

Variability in the chemistry of estuarine plants and its effect on feeding by Canada geese

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Summary. We investigated the influence of interspecific and seasonal variations in plant chemistry on food choices by adult and gosling Canada Geese, *Branta canadensis*, on Cape Cod, Massachusetts. The geese fed primarily on the abundant marsh grasses, *Spartina* spp., and rushes, *Juncus gerardi*, early in the growing season and switched to a greater dependence on eelgrass, *Zostera marina*, later. Forbs were generally avoided all season even when growing within patches of abundant species. The avoidance of forbs was related to their low abundance and their high concentrations of deterrent secondary metabolites. Differences in plant chemistry also determined the switch from marsh graminoids to *Z. marina* during the growing season. Marsh grasses were higher than *Z. marina* in nitrogen, particularly in the spring when the nitrogen requirement of geese is especially high. *Z. marina* was a better source of soluble carbohydrates and was the preferred food during the summer when the need to build up energy reserves may be more critical to geese than protein intake. Goslings, which require a diet higher in nitrogen than do adults, fed on marsh graminoids later into the growing season than the adults. The nitrogen content of the diets of goslings was significantly higher than that available to them in the plants, indicating that they selected for nitrogen. The diets of non-breeding adults in the spring and all geese in mid summer closely reflected the nutrient content of the plants. The diet of breeding adults was more similar to that of their goslings than to that of non-breeding adults. The effects of plant chemistry and the nutritional needs of geese on food choices were modified by the need to select a safe feeding site.

Variability in the chemical constituents of plants has profound effects on the food choices of herbivores (Atsatt and O'Dowd 1976; Denno and McClure 1983). Variation can occur on a number of levels. Interspecific variation among plants in the same community results in selection by herbivores for those particular species that provide feeding stimulents and either lack deterrents or have deterrents to which the herbivores are at least partially adapted (Atsatt and O'Dowd 1976; Rosenthal and Janzen 1979). Intraspecific

variation causes selection for those patches of a species that are most nutritious (Vince et al. 1981; Buchsbaum et al. 1981; Denno 1983) or low in deterrents (Cooper-Driver and Swain 1976; Arnold and Hill 1972). Variation within individual plants engenders selection for particular plant parts (McKey 1979; Denno 1983). Temporal variations in plant chemistry cause seasonal changes in the use of different species of plants by herbivores (Cooper-Driver et al. 1977; Ottosson and Andersen 1983).

In this paper we examine the effect of interspecific and temporal variation in the chemistry of a community of plants on feeding by adult and gosling Canada geese, *Branta canadensis*, in a coastal habitat on Cape Cod Massachusetts, U.S.A. Canada geese are almost entirely herbivorous (Owen 1980) and discriminate readily among different foods (Owen 1980; Sedinger and Raveling 1984; Buchsbaum et al. 1984). The value of food to geese may depend on its content of protein, (Harwood 1977; Owen et al. 1977; Buchsbaum et al. 1981; Sedinger and Raveling 1984), energy (Owen 1980) or deterrents (Buchsbaum et al. 1984). The relative importance of these constituents may depend on seasonal and age related variations in the nutritional needs of geese (Raveling 1979; Janzen 1979).

Material and methods

Study animals and field site

A population of 30–80 Canada geese inhabit West Falmouth Harbor (WFH) and Great Sippewissett Marsh (GSM) on the western shore of Buzzards Bay, Massachusetts (lat. 41°35'N, long. 70°W) in the spring, and remain in WFH throughout the summer to molt and rear goslings. In 1981, the population consisted of 17 non-breeding adults, 15 goslings, and 6 breeding adults during the molt period. In 1983, the numbers were 35, 19, and 8 respectively. The major feeding areas of the geese, especially during the molt period when their movements are restricted to WFH, are the shallow subtidal *Zostera marina* beds and the salt marshes that fringe much of the periphery of the harbor. *Z. marina*, growing at depths of 1–2 m at low tide, covers about 270,000 m² in WFH. The total area of salt marsh in WFH is 80,000 m². GSM vegetation covers 302,900 m² 1 km south of WFH. *Spartina alterniflora* is the dominant plant of the regularly flooded intertidal zones of the marshes. *S. patens* dominates at higher elevations that are inundated less often. *Juncus gerardi* grows in narrow bands

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along the upper edges of marshes. Forbs, such as *Salicornia* spp., *Limonium carolinianum*, and *Solidago sempervirens*, grow in scattered clumps in the salt marsh, covering <5% of the total area. *Poa pratensis* and other cultivated grasses grow adjacent to the marsh.

Determining the plants selected by geese

Surveys to determine the plant species eaten by Canada geese and to note seasonal changes in preferred foods were carried out 5 days during the 1981 and 6 days during the 1983 growing seasons. Since feeding patterns were more dependent on tides than on time of the day (Buchsbaum 1985), observations were carried out over complete tidal cycles. We surveyed the entire study area with a spotting scope each h (1981) or half h (1983) during daylight, noting the location and activity of as many geese as possible at each time interval. The activity of each goose as it was first observed was considered its activity for that h (1981) or half h (1983). If a goose was feeding, the species of plant on which it fed was recorded. Since most of the vegetated areas of WFH and GSM are dominated by one species of plant, the species eaten could usually be determined by noting the exact location of the feeding. Where two or more plants occurred together, we determined what the geese had eaten by looking for clipped plants after the geese had departed from the area. Geese feeding on the open water of the bay fed on *Z. marina*, the only plant growing in abundance there. Relative preference for a species of plant on a survey day was calculated as the percent of feeding observations on that species compared to the total number of feeding observations on all plants on that day.

Geese were divided into four categories. From early May through mid-July, we could distinguish non-breeding adults, breeding adults (parents), and goslings. After mid-July, these three groups were no longer easily distinguishable through our spotting scope, and all geese were pooled into a "mid-summer" category.

Our method of quantifying feeding behavior allowed us to note the food choices of a large number of individuals over the course of a tidal cycle. We made a total of 1650 feeding observations and kept track of the activities of most of the 30–80 geese present in WFH throughout a given survey day.

Collection of plant material for chemical analysis

Plants were categorized as either palatable (at least 5% of diet) or unpalatable based on the feeding observations. The more common representatives from both these categories were sampled repeatedly from April to September at several sites in West Falmouth Harbor and Great Sippewissett Marsh. The plants collected were *Zostera marina*, *Spartina alterniflora*, *S. patens*, and *Juncus gerardi*, *Salicornia europaea*, *Limonium carolinianum* and *Solidago sempervirens*. About 50 leaf blades from palatable species were collected biweekly from about 25 randomly selected culms of each species at each site and were placed in plastic bags to prevent water loss. The unpalatable species plants were sampled less often. Samples of *Spartina* spp. were always the uppermost and second uppermost fully emergent blades of a culm. These are the most frequently consumed leaves on the grass (Buchsbaum 1985). *J. gerardi*, *Z. marina*, and *L. carolinianum* leaves were clipped at ground level. All aboveground parts of the succulent, *S. europaea*, were col-

lected, but only the leaves from *So. sempervirens*. The samples were brought back to the laboratory within 2 h, were weighed, and were then dried at 45° C.

Measurement of chemical constituents

All dried plant material was ground through a 60 mesh screen in a Wiley mill. Plants categorized as palatable were then analyzed for three constituents that might stimulate feeding and for two potential deterrents. Unpalatable plants were analyzed only for potential deterrents because our previous results indicated that their unpalatability was unrelated to nutrient content (Buchsbaum et al. 1984).

The potential feeding stimulents we measured were water, nitrogen and soluble carbohydrates. Water content was the difference between fresh and dry weight. Total nitrogen content was determined with a Perkin-Elmer elemental analyzer. To quantify soluble carbohydrates, 100 mg of dried plant material were extracted twice in 80% methanol at 85° C. Residues were saved for fiber analysis, and the supernatants were pooled and analyzed for soluble carbohydrates using the phenol-sulfuric acid reaction (Strickland and Parsons 1972).

The potential inhibitory constituents were fiber and phenolics. Fiber was quantified gravimetrically after treating the residues from the methanol extraction with chloroform:ether (3:1), then ether alone, and finally 3% sulfuric acid for 30 min at 100° C (Buchsbaum et al. 1984). Phenolic content was measured on the 80% methanol extracts as both total phenolics (Swain and Goldstein 1964) and astringency (Bate-Smith 1973).

The nutrient content of the diet of geese and the weighted availability of nutrients

Once we determined the contribution of different plants to the diet of geese and the composition of carbohydrates and nitrogen in those plants over the growing season, we calculated the content of these nutrients in the diet of geese at different times during the growing season. We also calculated the overall availability to geese of carbohydrates and nitrogen in plants, weighted to reflect the relative abundance of the edible biomass of different species. These calculations revealed whether geese selected species with high carbohydrate or nitrogen content or whether their diets merely reflected what was available to them from the plants.

The nutrient content of the diet of geese was calculated by

$$\sum(o_p/o_t)*n_p$$

where

$$o_p = \text{number of feeding observations on plant species } p$$

$$o_t = \text{total number of feeding observations on all species}$$

$$n_p = \% \text{ carbohydrate or nitrogen content in species } p.$$

In calculating the weighted availability of a nutrient, we included all plants that were eaten by geese at least once during the growing season or that contributed at least 5% to the total edible biomass of the habitat. The calculation of weighted availability of a nutrient was as follows:

$$\sum(a_p*b_p*e_p/eb_t)*n_p$$

where

a_p = area covered by plant species p in m^2

b_p = biomass of plant species p per m^2

e_p = fraction of the biomass of species p that is edible to geese

eb_t = total edible biomass of all plants in the habitat, i.e. the sum of $a_p * b_p * e_p$ for all species

n_p = nutrient content of plant species p

The area covered by each species (a_p) was determined by mapping the vegetation of WFH and quantifying the area covered by each species by planimetry. Literature values were used to determine the biomass per m^2 of each species (b_p). The biomass per m^2 of the two *Spartina* species were taken from values for GSM (Vince et al. 1981). Based on our experience in GSM, we took the aboveground biomass of *J. gerardi* to be similar to that of *S. patens*, and therefore used values from Vince et al. (1981) in calculating its biomass. Estimates of the biomass of *Z. marina* per m^2 were taken from *Z. marina* beds in Woods Hole Harbor (Dennison and Alberte 1982) and Rhode Island (Harlin and Thorne-Miller 1981). Calculations of the percent of the biomass of each species that is edible (e_p) had to take into account which parts of individual grass plants are normally eaten by geese and how deeply geese are able to reach down into the water to feed on a submerged plant like *Z. marina*. In our study area geese eat only the apical half of blade tips of *Spartina* spp. and rarely feed on belowground tissues during the growing season (Buchsbbaum 1985). The percent of the biomass of apical halves of *S. alterniflora* and *S. patens* relative to total aboveground plant biomass varied from about 25% early in the growing season to about 10% in September (Buchsbbaum 1985). *J. gerardi* does not have a rigid, inedible stem such as that found in *Spartina* spp., hence we assumed that the geese ate 40% of the aboveground biomass of this plant, as described for plants of similar morphology in Ebbinge et al. (1975). *Z. marina* is subtidal in WFH, and we calculated that geese could reach down about 0.5 m below the water surface when "tipping up" for this plant, since the body length of the larger races of Canada geese is about 1 m from the tip of their bill to the tip of their tail (Belle-rose 1976). Thus at water depths of 1 m, half the biomass of *Z. marina* was available to geese and at 2 m, only one fourth. Only *Z. marina* growing at depths less than 1.5 m was available to geese in May because this plant only starts growing in late April or early May in WFH.

Results

Diets of adult geese and goslings

Geese grazed primarily on emerging grasses and rushes early in the season and switched to the submerged angiosperm, *Z. marina*, later (Table 1, Figs. 1 and 2). In May, geese fed heavily on *Sp. alterniflora*, *Sp. patens*, and *J. gerardi* in marshes, and on *Poa pratensis* in lawns near the harbor. By mid June, *Po. pratensis* was not eaten because all birds were molting and flightless and thus restricted to feeding on plants that grew in the water or in marshy areas very close to water. Later in the season *Z. marina* became increasingly important to geese, and by the end of August in both years, about 75% of the feeding observations were of this plant. The green algae, *Enteromorpha* spp., comprised a small but consistent part of the diets of the geese

Table 1. List of common plants of West Falmouth Harbor along with their value as food to geese

Phylum Tracheophyta

Graminae:

Distichlis spicata – regularly eaten in late summer.

Phragmites communis – no evidence of consumption.

Poa pratensis and other cultivated grasses – regularly eaten in the spring, fall, and winter.

Spartina alterniflora – regularly eaten in the spring, consumed in smaller amounts throughout the summer.

Spartina patens – regularly eaten in the spring, consumed in smaller amounts throughout the summer.

Juncaceae:

Juncus gerardi – regularly eaten in the spring.

Juncaginaceae:

Triglochin maritima – leaves are occasionally eaten in the spring, seeds are consumed in mid summer.

Zosteraceae:

Zostera marina – consumed heavily in late spring and summer, less so in fall.

Chenopodiaceae:

Salicornia bigelovii – no evidence of consumption.

Salicornia europaea – a few summer feeding observations.

Salicornia virginica – one summer feeding observation.

Plantaginaceae:

Plantago oliganthos – occasionally eaten in late summer.

Plumbaginaceae:

Limonium carolinianum – no evidence of consumption.

Compositae:

Iva frutescens – occasionally eaten by goslings in spring.

Solidago sempervirens – no evidence of consumption.

Phylum Chlorophyta

Enteromorpaceae:

Enteromorpha spp. – regularly eaten in spring and summer.

Phylum Phaeophyta

Fucaceae:

Ascophyllum nodosum – no evidence of consumption.

Fucus vesiculosus – no evidence of consumption.

throughout the season. Forbs tended to be avoided, even when they grew within patches of the more abundant marsh graminoids.

There were some differences in the diets of goslings and non-breeding adult birds. Goslings relied more heavily than non-breeding adults on *J. gerardi* and did not feed on *P. pratensis* in upland areas (Figs. 1 and 2). Goslings switched to *Z. marina* later in the season than adult birds. The first goslings to feed on this submerged plant were 5 week old birds that ate plants their parents had plucked and brought up to the surface of the water.

The diet of parents was more similar to that of goslings than to that of non-breeding adults (Figs. 1 and 2, bottom). Parents fed on *J. gerardi* rather than on *P. pratensis* in May and did not switch to *Z. marina* as early in the growing season as non-breeders. Parents generally fed on a smaller number of plant species than goslings (Figs. 1 and 2).

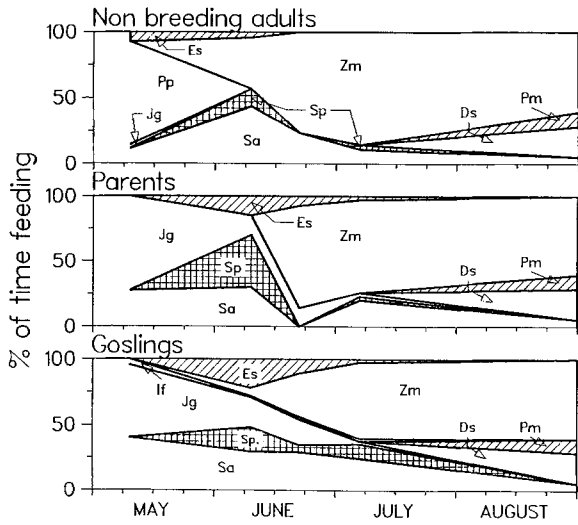


Fig. 1. Seasonal changes in plants selected by non-breeding adult, parent, and gosling Canada geese over the growing season in 1981. Selection was determined by the % of time geese spent feeding in patches of different plants during survey days. *Ds* *D. spicata*, *Es* *Enteromorpha* spp., *If* *I. frutescens*, *Jg* *J. gerardi*, *Pm* *Pl. oliganthos*, *Pp* *Poa pratensis*, *Sv* *Sa. virginica*, *Sa* *Sp. alterniflora* *Sp* *Sp. patens*. For surveys carried out in late July and August, the 3 groups of geese were no longer distinguished and were pooled together into a "mid-summer" category

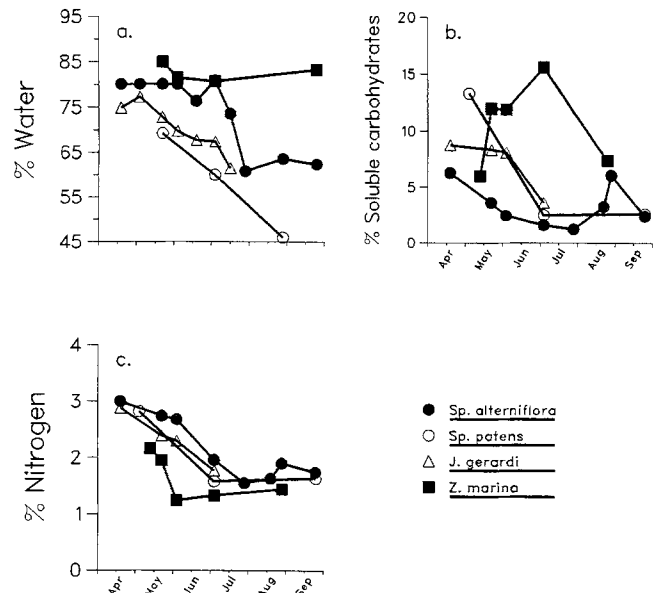


Fig. 3a-c. Seasonal changes in the concentrations of water, soluble carbohydrates, and nitrogen in palatable plants in West Falmouth Harbor. Standard errors were less than size of symbols

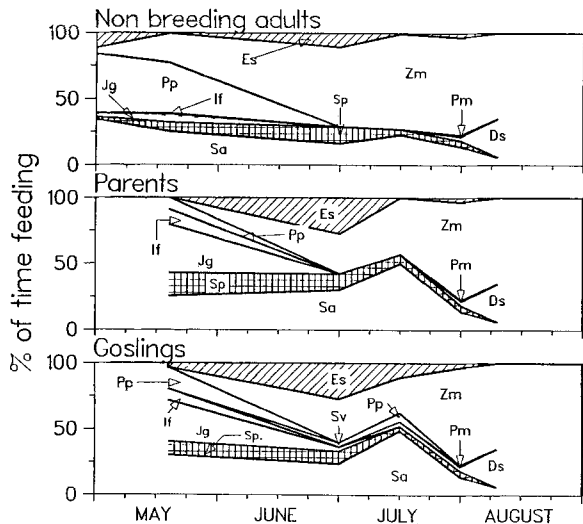


Fig. 2. Seasonal changes in plants selected by Canada geese over the growing season in 1983. Symbols as in Fig. 1

Seasonal changes in the chemical constituents of plants

Analysis of palatable plants for water, soluble carbohydrates, and nitrogen indicated that *Z. marina* differed from the three marsh graminoids in the quantity and seasonal distribution of these constituents. The water content of *Z. marina* remained above 80% throughout the growing season (Fig. 3a). In contrast, water contents of the 3 marsh graminoids were about 80% in the spring, but declined substantially later in the growing season. The soluble carbohydrate content of *Z. marina* was higher than that of marsh graminoids through most of the growing season (Fig. 3b). The seasonal trends in concentration also differed, soluble

carbohydrates peaking in mid summer in *Z. marina*, but in the spring in marsh graminoids. Total nitrogen declined from spring to summer in all plant species (Fig. 3c). In contrast to its higher levels of soluble carbohydrates, *Z. marina* was consistently lower in total nitrogen than any of the marsh plants.

Of potential feeding deterrents, the fiber content of *Z. marina* was lower than that of the marsh graminoids throughout the growing season, and did not show any seasonal trends (Fig. 4a). The fiber content of *S. alterniflora* and *S. patens* varied between 30–47%. The absence of a seasonal increase in fiber in these two species (as might have been predicted from their lowered water content) is probably related to selecting only young leaves for analysis. Only fiber in *J. gerardi* exhibited a consistent seasonal change, increasing rapidly in June, the same time its water content declined. The phenolic content of the palatable plants remained fairly constant at less than 2.5% over the growing season, with *Z. marina* containing the lowest concentration of this constituent (Fig. 4b). None of the palatable plants were astringent at any time during the growing season.

The unpalatable forbs differed from the palatable plants in the content of potential deterrents over the growing season. The forbs were consistently lower in fiber than the graminoids (Fig. 4c) but maintained relatively high levels of phenolics and astringency (Fig. 4d). Thus phenolics apparently had a greater role than fiber in deterring feeding on unpalatable plants.

Seasonal trends in feeding vs chemical changes in plant

The average carbohydrate content of all species of plants in our study area (weighted to reflect relative abundances of different species) increased early in the season, peaked in July, then declined in August (Fig. 5a). The weighted average nitrogen content declined (Fig. 5b). The extent to

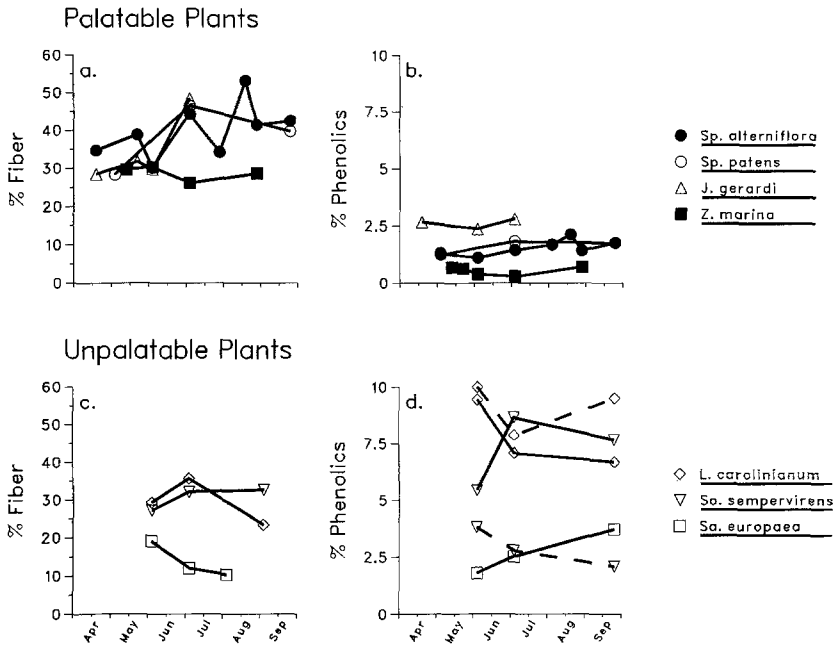


Fig. 4a-d. Seasonal changes in potentially inhibitory substances in palatable (a and b) and unpalatable (c and d) plants. *Solid lines* in (b, d) represent total phenolic content (Folin-Denis) and *broken lines* represent astringency (tanning activity). Note that none of the palatable plants in (b) nor *Sa. europaea* in (d) were astringent. Standard errors were less than size of symbols

which the nutrient content of the diets reflected the availability of nutrients depended on the age of the geese. The soluble carbohydrate content of the diets of non-breeding adults, parents, and mid-summer geese was not significantly different than the weighted available soluble carbohydrate content of the plants (Fig. 5a and Table 2). In fact, the pattern in non-breeding adults combined with mid-summer birds followed available carbohydrates fairly closely (Fig. 5a, open circles and diamonds). Feeding by parents in relation to available carbohydrates was more random (Fig. 5a,

open squares). Goslings, in contrast, selected a diet significantly lower in soluble carbohydrates than that available (Fig. 5a, open triangles, and Table 2). This was probably a result of their feeding less on *Z. marina*, the abundant, high soluble carbohydrate plant, than the other geese.

The relationship between available nitrogen and dietary nitrogen also differed among non-breeding adults, parents, and goslings (Fig. 5b and Table 2). The nitrogen contents of the diets of non-breeders and parents were not significantly different from the weighted available nitrogen of the

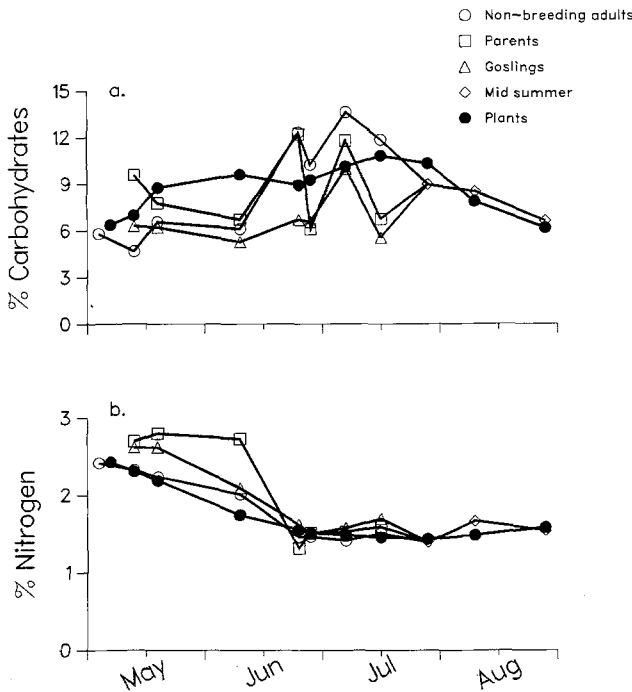


Fig. 5a, b. Seasonal changes in the availability of soluble carbohydrates and nitrogen in plants at West Falmouth Harbor compared to seasonal changes in the amounts of these two constituents in the diets of geese

Table 2. Paired *t* test comparing the % soluble carbohydrates and % N in the diet of geese at various dates during the growing season vs the weighted average amount of those constituents in marsh plants at the same dates. The contents of the diets of goslings and non-breeding adults is also compared. Feeding observations from 1981 and 1983 combined for this analysis

Goose	<i>n</i>	Average difference	Std error of difference	<i>t</i> value	Significance
<i>% Soluble carbohydrates in diet vs in plants</i>					
Non-breeders	8	0.04	0.93	0.04	NS
Parents	7	0.51	0.45	1.14	NS
Goslings	7	-2.56	0.69	-3.73	<i>P</i> < 0.05
Mid-summer	3	0.09	0.63	0.14	NS
<i>% soluble carbohydrates in diet of goslings vs non-breeders</i>					
	7	-2.69	1.09	-2.45	<i>P</i> < 0.05
<i>% N in diet vs in plants</i>					
Non-breeders	8	0.04	0.04	-1.11	NS
Parents	7	0.28	0.16	1.74	NS
Goslings	7	0.19	0.06	3.25	<i>P</i> < 0.05
Mid-summer	3	0.03	0.07	0.45	NS
<i>% N in diet of goslings vs non-breeders</i>					
	7	0.18	0.04	4.10	<i>P</i> < 0.05

plants (Fig. 5b and Table 2). For non-breeders, most of the points representing the % nitrogen in the diets at different available nitrogen contents fell very close to the line that represents the amount available to them. Thus, the nitrogen content of the diet of non-breeding adults was closely related to the availability of nitrogen in the plants. For parents, the lack of difference between dietary and available nitrogen was a reflection of the variability in their dietary content in relation to availability (note the relatively large standard error of difference in Table 2). Goslings, in contrast, selected a diet that was significantly higher in nitrogen than non-breeding adults and higher than the average nitrogen content available to them in their plant food (Fig. 5b and Table 2). Note that most of the open boxes representing the % nitrogen in the diet of goslings lie above the line representing the amount available to them in the plants. This occurred because goslings fed on marsh graminoids, which are higher in nitrogen than *Z. marina*, longer into the growing season than other geese.

Discussion

Interspecific variation in plant chemistry and feeding by geese

Canada geese at West Falmouth fed on grasses, rushes, eelgrass, and green algae and generally avoided forbs (Table 1). This pattern of selection was partly related to the much greater abundance of graminoids and partly to chemical defenses of forbs. Over 95% of the plant biomass in the habitat consisted of graminoids (R. Buchsbaum unpublished work), thus geese can harvest graminoids with much less effort than would be required to harvest scattered clumps of forbs. Abundance alone, however, does not explain the avoidance of forbs because geese will occasionally feed intensely on a less abundant marsh species if that species provides a sufficient nutrient reward (Buchsbaum et al. 1984). Forbs are often higher in nitrogen and soluble carbohydrates and lower in fiber than graminoids (Fig. 4 and Buchsbaum et al. 1984), thus would appear to be high quality foods, however a number of the more common forbs contain concentrations of tannins that are deterrent to geese (Fig. 4 and Buchsbaum et al. 1984). The complete avoidance of these plants by grazing geese even when they grow within patches of heavily grazed graminoids indicates that geese find them repellent.

The presence of tannins in less abundant salt marsh plants and their absence in more abundant plants contradicts the idea that tannins are more likely to be found in "apparent" plants (Feeny 1976, Rhoades and Cates 1976). Tannins might be particularly effective defenses against geese because the dominant plants in habitats where geese typically graze (i.e. grasslands and marshes) do not contain tannins. In general, we predict that herbivores of forests will be more tolerant of tannins than grassland herbivores because the dominant vegetation in forests tends to contain tannins (Swain 1979). Bernays and Chapman (1978), for example, found that the graminivorous grasshopper, *Locusta migratoria*, was more sensitive to tannins than closely related grasshoppers that had a more diverse diet. Thus the effectiveness of tannins in protecting a particular plant species against herbivory is determined to some extent by the types of defenses found in other members of the plant community.

Temporal variation in plant chemistry and feeding by geese

The dominant salt marsh graminoids, the submerged angiosperm, *Zostera marina*, and the green algae *Enteromorpha* spp. were all palatable to geese for at least part of the growing season. The switch from an early season diet dominated by marsh graminoids to a later season diet of *Z. marina* reflected the variations in the nutritional quality of the plants at different times of the year. Our measurements of soluble carbohydrates and nitrogen content (Fig. 3) indicated that the nutritional quality of the three marsh plants declined over the season. In contrast, the mid-summer increase in soluble carbohydrates in *Z. marina* may make it more nutritious at that time than in the spring. *Z. marina* is also substantially lower in fiber and higher in water content than the marsh plants (Figs. 3 and 4), thus may be more digestible than any of the marsh plants for most of the growing season.

Grasses often increase in palatability-reducing components such as fiber and phenolics over the growing season (Van Soest 1982; Berger et al. 1977; Hartley and Jones 1977). We did not observe consistent increases in fiber or phenolics in the marsh graminoids (Fig. 5). Other chemical changes, however, might contribute to the reduced palatability of marsh plants to geese. We have noted, for example, that *S. alterniflora* can accumulate up to 1% dry weight concentrations of aconitic acid, a TCA cycle intermediate, during the summer perhaps as a response to water stress (Buchsbaum 1985).

A certain minimum threshold water content may be necessary for a plant to be palatable. This would explain why *J. gerardi* is not consumed at all during the summer (Figs. 1 and 2) despite its chemical similarities to the other graminoids. *J. gerardi* flowers and starts to senesce about 6 weeks earlier than the two *Spartina* species in this study. Changes in its water content and the pattern of its consumption by geese reflects its phenology. Geese in Europe show a similar seasonal pattern of feeding on *Juncus* only early in the growing season (Owen 1980). In general, once a plant dropped below 60% water, it never constituted more than 10% of the diet of geese (Buchsbaum 1985). Water itself does not appear to be limiting, thus the effect of low water content in plants is likely to be related to increased difficulty in harvesting and swallowing such plants.

Changes in the nutritional needs of geese in relation to food choices

The impact of temporal and interspecific variations in plant chemistry must also be understood within the context of changes in the nutritional needs of a herbivore. The protein requirements of geese are higher in the spring than in the summer (Raveling 1979), thus the relatively low protein content of *Z. marina* compared to marsh graminoids explains why this species is not an important food source until summer. In the summer, geese often switch to a high carbohydrate diet, such as grains and seeds, as they build up energy reserves for fall migration (Raveling 1979). *Z. marina* contains soluble carbohydrate levels during the summer that are very similar to those of some grains and seeds (Van Soest 1969; Thomas and Prevatt 1980; McKey et al. 1981; Sedinger and Raveling 1984). Thus the switch from marsh plants to *Z. marina* during the summer by maritime

geese is dietetically similar to the switch to grains by geese in the interior of the continent (Owen 1980; Thomas and Prevatt 1980; Sedinger and Raveling 1984).

In addition to being a better source of digestible energy, *Z. marina* may also require less energy to harvest, particularly in midsummer. A greater percentage of the biomass of the submerged *Z. marina* is within reach of surface feeding herbivores as the plants grow toward the surface of the water during the season. In contrast, salt marsh plants are more difficult to harvest as the season progresses because more of their biomass becomes tied up in inedible stems.

Geese may need to include small amounts of some foods in their diets to meet requirements for micronutrients. For example, geese generally consumed a small amount (<10 of their feeding time) of the green algae *Enteromorpha* every survey day. This algae contains high concentrations of mineral nutrients (Ranwell and Downing 1959) that may not be present in other foods.

Differences in the plants selected by adults and goslings are influenced by nutritional considerations. Juvenile herbivores often show a greater selection for nitrogen than adults of the same species (Janzen 1979). Goslings in this study fed on salt marsh plants later into the growing season than non-breeding adults, probably to take advantage of the higher nitrogen content in these plants compared to *Z. marina* (Fig. 5 and Table 2). This choice is a trade off for goslings, since plants higher in nitrogen were lower in carbohydrates than the alternative. Sedinger and Raveling (1984) related preference for *Triglochin maritima* by gosling cackling geese (*Branta canadensis minima*) to the relatively high nitrogen content of this plant. Goslings in West Falmouth occasionally eat the leaves of *T. maritima* and *Iva frutescens* (Table 1), both of which are higher in nitrogen than plants that are regularly part of their diet (Buchsbaum et al. 1984).

Breeding arctic-nesting geese (particularly females) often go through a period of intense feeding ("hyperphagy") after their goslings hatch (Harwood 1977). This replaces nutrient reserves lost during migration and incubation. Parents at WFH spent less of their time feeding than either non-breeding adults or goslings (Buchsbaum 1985), thus did not exhibit the such post-breeding feeding. Feeding by parents at West Falmouth is probably governed by the selection of appropriate feeding sites for their goslings.

Factors other than plant chemistry and nutritional needs are likely to influence feeding choices by geese. The open water habitat in which *Z. marina* grows is a refuge from predators and other forms of disturbance, and thus may be a highly desirable feeding site. In contrast, geese prefer to avoid areas of tall grass (Owen 1975), as found in marshes in mid to late summer, perhaps because their ability to survey their surroundings is reduced. Safety may also have contributed to the relatively low amount of feeding on *P. pratensis* in the spring by goslings; the more vulnerable young birds would have had to graze further from the security of water. Thus the choice of a nutritious diet by geese is likely to be modified by the need to select a relatively undisturbed feeding site.

Our research indicates that geese track the chemical constituents of their food plants well. They select feeding sites where their favorite foods are the most abundant species and where they are moderately safe from disturbance. They avoid plants that have chemical deterrents. They respond to the declining quality of early season foods and to their

own changing nutritional needs by switching to another food source that has a different chemical profile.

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