HABITAT AND FOOD SELECTION BY EMPEROR GOOSE GOSLINGS[1]

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Abstract. The habitat and diet of Emperor Goose (*Chen canagica*) goslings were studied on the Yukon-Kuskokwim Delta, Alaska in 1985 and 1986. We studied diet selection and nutrient content of potential food plants to determine whether Emperor Goose goslings selected food plants to increase nutrient intake. Broods moved from inland nest sites to coastal salt marsh within one week of hatching. This movement resulted in abandonment of areas that contained high densities of *Triglochin palustris,* a food that was selected in a feeding trial. Wild goslings selected vegetated mudflats in coastal salt marsh, spending 80–82% of their feeding time there, although mudflats covered only 5% of the study area. The relative densities of *Puccinellia phryganodes* and *Carex subspathacea,* the two mudflat plant species available on a feeding trial plot, changed over the two years of the study, with *P. phryganodes* increasing from 65% in 1985 to 84% in 1986. Captive goslings selected *C. subspathacea* more often than *P. phryganodes* in 1985, but ate primarily *P. phryganodes* in 1986. *Triglochin palustris* was significantly higher in total nitrogen and water content and lower in cell wall content than other available species, but productivity and nutrient value of *P. phryganodes* and *C. subspathacea* might increase with grazing. Emperor Geese may leave areas where *T. palustris* is available to avoid predation or competition. By feeding repeatedly on coastal mudflats goslings are likely to find recently fertilized, nitrogen-rich plant food in a habitat providing refuge from predators.

Key words: Chen canagica; Emperor Goose; habitat selection; food selection; plant nutrients; herbivory.

INTRODUCTION

Goslings of geese nesting at northern latitudes must acquire enough nutrients for growth within a limited fledging period, yet they are among the few vertebrates which rely almost entirely on plant protein for growth (Owen 1980). This is noteworthy because geese face particular problems gaining sufficient nutrients from plant food. Plant foliage is generally lower in protein than animal food, and the high fiber content of plant foliage makes it less digestible (Demment and Van Soest 1985). Geese are small (1–6 kg) vertebrate herbivores, as defined by Demment and Van Soest (1985). Small herbivores are constrained by a small digestive capacity relative to their size and reduced ability to digest plant fiber compared to larger herbivores (Demment and Van Soest 1985). Although geese digest protein as rapidly and efficiently as other vertebrate herbivores (Buchsbaum et al. 1986), the generally low protein and

high fiber content of their food requires that they maintain a high rate of food intake to obtain sufficient nutrients (Buchsbaum et al. 1986, Sedinger and Raveling 1988).

Goslings may not completely compensate for the low protein content of their food by increasing intake, because intake rate is apparently limited by the processing rate of the digestive tract (Sedinger and Raveling 1988). Goslings might therefore benefit by selecting plants highest in digestible protein, which is a major requirement for growth (Sedinger 1992). Sedinger and Raveling (1984) found that Cackling Canada Goose goslings (*Branta canadensis minima*) on the Yukon-Kuskokwim Delta in western Alaska selected plant species high in protein and low in fiber content.

Emperor Geese (*Chen canagica*) nest sympatrically with Cackling Geese. However, Emperor Geese differ from Cackling Geese and other goose species nestling on the Yukon-Kuskokwim Delta in that Emperor Geese remain in maritime areas in Alaska and Siberia during winter (Bellrose 1980), and have been observed to feed on intertidal invertebrates during winter and in migration (Cottam and Knappen 1939, Petersen 1983). Given the limitations of plants as a diet for young

geese, the possibility existed that goslings of Emperor Geese depend on invertebrates to meet protein requirements for growth. The purpose of this study was to examine this possibility by describing the habitat and diet of Emperor Goose goslings. When it was established that Emperor Goose goslings depend on plants for food, the availability and nutrient content of potential food plants were examined in relation to diet to determine the extent to which goslings selected food plants to increase nutrient intake.

STUDY AREA

We collected data on the south shore of Kokechik Bay (61°37′N, 165°50′W) on the Yukon-Kuskokwim Delta, Alaska. The study area was within 500 km of that described by Eisenhauer and Kirkpatrick (1977). Jackson (1981) described vegetation at Kokechik Bay. Our study area included lowland marsh (<1 m above mean high-tide level) and Kokechik Bay.

Lowland areas consisted of meadow intermixed with tidal sloughs, mud flats and ponds. Meadows were dominated by the sedge *Carex ramenskii,* growing up to 30 cm in height, or by the grass *Elymus arenarius* along slough banks. Mud flat vegetation consisted of pure or mixed patches of *Puccinellia phryganodes* and *Carex subspathacea* scattered within large areas of bare mud. Plants on mud flats were less than 5 cm tall, and were not observed flowering. Mud flats were inundated daily by high tides, while meadows were flooded two or three times each summer.

Lowland marsh was bordered by Kokechik Bay on the north. The border between lowland and the bay was clearly marked by a steep 2-m bank. At low tide a large expanse of unvegetated mud was exposed on the bay.

METHODS

HABITAT SELECTION BY WILD GEESE

Habitat availability. We defined four habitats within the lowland brood-rearing area: meadow, vegetated mud flats, unvegetated mud flats combined with ponds and sloughs, and Kokechik Bay. We recorded habitat and behavior of Emperor Goose broods within a 300 m radius centered on an observation tower 120 m south of the bank which defined the edge of the bay. To determine relative availability of the four habitats within the observation area, we digitized an aerial infra-

red photograph to determine the number of pixels covered by meadow, bay and the circular study area, respectively. We obtained the area covered by all mud flats, ponds and sloughs by subtraction. Finally, we determined the proportion of mud flat that was vegetated using 10 line transects placed parallel to the coast at randomly chosen points on a 420-m line perpendicular to the coast. Each transect was sampled at 1-m intervals (estimated by walking stride) and categorized as either vegetated or not vegetated. We skipped a transect sample point when meadow was encountered and continued the transect again when a mud flat, pond or slough was reached, so that each transect had 200 points.

Habitat use by wild geese. Emperor Goose families were observed from a 3.5-m tower by one of two observers. Brood movements at Kokechik Bay were poorly known prior to this study, so the observation tower was first set up 500 m inland from Kokechik Bay, and was moved within 120 m of the coast when it became clear that Emperors had moved there. For this reason, observations subject to analysis in 1985 began 12 July, 13 days after the peak of hatch calculated from modal nest initiation in the area (M. R. Petersen, pers. comm.). In 1986, observations began 29 June, near the peak of hatch (M. R. Petersen, pers. comm.). Observations ended 10 August 1985 and 12 August 1986, approximately one week prior to fledging of goslings.

We made observations on goose families in which adult females had been neck-collared for another study (Petersen 1992). We used binoculars and a telescope to observe these families when they were within 300 m of the tower between 06:00 and 23:30 hr. We observed families for 30- to 70-min periods, recording the habitat and behavior of each adult and the habitat and behavior of a majority of goslings every 20 sec (Altmann 1974). Behavior was recorded as feeding only when birds had their heads down in the vegetation. Observers remained in the tower or in a tent at the tower's base for 2–4 days to minimize disturbance to geese.

FOOD SELECTION BY CAPTIVE GOSLINGS

Plant species composition. We examined food selection by captive goslings on two plots established approximately 1 km from the observational study area. We established and sampled Plot 1 (20 × 20 m) on 9 July 1985 in grass and sedge meadow 500 m from the coast where tidal

lowland graded into upland (>1 m above mean high-tide level) because Emperor Geese were found in this area during movements from nests after hatch.

When it became clear that Emperor Goose families moved from upland areas to the coast, we established Plot 2 in lowland marsh 100 m from the coast. Beginning on 19 July 1985 and throughout 1986 all feeding trials took place on Plot 2, which was larger (24 × 54 m) than Plot 1 to allow for large areas of unvegetated mud flats. We sampled Plot 2 for plant species composition on 4 August in 1985 and on 25 July in 1986 because plant phenology was approximately 10 days earlier in 1986 than in 1985.

We mapped plots to determine the proportion of area occupied by meadow and mud flats. We determined plant species composition within meadow and mud flat communities by counting all individual shoots and the number of leaves per shoot within a 15-cm² wire rectangle placed at the intersection of randomly selected pairs of coordinates on the plot (Plot 1, $n = 20$; Plot 2, $n = 30$). Mud flat samples that contained no plants were included to estimate the proportion of bare versus vegetated mud flats.

Feeding trials. We obtained 12 goslings from seven nests in 1985 and 17 goslings from nine nests in 1986 at hatching between 26 and 29 June each year. Goslings were imprinted on investigators and raised at a field camp 1 km inland from the feeding plots. Goslings grazed on wild plants, but the diet was augmented with commercial turkey starter because goslings were penned when investigators were not at camp to watch them.

We transported groups of 3–5 goslings to the feeding plot at the ages of 10, 20, 30 and 40 days. Goslings fed freely near (but not in) the plot for 4–6 hr before trials. They were then placed in an enclosure with no food available for 1 hr. When released onto meadow habitat in the center of the plot they were allowed to graze freely until they stopped feeding, generally about 30 min. During feeding trials the investigator stood on meadow in the center of the plot and monitored the amount of time goslings spent on meadow and mud flats. We sacrificed goslings when they stopped feeding.

In 1985, we preserved esophageal contents immediately by injecting 20 cc of formalin into esophagi, then removed esophageal contents from carcasses within 6 hr of collection and stored them in 10% formalin. In 1986, we injected 80% ethyl alcohol into the esophagi, then removed, rinsed and stored esophageal contents frozen within 6 hr of collection. This change in procedure was made so that plant components could be analyzed without contamination by formalin.

Collection of available plant species. We collected plant samples in 1986 from meadows and mud flats for component analysis. Exclosures (1 m²), six in meadow and eight in mud flats, were constructed of wire mesh on 25 June. We collected vegetation samples by clipping all plants to litter level within 20 × 25-cm quadrats. On 25 June, 15 July, and 14 August we clipped one quadrat inside and one quadrat outside each enclosure to examine effects of grazing by geese. Quadrat location was randomly chosen inside exclosures and arbitrarily placed within 2 m outside exclosures. We froze all samples within 2 hr of collection.

LABORATORY ANALYSES OF PLANT SAMPLES

We rinsed and blotted dry esophageal contents and clipped vegetation samples, then sorted them by species, weighed and freeze-dried them to constant mass at the University of California, Davis. For clipped samples only live material was analyzed. We calculated water content as the difference between fresh and dry mass. As an index to protein content, samples were ground in a Wiley mill with a 40-mesh sieve, then analyzed for total nitrogen content using high performance liquid chromatography (HPLC) (Goyal et al. 1988). We estimated cell wall content (or neutral detergent fiber: NDF) by neutral detergent analysis using samples ground in a Wiley mill with a 20-mesh sieve (Goering and Van Soest 1970, Robertson and Van Soest 1980). Amylase was used in the neutral detergent procedure. We did not determine cell wall content for esophageal samples because of the small amount of material collected, and because samples collected in 1985 were stored in formalin, which would cause an overestimation of cell wall content.

STATISTICAL ANALYSES

We used the percentage of time spent by wild geese in each of the four habitats during focal observations as an index to habitat use. For analysis, we combined all data collected for a marked brood throughout a season. We calculated habitat availability as the percentage of each habitat in the observation study area. We analyzed se-

lection of habitats by wild goslings using the Friedman Test and an accompanying multiple comparison test (Conover 1980) to test the null hypothesis that the ranks of the differences between habitat use and availability were the same for all habitats (Alldredge and Ratti 1986). In other words, habitats constituted treatments (k = 4) and broods constituted blocks (n = 5 in 1985 and n = 7 in 1986).

We analyzed plant selection data collected during feeding trials of captive goslings using nonparametric statistics (Conover 1980) because these percentage data were not normally distributed, even when transformed. We analyzed leaves, rather than shoots, because goslings ate individual leaves. We used the Wilcoxon matched-pairs signed ranks test to compare the availability of leaves of *P. phryganodes* and *C. subspathacea* found on mud flats on Plot 2 within each year. The Mann-Whitney U-test was used to compare percentage of leaves of each plant species eaten by goslings in feeding trials between years. We compared the relative abundance of plant species eaten by goslings in feeding trials to availability of each plant species (percentage of leaves counted in 30 samples each year) using a Wilcoxon signed ranks test. We used Kruskal-Wallis tests to identify differences in the percentage of each species in the diet among dates, within each year.

We did not perform statistical analyses on chemical composition of esophageal samples because the small amount of material collected made it necessary to combine samples within dates (and across dates in one case) for chemical analysis. Water content, nitrogen and cell wall content data from plants clipped from exclosures had homogeneous variances (F_{max}-test; Sokal and Rohlf 1981) and were normally distributed (Kolmogorov-Smirnov goodness-of-fit test; Sokal and Rohlf 1981). Therefore we compared all species for each constituent by means of parametric analysis of variance (ANOVA) using SAS statistical software (SAS Institute 1985).

We used plant species and sampling date as ANOVA main effects. Exclosure locations were nested within species effect. Initial analyses indicated no interaction between species and sampling date for any constituent, and no difference between samples inside and outside exclosures, which were not frequented by geese, so we did not include these factors in the final analyses. SAS Procedure GLM, which calculates ANOVA

for unequal numbers of samples, was used because some samples did not have enough material for analysis (SAS Institute 1985). When significant F-values were obtained from the ANOVA, we used the Tukey-Kramer multiple comparison test (Sokal and Rohlf 1981) to determine which species differed.

RESULTS

HABITAT SELECTION BY WILD GEESE

Emperor goose broods observed after hatch moved within one week from upland nest sites to tidally influenced salt marsh within 500 m of Kokechik Bay, where they remained throughout brood-rearing. We observed five broods for a total of 11 hr in 1985; in 1986, we observed seven broods for 30 hr. Selection among the four habitats by goslings differed from availability in both 1985 and 1986 (Table 1) (Friedman test, 1985: n = 5 broods, T = 6, P < 0.01; 1986: n = 7 broods, T = 7.61, P < 0.01). Multiple comparison tests indicated that goslings spent more time on vegetated mud flat than its availability would suggest (Table 1). Similar selection of vegetated mud flats emerged when feeding behavior alone was analyzed (Table 1) (Friedman test, 1985: T = 16.83, P < 0.01; 1986: T = 24, P < 0.01).

FOOD SELECTION BY CAPTIVE GOSLINGS

Feeding trial at Plot 1, 9 July 1985. Although sedge meadow had a high density of vegetation (Table 2), and constituted 51% of this inland plot, none of the three goslings fed in sedge meadow. Each gosling fed entirely in open grass meadow habitat, selecting 100% *Triglochin palustris* leaves. Although *T. palustris* was the most common leaf type in grass meadow (Table 2), its leaves were much smaller than any other species present. Selection of *T. palustris* was consistent with observations of captive goslings at the field camp throughout both summers. *T. palustris* was always selected over other species when available.

Feeding trials at Plot 2. Fifty-four percent of coastal Plot 2 was covered by sedge meadow, while 48% was vegetated or bare mud flat. Goslings always moved off the meadow immediately and spent the entire trial feeding in mud flat habitat.

Fourteen of 30 samples (47%) taken on mud flats contained plants in 1985, while 19 of 30 (63%) contained plants in 1986. There was no

TABLE 1. Estimated percentage of time spent in available lowland marsh habitats by wild Emperor Goose goslings ($\bar{x}\%$ ± SE). n = five families in 1985; seven families in 1986. Ranks of differences between habitat use and availability were significantly different when habitats did not share a capital letter within a column (Friedman ANOVA multiple comparison test, α = 0.01).

Habitat	% of total area available	% of total time spent in habitat		% of feeding time spent in habitat	
		1985	1986	1985	1986
Meadow	41	21 ± 6 AB	33 ± 9 A	8 ± 3 A	11 ± 5 A
Mud, ponds	29	2 ± 2 A	4 ± 1 A	0 AC	0 A
Vegetated mud	5	51 ± 6 B	53 ± 9 B	80 ± 4 B	82 ± 6 B
Bay	25	18 ± 12 AB	5 ± 2 A	9 ± 6 BC	4 ± 3 C
Unidentified	—	8 ± 3	5 ± 1	3 ± 2	3 ± 1

difference detected in the availability of leaves of the two species in 1985 (Wilcoxon paired test, n = 14, T = 51, P > 0.10), but a difference was detected in 1986 (n = 19, T = 35, P < 0.05), when *P. phryganodes* was more common (Table 3).

Selection of plants by goslings varied between years (Table 4; Mann-Whitney U-test 1985: n = 9 goslings; 1986: n = 17 goslings; T = 18, P < 0.002). In 1985, goslings selected *C. subspathacea* leaves more often than predicted by their availability (Wilcoxon signed-ranks test: n = 9 goslings, T = 0, P < 0.008). Goslings frequently selected *Carex* leaves by feeding along the border between meadow and mud flat, rather than by searching for plants scattered in the middle of mud flat habitat.

In contrast to goslings observed in 1985, goslings in 1986 fed primarily on *P. phryganodes* (Table 4). Goslings selected this species approximately in proportion to its availability (Wilcoxon signed-ranks test: n = 17 goslings, T = 39.5, 0.051 < P < 0.098). Thirteen goslings in 1986 ate *P. phryganodes* in greater proportions than predicted by its availability, but three of the five 10-day old goslings selected mostly *C. subspathacea*. When 10-day old goslings were excluded

from the analysis, usage and availability were significantly different (Wilcoxon signed-ranks test: n = 12 goslings, T = 0, P < 0.009), suggesting strong selection of *P. phryganodes* by older goslings.

The three 10-day old goslings in 1986 that preferred *C. subspathacea* were responsible for the only large difference in diets among ages in either year. Kruskal-Wallis tests for differences in diet among ages in 1985 indicated no differences (k = 3 dates, H = 0.41, P > 0.10) but diets varied among ages in 1986 (Table 4; k = 4 dates, H = 10.75, P < 0.025).

CHEMICAL COMPOSITION OF PLANTS

Concentrations of water, nitrogen and cell wall all varied significantly among species (Table 5). Nitrogen content did not vary significantly among sampling dates (Table 5). Water content was the only constituent which varied among dates and among sampling exclosures (Table 5).

T. palustris was significantly higher in nitrogen and water content than other species, and lower in cell wall than all species except *Potentilla egedii* (Table 5). *Elymus arenarius* had the lowest mean values for nitrogen and water content of any species (Table 5). Plants from gosling esoph-

TABLE 2. Plant species composition (mean number of leaves per sample ± SE) of meadow portions of feeding trial plots. n = 20 samples for Plot 1 sampled on 9 July 1985; n = 30 samples for Plot 2 sampled on 4 August 1985.

Plant species	Plot 1 (inland)		Plot 2 (coastal) Sedge meadow
	Grass meadow	Sedge meadow	
Triglochin palustris	5.0 ± 1.0	0.6 ± 0.3	0.4 ± 0.3
Puccinellia phryganodes	1.2 ± 0.1	0.3 ± 0.2	1.0 ± 0.6
Elymus arenarius	3.4 ± 0.8	0	0.1 ± 0.1
Carex ramenskii	2.7 ± 0.9	19.3 ± 2.6	21.2 ± 3.1
Carex subspathacea	0.9 ± 0.9	0	1.5 ± 0.8
Stellaria humifusa	1.3 ± 0.7	3.5 ± 1.3	3.7 ± 3.5
Potentilla egedii	3.9 ± 2.0	5.5 ± 2.3	7.1 ± 12.3

TABLE 3. Plant species composition (mean number of leaves or shoots ± SE) of mudflat portion of feeding trial Plot 2. n = 30 samples each year.

Plant species	Year	Number of leaves per sample	Number of shoots per sample
Puccinellia phryganodes	1985	19.3 ± 8.0	5.0 ± 2.1
	1986	36.7 ± 9.5	9.8 ± 2.6
Carex subspathacea	1985	10.4 ± 4.2	2.5 ± 1.0
	1986	7.0 ± 3.2	1.8 ± 0.8

agi consistently contained higher nitrogen and water content than clipped plants (Tables 5, 6).

DISCUSSION

IDENTIFICATION OF PLANT SPECIES

Use of tidal mud flats along the Kokechik River and Kokechik Bay by Emperor Goose broods was described in earlier studies (Eisenhauer and Kirkpatrick 1977, Frazer and Kirkpatrick 1979). However, there are discrepencies in the identification of plant species between those studies and the present one. Frazer and Kirkpatrick (1979) reported that Emperor broods used areas of "stalkless *Carex rariflora*" on mud flats, and Eisenhauer and Kirkpatrick (1977) listed *C. rariflora* as the most important plant eaten by Emperors between May and July. It is probable that "stalkless *C. rariflora*" referred to *C. subspathacea*, and possibly to *P. phryganodes*, which rarely flowers (Jefferies and Gottlieb 1983) on mud flats. Identification of *Carex* species are difficult for several reasons. *C. subspathacea* rarely flowers on tidal mud flats (Kotanen and Jefferies 1987). In addition, *C. subspathacea* and *C. ramenskii* (cf. Hulten 1968:252) are considered one species by Polunin (1940:133), who noted that the mor-

phology of *C. subspathacea* growing at the border between mud flats and meadows appears to grade into *C. ramenskii* on adjacent meadows. *Carex ramenskii* meadows at Kokechik Bay, identified by J. Tande, T. Jennings and S. Fleischman of the U.S. Fish & Wildlife Service during this study, were called *C. rariflora* meadows by Jackson (1981) during studies in the 1970s, when Eisenhauer and Frazer were working there. Extensive *C. rariflora* meadows do occur inland from tidal marshes at Kokechik Bay.

MOVEMENTS FROM UPLAND NESTING AREAS TO COASTAL MARSHES

Post-hatch movement of Emperor Geese to the tidal marshes of Kokechik Bay and to the banks of the Kokechik River drainage was documented as early as 1924 (Murie 1924), and later confirmed by aerial surveys (Eisenhauer and Kirkpatrick 1977) and ground observations (Frazer and Kirkpatrick 1979). By moving to coastal marshes, Emperor Geese abandoned areas which contained high densities of *T. palustris*, a major food of Cackling Canada Geese during brood-rearing on the Yukon-Kuskokwim Delta (Sedinger and Raveling 1984). *Triglochin palustris* was

TABLE 4. Comparison of availability (percentage of total [and actual number] leaves counted in 30 samples each year) and consumption (mean percentage ± SE) of plant species (and number of goslings) by captive Emperor Goose goslings during feeding trials on Plot 2. Consumption on different dates within a year are significantly different if they do not share a capital letter (Kruskal-Wallis test, α = 0.02).

	1985		1986	
	Puccinellia phryganodes	*Carex subspathacea*	*Puccinellia phryganodes*	*Carex subspathacea*
Availability	65 (578)	35 (312)	84 (1,102)	16 (210)
Consumption Age (days)				
10	*	*	52.4 ± 20.3	47.6 ± 20.3 (5) A
20	19.0 ± 4.6	81.0 ± 4.6 (3) A	98.6 ± 0.7	1.4 ± 0.7 (5) B
30	23.7 ± 5.7	76.3 ± 5.7 (3) A	94.0 ± 1.9	4.8 ± 1.9 (4) AB
40	22.3 ± 7.3	77.7 ± 7.3 (3) A	98.0 ± 2.0	2.0 ± 2.0 (3) B

* No feeding trial on Plot 2 took place on this date.

TABLE 5. Components of plants (percent [unweighted mean[a]] ± SE) available to Emperor Geese during brood-rearing. Results for species within a column not sharing a capital letter are significantly different (Tukey-Kramer test, $\alpha = 0.05$).

Species	Water (% fresh mass)	Nitrogen (% dry mass)	Cell wall (% dry mass)
Triglochin palustris	90.3 ± 0.4 A	4.7 ± 0.2 A	30.4 ± 2.0 A
Puccinellia phryganodes	83.3 ± 0.3 C	2.5 ± 0.1 BC	46.8 ± 1.5 B
Elymus arenarius	71.4 ± 0.5 D	1.7 ± 0.2 D	50.9 ± 1.9 B
Carex ramenskii	84.0 ± 0.3 BC	2.4 ± 0.1 CD	53.0 ± 1.5 B
Carex subspathacea	86.1 ± 0.3 B	3.1 ± 0.1 B	51.6 ± 1.6 B
Potentilla egedii	87.0 ± 0.6 B	2.2 ± 0.2 CD	27.5 ± 2.1 A
ANOVA results			
Species	$F = 231.7\ P = 0.001$	$F = 92.5\ P = 0.001$	$F = 496.5\ P = 0.01$
Date	$F = 7.3\ P = 0.05$	$F = 5.1$ ns	$F = 2.8$ ns
Sampling location within species	$F = 19.9\ P = 0.01$	$F = 2.8$ ns	$F = 15.6$ ns

[a] For each species, mean and standard error were obtained by finding the mean value for each of the three collection dates, and then taking the mean of those means.

higher in total nitrogen, water (Table 5) and soluble carbohydrate content (Sedinger and Raveling 1984) and lower in cell wall content (Table 5) than other available plants, making it appear to be an ideal food during growth. Emperor Goose goslings in this study selected *T. palustris* when available.

Factors other than nutritional preferences, such as escape from predators, influence the choice of brood-rearing areas by geese (Buchsbaum and Valiela 1987). Molting geese frequently run to ponds or lakes to escape from predators (Derksen et al. 1982, Giroux et al. 1986). When alarmed by arctic foxes (*Alopex lagopus*), human pedestrians or low-flying airplanes, Emperor Geese in this study ignored nearby ponds. Instead they ran as far as 400 m to the bay, where they remained in large groups for up to an hour after disturbance. They may have avoided going further inland, where *T. palustris* was more fre-

quently available, because doing so would have increased the distance to the bay beyond 500 m.

By moving to coastal marshes Emperor Geese avoided potential competition for food with Cackling Geese. Sedinger and Raveling (1988) found that grazing by Cackling Goose goslings limited the availability of *T. palustris* during brood-rearing. *Triglochin palustris* was not known to occur on the Yukon-Kuskokwim Delta (e.g., Hulten 1968, Jackson 1981) until D. Murray and A. Batten identified it for Sedinger and Raveling (1984). It may have been missed due to intense grazing when goose densities were high prior to the late 1970s.

If the Emperor Goose broods in this study avoided competition with Cackling Geese by staying on the coast, they nevertheless shared food resources with Black Brant (*Branta bernicla nigricans*) broods, which fed intermittently at the same vegetated mud flats as Emperor Geese. At

TABLE 6. Components of plants collected from esophagi of Emperor Goose goslings after feeding trials (mean percentage ± SE). Means were generated by finding the mean of the means for goslings sampled on each date.

Species	Number of feeding trial dates	Water (% fresh mass)	Nitrogen (% dry mass)
1985			
Triglochin palustris	1	93.1	6.7
Puccinellia phryganodes	3	87.2 ± 0.8	4.1 ± 0.5
Carex subspathacea	3	85.2 ± 1.7	5.2 ± 0.5
1986			
Puccinellia phryganodes	4	89.4 ± 1.2	4.0 ± 0.5
Carex subspathacea[a]	4	90.7	4.2

[a] Samples were combined for analysis because of the small amount of material collected.

high densities of geese, the potential for competition between these two species is likely.

HABITAT SELECTION WITHIN COASTAL MARSHES

Adult geese controlled the larger movement of goslings from upland to coastal lowland areas, and in lowland areas they probably controlled whether goslings used Kokechik Bay or coastal marshes; goslings remained within 5 m of adults most of the time. However, within the coastal lowland marsh, mud flat and meadow habitats were interspersed enough to provide choices for goslings without forcing them to move away from adults.

Geese often avoid tall vegetation, perhaps because their ability to detect predators is reduced (Owen 1975). Both wild and captive goslings at Kokechik Bay avoided dense sedge meadow in favor of open mud flats, and fed almost entirely on mud flat vegetation.

Goslings apparently gained more nutrients from mud flat vegetation than they would have from meadow plants. *Carex ramenskii* and *P. egedii* contained lower total nitrogen levels than mud flat species, and *C. ramenskii* contained more cell wall material (Table 5), indicating that less nitrogen was available for digestion. In addition, the nitrogen available in mud flat species may be higher than reported in Table 5. A recent series of studies on *P. phryganodes* and *C. subspathacea* heavily grazed by Lesser Snow Geese (*Anser caerulescens caerulescens*) during brood-rearing demonstrated that deposition of goose feces during grazing accelerated nitrogen recycling, resulting in higher above-ground production and nitrogen content of grazed versus ungrazed vegetation despite the loss of plant tissue caused by grazing itself (Bazely and Jefferies 1985, 1986, 1989; Jefferies 1988; Ruess et al. 1989). Mud flat vegetation grazed repeatedly by geese is likely to be higher in nitrogen than that measured in this study, which was taken from exclosures not frequented by geese. Whether grazing the tops of 30-cm *C. ramenskii* leaves would cause such a compensatory response is unknown. *P. egedii* did not respond to grazing with regrowth (Bazely and Jefferies 1986).

By repeatedly selecting the same area of mud flats throughout brood rearing, Emperor Goose goslings fed in an open habitat, close to refuge from predators, with a high likelihood of finding recently fertilized, nitrogen-rich plant material.

Records of locations of marked broods and the presence of feces suggest that Emperors remain in specific areas during brood-rearing, regrazing vegetation on the mud flats (Laing, unpub. data). Nearby areas apparently identical to the study area were nearly devoid of geese (as determined by observations and absence of feces) throughout each season.

PLANT SPECIES SELECTION

Selection by Emperor Goose goslings for *T. palustris*, when available, was similar to findings of other studies in which geese grazed selectively on marsh and meadow plants with high nitrogen content (Lieff et al. 1970, Owen et al. 1977, Sedinger and Raveling 1984, Teunissen et al. 1985, Kotanen and Jefferies 1987) or low levels of secondary compounds (Buchsbaum et al. 1984), perhaps by using water content or relative toughness as indicators of nutrient content and digestibility (Owen 1976). Selection for nitrogen by goslings is further implied by the high nitrogen content of esophageal contents of goslings compared to clipped plants (Sedinger and Raveling 1984; Buchsbaum and Valiela 1987; this study Tables 5, 6), although an unknown proportion of this nitrogen may be due to contamination by saliva (Moss 1972).

Levels of nitrogen, water and cell wall (Table 5) do not suggest that there should be great differences in selection between *P. phryganodes* and *C. subspathacea*. Cargill and Jefferies (1984) reported variable total nitrogen values for ungrazed *C. subspathacea* (1.3–3.5% over two years) and for *P. phryganodes* (0.8–3.1%) at La Perouse Bay, Canada, where Lesser Snow Geese fed heavily on both species (Jefferies 1988). Peck rates and defecation rates by Lesser Snow Goose goslings feeding on the two species were similar (Ruess et al. 1989). In northern Alaska, Kiera (1982) found no difference in selection by Black Brant goslings between the two species, which were comparable in total nitrogen content.

Differences in selection by Emperor Goose goslings for the two species between the two years of this study may be explained by changes in local conditions on the feeding trial plot (Plot 2). There were more *P. phryganodes* shoots growing on the plot in 1986 than in 1985 (Table 3), perhaps due to changes in weather conditions or tidal flooding. *Puccinellia* species are more tolerant of saline conditions than other marsh species (Snow and Vince 1984). Whatever changes

influenced the difference in growth may also have affected nitrogen content of the two species. Nitrogen content was not measured on the feeding plot.

SIGNIFICANCE FOR GOOSE POPULATION MANAGEMENT

Geese feeding on *P. phryganodes* and *C. subspathacea* not only increase productivity and food quality of their preferred forage by grazing and defecating, but also retard plant succession, maintaining graminoid plant communities required for gosling growth (Jefferies 1988, Bazely and Jefferies 1989). Such interaction between geese and their forage plants implies that extreme population fluctuations of geese may have greater significance than formerly thought. Currently low populations of Emperors and Black Brant on the Yukon-Kuskokwim Delta (Pamplin 1986) could have both short-term effects on plant nutritional quality and long-term effects on the abundance of preferred forage species.

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