings' diets among the three mesic habitats sampled can be explained by differences in plant availability and nutritional quality. Mesic meadows had the highest availability and corresponding highest gosling consumption of grasses. Rushes were the main plant taxon consumed in heath tundra (36%), but were a very small component of the diet in mesic meadows (5%), even though their availability was similar in both habitats (4%–5%). This disparity could be due to the large difference in availability of grasses between the two habitats, which were seven times less abundant in heath tundra than in mesic meadow. Hence, even though plants in the Juncaceae had lower nutritional quality than Gramineae (less nitrogen and more fiber), goslings may have partly favored this taxon to maximize their feeding efficiency in response to the scarcity of Gramineae in heath tundra. This could also explain why species in the Polygonaceae, which were little consumed in other habitats, were highly sought after by goslings in heath tundra, even though the availability of plants in this family changed little across habitats. The abundance of plants of low palatability for geese (such as mosses, *Salix* spp., and *Cassiope tetragona*), combined with the scarcity of palatable plants (such as species in the Gramineae, Juncaceae, and Polygonaceae) in heath tundra, increased the apparent selectivity of goslings. Indeed, it is in this habitat that we found the highest selection ratio values. The high abundance of legumes (11% of plant cover) in *Salix*-legume tundra combined with their good nutritional attributes (high nitrogen content) and the low availability of grasses may explain why geese fed pre-

TABLE 3. Food items consumed (based on esophageal contents) by wild Greater Snow Goose goslings along with availability (percent cover) and selectivity coefficients (W_i ; Manly et al. 2002) of major plant taxa in four periods of the brood-rearing season on Bylot Island, Nunavut, Canada (no goslings were collected in period 1 and periods 4 and 5 were pooled because of small sample sizes). A $W_i > 1$ indicates a food item selected and $W_i < 1$ a food item avoided by goslings ($* = P < 0.05$). Values with the same letter within a column are not significantly different ($P > 0.05$). The F -statistic tests for differences in consumption of items among periods of the summer. The number of goslings collected is given beside the dates of each period.

Food item	2		3		4 and 5					
	15–22 July (<i>n</i> = 29)		23–30 July (<i>n</i> = 27)		3–13 August (<i>n</i> = 10)					
	Consumed (%)	Available (%)	<i>W_i</i>	Consumed (%)	Available (%)	<i>W_i</i>	<i>F</i> _{2,63}			
Plant taxa										
Gramineae ^a	47.7	2.8	12.9* ab	50.4	4.5	4.5 ab	64.2	5.6	10.9* ab	1.6
Juncaceae ^b	4.4	5.6	0.8 cd	11.0	3.7	6.2 a	3.8	6.6	0.8 bc	2.3
Leguminosae ^c	0.3	2.1	0.2* d	0.2	2.6	0.2* bc	5.9	1.9	2.1 abc	3.5*
Polygonaceae ^d	22.1	1.4	12.8* a	16.3	1.0	12.6* a	6.9	0.5	18.4* a	3.5*
<i>Stellaria longipes</i>	1.3	0.8	2.6 bcd	1.2	0.6	5.8 abc	4.7	0.7	6.6 abc	2.3
Cruciferae ^e	4.4	0.8	5.6 abc	4.7	0.3	17.8 ab	8.7	0.4	24.2* a	1.3
<i>Salix</i> spp. ^f	1.3	17.5	0.1* d	0.8	19.7	<0.1* c	0.5	12.8	<0.1* c	0.7
Saxifragaceae ^g	2.9	0.8	7.2* abc	1.2	0.3	8.1 abc	0.1	0.4	0.5 bc	1.8
<i>Equisetum</i> sp.	6.6	0.7	15.1* ab	5.9	0.1	45.4 abc	0.0	0.0	na	<0.1
Other plants ^h	8.7	67.6		8.3	67.3		4.1	71.0		0.7
Insects	0.8	na		0.0	na		1.0	na		<0.1
Plant part										
Leaves	71.4	na		64.1	na		80.7	na		2.2
Flowers ⁱ	19.8	na		28.5	na		11.8	na		3.5*
Stems	0.1	na		0.5	na		3.3	na		4.3*
Other parts ^j	8.7	na		6.9	na		4.1	na		0.4

^a *Arctagrostis latifolia*, *Hierochloa alpina*, *Poa arctica*, *Alopecurus alpinus*, and *Festuca brachyphylla* (species always listed from most to least fed upon by wild goslings).
^b *Luzula confusa* and *L. nivalis*.
^c *Oxytropis maydelliana* and *Astragalus alpinus*.
^d *Oxyria digyna* and *Polygonum viviparum*.
^e *Eutrema edwardsii*, *Cardamine bellidifolia*, and *Draba* spp.
^f *Salix arctica*, *S. herbacea*, and *S. reticulata*.
^g *Saxifraga cernua*, *S. foliolosa*, *S. hirculus*, *S. oppositifolia*, and *Chrysoxylum* sp.
^h Other plants consumed included *Papaver radicum*, *Eriophorum* sp., *Ranunculus* sp., *Pedicularis* sp., *Carex* sp., lichens, mosses, *Cerastium alpinum*, roots, *Cassiope tetragona*, and litter.
ⁱ “Flowers” category includes some fruits and seeds.
^j Other parts consumed included *Equisetum* sp., lichens, insects, mosses, roots, and litter.

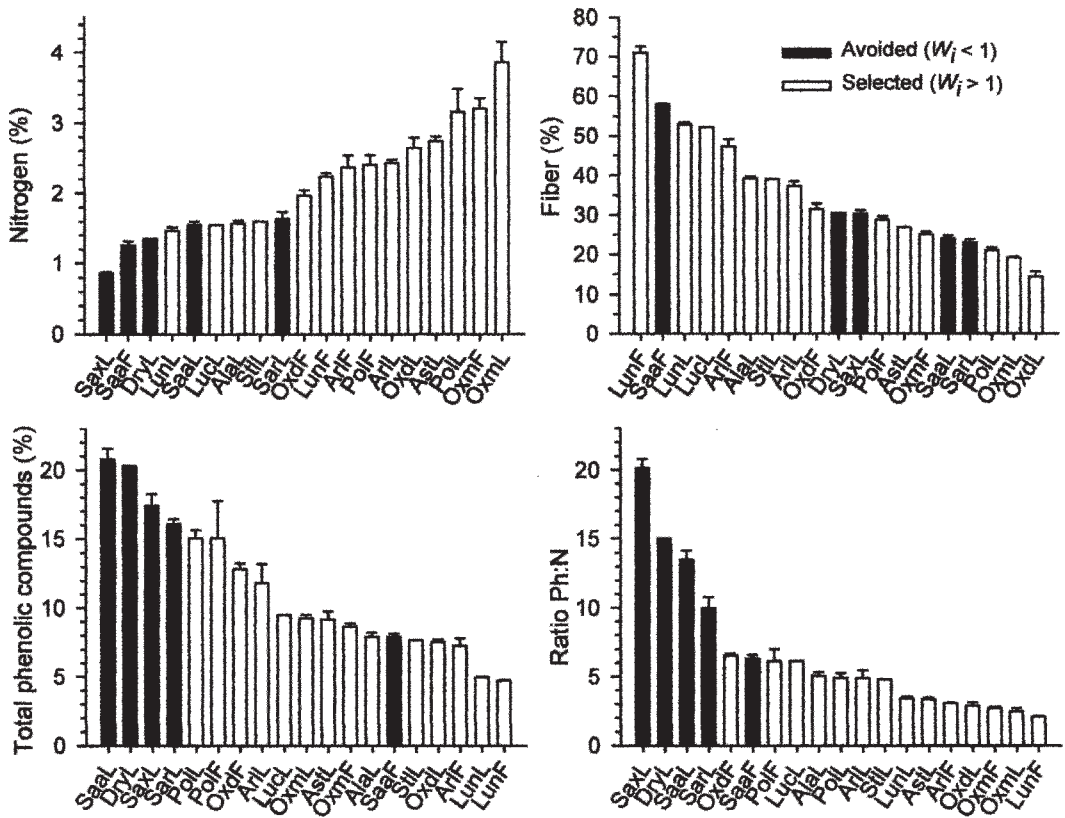


FIGURE 2. Mean \pm SE nitrogen, neutral detergent fiber, total phenolic compounds, and ratio of phenolic compounds to nitrogen (ration Ph:N) in leaves or flowers of 13 plant species harvested midsummer (24 July–4 August 2002–2003) on Bylot Island, Nunavut, Canada. Distinction between plants selected and avoided by Greater Snow Goose goslings was made following selection ratios (W_i) calculated on the global diet of captive goslings. Sample sizes per species range from one to four. Plant species codes are Ala: *Alopecurus alpinus*, Arl: *Arctagrostis latifolia*, Ast: *Astragalus alpinus*, Dry: *Dryas integrifolia*, Luc: *Luzula confusa*, Lun: *Luzula nivalis*, Oxd: *Oxyria digyna*, Oxm: *Oxytropis maydelliana*, Pol: *Polygonum viviparum*, Saa: *Salix arctica*, Sar: *Salix reticulata*, Sax: *Saxifraga oppositifolia*, and Stl: *Stellaria longipes*. The letter “L” stands for leaves and “F” for flowers at the end of three-letter codes (flowers include seed heads). Plant species are presented in increasing order of nutritional value from left to right for each attribute.

dominantly on legumes in this habitat. Therefore, it appears that mesic meadow and *Salix*-legume tundra are higher-quality gosling habitats than heath tundra, where goslings may have to spend more time searching for palatable plants.

SEASONAL VARIATION IN DIET

The diversity of the diet of captive goslings decreased considerably over time. Plants that decreased in the diet (mosses, *Salix* spp., and *Cassiope tetragona*) were also those that were avoided ($W_i < 1$). It thus appears that young, inexperienced goslings fed on almost anything available, but as they grew older and gained

experience, they became more selective and concentrated on the most nutritious plants (members of the Gramineae and Leguminosae; see also Buchsbaum 1985, Giroux and Bédard 1988, Cadieux et al. 2005). The high proportion of mosses in the diet of young goslings (5–8 days old) is surprising, as mosses are considered to be of low nutritional quality for geese (Prop and Vulink 1992). However, goslings fed mostly on sporophyte capsules of mosses rather than on moss stems, a feeding behavior also observed by Martin and Hik (1992) in Willow Ptarmigan (*Lagopus lagopus*) chicks. These authors suggested that moss capsules, with their small size, may represent a source of

adequate nutrition that is easy to consume at a time when handling larger or coarser food items is difficult for small chicks. Thus, moss capsules may be a regular food item in the diets of young goslings in habitats where mosses are abundant, such as in mesic meadows.

That food handling may be a problem for young goslings is supported by the high proportion of unsuccessful pecks (>21%) recorded in captive goslings 5–8 days old. We frequently observed young goslings trying several times to cut relatively coarse plants like *Salix* spp. or even *Arctagrostis latifolia*. Some unsuccessful pecks also occurred when goslings acquired plant fragments but dropped them rather than ingesting them, presumably because they judged the items to be unpalatable. The reduction over time in unsuccessful pecks indicates that foraging is a learning process, during which individuals acquire experience in selecting the best plants as well as strength and agility in cutting plant parts, thus reducing the need to sample alternative food items as they mature (Groves 1978, Goss-Custard and Durell 1987, Giroux and Bédard 1988, Bennetts and McClelland 1997).

Members of the Juncaceae, one of the plant families preferred by goslings, showed a marked decline in the diet in late summer. Goslings primarily consumed the flowering parts of rushes, but by late summer flowering had almost ceased, which may explain why consumption of these species decreased. Generally, flowering parts decreased in the diet of captive goslings throughout the summer in favor of leaves. However, wild goslings consumed more and different flowers than captive goslings in midsummer (20%–29% of the diet vs. 3%–7%, respectively), which suggests that flowers were underrepresented in the diet of captive goslings (see below). Thus, goslings may preferentially feed on the flowering parts of some species (especially forbs) in mesic tundra, as previously suggested by Gauthier (1993) and Duclos (2002). In contrast, stems were rarely eaten, presumably because they are the most fibrous part of plants and their coarseness makes them difficult to handle.

Several studies have reported that goslings include berries, a food source rich in lipids and soluble carbohydrates, in their diet near or after fledging (Sedinger and Raveling 1984, Sedinger and Bollinger 1987, Cadieux et al. 2005). The

only species producing berries in our study site is *Vaccinium uliginosum* (blueberry), but its abundance is low (Duclos 2002) and it was absent from our study plots in mesic tundra. Furthermore, only a few wild goslings were collected at the end of the summer when berries started to ripen and goslings were close to fledging. Therefore, we cannot compare gosling use of berries in our mesic tundra study sites, although due to their scarcity, berries are probably a negligible portion of the diet here.

VALIDATION OF THE DIRECT OBSERVATION TECHNIQUE

The observation of individual pecks by captive goslings to determine the diet was an innovative technique, therefore it needed to be validated. Comparisons of the diet determined by observations of pecks vs. esophageal contents in the same birds indicated that direct observations by trained observers provided a reliable measure of plants actually eaten by captive goslings. The higher number of pecks observed compared to the number of plant fragments found in the esophagi could be due to some unsuccessful pecks that were misclassified or, more likely, to the passage into the gizzard of the first fragments consumed after 10 min of observations.

The similarity between the diets of captive and wild goslings collected in the same periods of the summer suggests that the diet of captive goslings determined by direct observations was representative of the population. Nevertheless, there were a few notable differences in results between the techniques, with species in the Polygonaceae more abundant in the diet of wild than captive goslings, but Leguminosae more abundant in the diet of captive goslings. One reason for these differences may have been our inability to collect equal numbers of wild goslings across the three mesic habitats due to the opportunistic nature of the sampling. For instance, we collected twice as many goslings grazing in heath tundra than in *Salix*-legume tundra. This could explain why the diet of wild goslings contained more members of the Polygonaceae (mostly grazed in heath tundra) and fewer of the Leguminosae (mostly grazed in *Salix*-legume tundra) than the diet of captive goslings. Therefore, one advantage of the direct observations method is that it allows an evaluation of variation in diet across habitat

patches and over time with a rigorous sampling design.

The similarities in the selection ratios (W_i) obtained for captive and wild goslings further suggest that both techniques gave reliable results. Selection ratios were probably more accurate for captive than for wild goslings because the former were confined to an enclosure where plant availability could be measured more accurately. However, the latter assertion assumes that plots were large enough and the feeding trials short enough to prevent depletion of preferred food items by goslings, which was likely the case in most experiments.

One limitation of the direct observations method using captive, imprinted chicks is the absence of parents from which goslings could learn the best food items to consume. This could partly explain the high proportion of seemingly less nutritious plants in the diet of young captive goslings. Goslings were also forced to feed in sites chosen by experimenters, which could have differed somewhat from those that would have been selected by parents. For instance, the higher proportion of flowers in the diet of wild goslings may be because parents selected feeding sites with a higher proportion of flowers than those we used for the feeding trials, although early depletion of flowers by goslings in our experimental plots is also possible. The diet of wild goslings collected in mesic tundra also included some plants typical of wetlands (*Equisetum variegatum* and *Eriophorum* spp.) that were not found in the diet of captive goslings. This supports the observations of Hughes et al. (1994) and Mainguy et al. (2006b), who found that even when foraging in mesic tundra, geese exploited isolated wet patches, streams, and gullies whenever possible. *E. variegatum* is known for its low fiber and high protein and mineral content, which is of particular importance for growing goslings (Prevett et al. 1979, Thomas and Prevett 1982, Cadieux et al. 2005).

PLANT NUTRITIONAL QUALITY AND FOOD SELECTION

Geese are well known for being highly selective in their feeding (Buchsbaum et al. 1984, Sedinger and Raveling 1984, Prins and Ydenberg 1985, Gauthier and Bédard 1990). Our results showed that goslings are also selective in tundra habitats offering a high diversity of

plant species. In contrast to wetlands, mesic tundra is comprised primarily of shrubs and forbs, which often contain high concentrations of secondary metabolites like phenolic compounds that act as feeding deterrents (Buchsbaum et al. 1984, Robbins et al. 1987). We found that goslings preferred plants with high nitrogen content and avoided those high in phenolic compounds. Buchsbaum et al. (1984) suggested that plant palatability for geese is determined by a hierarchy of feeding cues and that deterrent secondary metabolites have a dominant role over nutrients. In contrast, Gauthier and Hughes (1995) suggested that the ratio of the deterrent to the nutrient content in plant tissues is more important in the food selection process than the content of the deterrent alone. The stronger association of the food selection ratios with the ratio of phenolic compounds to nitrogen than with phenolic compounds alone supports Gauthier and Hughes's (1995) hypothesis. Therefore, it appears that goslings are willing to tolerate higher levels of deterring factors such as phenolic compounds in plants that have a high nitrogen content. Presumably, this allows them to maximize their intake of metabolizable nitrogen when the protein requirement imposed by their rapid growth is very high (Manseau and Gauthier 1993, Lesage and Gauthier 1997, Lepage et al. 1998).

Fiber, the major component of plants, can influence plant digestibility. Because geese are unable to digest most fiber constituents (Buchsbaum et al. 1986, Sedinger et al. 1989, 1995), plant digestibility is inversely related to fiber content (Bédard and Gauthier 1989, Sedinger et al. 1989, Piedboeuf and Gauthier 1999). Thus, fiber content has also been found to affect food selection by geese (Hardwood 1977, Owen 1978, Ydenberg and Prins 1981). However, we found little evidence that fiber content influenced food selection by goslings. Thus, despite the large interspecific differences in fiber content of leaves, it appears that goslings relied more on other plant constituents (nitrogen and total phenolic compounds) as feeding cues when foraging in mesic tundra.

To conclude, although mesic habitats had a more diverse floristic composition than wetlands and sparse graminoid cover, grasses remained the dominant item in the diet of goslings and were preferentially selected. Gos-

lings showed selection abilities at a young age and maximized their feeding efficiency by concentrating on plants with a low ratio of phenolic compounds to nitrogen content.

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