# The role of phenolic compounds and other plant constituents in feeding by Canada geese in a coastal marsh

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**Summary.** We have assessed the relative importance of phenolic compounds, other secondary metabolites, and gross nutrient levels as feeding cues to Canada geese. Phenolic content was the most significant constituent influencing feeding selection by geese. Nutrient content had little or no effect on feeding selection.

Correlative data showing the negative influence of plant phenolics on food choices by wild geese were supported by feeding preference tests. Extracts of unpalatable plants inhibited feeding by captive geese relative to extracts of palatable plants. In high phenolic plants, the phenolic containing methanol extract was more inhibitory than extractions made with petroleum ether. In a relatively low phenolic, unpalatable plant, an inhibitory factor was extractable in petroleum ether, indicating that for this species, another class of deterrents was involved. Preference tests with individual secondary metabolites showed that tannic acid and quebracho tannin were very effective in inhibiting feeding by geese and phenolic acids were slightly inhibitory, but a sesquiterpene lactone was not deterrent. These results point out the primacy of some secondary metabolites in determining food choices by geese.

## Introduction

The acceptability of a plant as food for a herbivore is determined by a combination of feeding incentives and deterrents. Plant secondary metabolites often deter herbivores by rendering a plant unpalatable, indigestible, or toxic to herbivores (Swain 1977; Rosenthal and Janzen 1979). These secondary metabolites include a wide variety of basic chemical structures, such as alkaloids, phenolics, and terpenoids, which are functionally grouped together due to their ecological effects.

The few field studies on the influence of plant secondary metabolites on feeding by herbivorous birds have indicated that these substances may affect avian food choices. Low levels of deterrent phenolic and terpene resins were more important than high nutritional content in determining food choices by five species of subarctic browsing gallinaceous birds (Bryant and Kuropat 1980). The existence of "bird proof" varieties of sorghum high in tannins (McMillan et al. 1972) also indicates that some kinds of birds are repelled by these important secondary substances. In con-

trast, Moss (1972) found that red grouse (*Lagopus lagopus*) did not select heather relatively low in soluble tannins, but in his experiment the range of tannin content of the heather (only about 25%) may not have been large enough to affect feeding selection.

Geese are almost entirely grazers and in certain areas are the ecological counterparts of large grassland ungulates. They will often select patches of a given plant species that are higher in nitrogen (Lieff 1973; Harwood 1975; Owen 1975; Buchsbaum et al. 1981), but nitrogen content does not consistently explain the selection of some plant species over others (McFarland and George 1966; Lieff et al. 1970; Owen et al. 1977). Owen (1980) suggested that selection by geese is related to easily extractable energy content of plants rather than protein but that deterrent compounds in plants could also play a role.

In this paper we evaluate the relative importance of nutritional factors and secondary metabolites from salt marsh plants in determining food choices by Canada geese (*Branta canadensis*). The advantage of carrying out this study in the salt marsh is in the relative taxonomic (hence chemical) simplicity of the plant community. Our earlier studies (Valiela et al. 1979; Buchsbaum et al. 1981) and the phytochemical literature (Bate-Smith and Lerner 1954; Hegnauer 1977; Seaman 1982) have indicated that the major secondary metabolites in the dominant marsh plants are likely to be phenolic acids, tannins, and terpenoids. We have correlated plant nutrients and potential deterrents with feeding choices by free living geese and have tested the reaction of captive geese to plant extracts and isolated secondary metabolites added to foods.

## Materials and methods

### Field observations of feeding by geese

Field observations of feeding Canada geese were carried out in West Falmouth Harbor and adjacent salt marshes, including Great Sippewissett Marsh. This area is located on the east shore of Buzzards Bay in Falmouth, Massachusetts and is heavily used by a population of 30 to 70 Canada geese in the spring and summer. The most widespread plants in the marshes are the tall and short forms of *Spartina alterniflora* (Poaceae) in the regularly flooded intertidal zone and *Sp. patens* at higher elevations inundated less often. *Zostera marina* (Zosteraceae) grows in extensive subtidal beds.

From 1980 through 1983, seven full day and two half day surveys were carried out in May and June to determine the plant species eaten by Canada geese. At either hourly or half hourly intervals on each survey day, we used a spotting scope to record the number of geese feeding on each species of marsh plant. Since much of the vegetation in New England salt marshes occurs in monospecific stands, the species of plants eaten by geese can be identified by noting the exact location of the feeding. Where two or more plants co-occurred in a feeding area, it was possible to tell what the geese had eaten by looking for clipped plants after the geese had departed from the area. In these field feeding studies, we kept track of at least 30 individual geese on any survey day and made a total of 1553 feeding observations. We included approximately equal numbers of low, mid, and high tide periods of observation because tide height rather than time of day had the strongest influence on daily movements.

*Chemical analyses*

Fresh samples of 15 common marsh and estuarine plants and macroalgae were collected within 10 days of June 1. Since there are a number of distinctions between the two growth forms of *Spartina alterniflora* (Valiela et al. 1978) we included in our analysis a tall form of this species growing along a creek bank and a short form growing at a slightly higher elevation. *Poa pratensis* was also included because it grew in lawns immediately adjacent to the bay and was eaten by geese. Samples representing at least 50 leaves or thalli from 25 different individuals were immediately placed in plastic bags in the field to prevent water loss. The samples were weighed and dried at 45° C for 48 h (or to constant weight). Dried samples were reweighed to determine water content and then either ground immediately or stored at 4° C.

Dried plant material was ground through a 60 mesh screen in a Wiley Mill. Extractions for most chemical analyses were carried out in duplicate in 80% methanol at 80° C for 10 min at a concentration of 10 to 25 mg plant material/ml. Two sequential extractions were carried out on the same plant material and the supernatants pooled. Soluble constituents in this paper refer to compounds which are soluble in 80% methanol, except for soluble protein. Insoluble residues were saved for the fiber assay.

Soluble carbohydrates were determined by the phenol-sulfuric acid assay described in Strickland and Parsons (1972). Total soluble amino acids were determined using the ninhydrin reagent (Spies 1957). Soluble proteins were quantified by the Lowry et al. (1951) method after extracting 25 mg of dried plant material in a 5 mM phosphate buffer at pH 8.0 for 30 min at 37° C and then precipitating the proteins with 5% trichloroacetic acid at 4° C. Total nitrogen was determined with a Perkin-Elmer elemental analyzer.

Acid normal fiber analyses were modified from Allen et al. (1974). Residues from methanol extractions were washed first in methylene chloride:ether (3:1) and then in ether alone to remove all lipid soluble compounds. The dried residues were next hydrolyzed in 3% sulfuric acid at 100° C for 30 min. After cooling, rinsing the samples in distilled water, and drying, the residues were weighed, ashed, and reweighed. The percent fiber was calculated by comparing the weight of this residue corrected for ash with the initial weight.

Ash was determined gravimetrically after combusting ground plant material at 500° C for 3 h (Allen et al. 1974).

Total soluble phenolics in the aqueous methanol extract were determined by the Folin-Denis assay as described by Swain and Goldstein (1964). Ferulic acid (Sigma Chemical Company) was used as a standard for all plants that lacked tannins, and tannic acid (Fisher Chemicals) was used for *Limonium carolinianum*. Individual phenolic acids and related compounds were identified by paper chromatography as described in Harborne (1973) and by gas-liquid chromatography using a 200 cm by 2 mm i.d. glass column filled with 3% OV-25 coated on a 60–80 mesh Chromosorb W support (Vande Casteele et al. 1976). The temperature program ran from 100° C (5 min initial time) to 250° C at 6° C per min.

Tannin activity was quantified using the haemanalysis assay of Bate-Smith (1973). Proanthocyanidins (condensed tannins) were detected and measured spectrophotometrically after treatment in hot acidic alcohol (Bate-Smith 1975). Gallotannins and ellagitannins were determined by methods described by Haslam (1965) and Bate-Smith (1972) respectively.

*Feeding studies with captive geese*

All feeding selection experiments with captive Canada geese were designed as choice experiments between two types of food. Three to six geese participated in each experiment. The geese were deprived of food for 15 to 30 min prior to each experiment and were then presented with pre-weighed experimental foods in large clay bowls. Since our observations of Canada geese indicated that they spend at least half their day feeding, we felt that the short starvation period before beginning each experiment was sufficient to motivate them to feed. Two or three replicate bowls were used for each food type. The experiments were run for 1 h with less than four geese, and for 40 min with more than five. The position of bowls of the two food types were reversed halfway through each experiment. Fresh water was available at all times during these feeding trials. The geese fed readily in all experiments and often switched bowls and sampled different foods. Immediately after each experiment, the food remaining in each bowl was weighed to determine how much the geese had eaten. The results are presented as the mean of two or three replicate experiments.

Three different sets of experiments were carried out. In the first set of trials, we directly compared the palatability of different marsh plants. Two species of plants collected just prior to the feeding trials were chopped into 2 cm pieces and presented to the geese. The tests were standardized by using the tall growth form of *Sp. alterniflora* as one of the two choices in most tests. A bowl containing each plant species was kept outside the cage during feeding trials to measure weight loss due to evaporation.

In the second set of experiments, we investigated whether extracts of avoided plants could inhibit feeding by geese. Geese were presented with a highly palatable grass (*Poa pratensis* in most cases) that had been impregnated with extracts of different marsh plants. The petroleum ether extracts, which contain relatively non-polar compounds such as lipids and terpenoids, were prepared in a Soxhlet apparatus. The sample was continually refluxed with petroleum ether until the solvent was clear. Aqueous methanol extracts, which contained relatively polar compounds like

phenolic acids and polyphenols, were prepared by taking the residue from the Soxhlet extraction and heating it up to 80° C in 80% methanol, cooling it to room temperature, saving the supernatant, repeating the extraction, and pooling the two supernatants.

We impregnated as much control grass as the original weight of the marsh plants that had been extracted. Extracts in solvent were poured slowly over the chopped up grass in a flat Pyrex dish, and the grass mixed around to distribute the extract evenly. The solvent was then evaporated off at room temperature and the impregnated grass stored at 4° C in plastic bags until ready for use.

In the final set of experiments, isolated phenolic compounds present in avoided marsh plants were tested for their ability to inhibit feeding by geese. Compounds that were commercially available were added to a highly palatable grass using the same protocol as with the plant extracts. Concurrently, a set of controls was prepared in which solvent alone without any compounds was added to grass. In addition to the phenolics, helenin (alantolactone, Sigma Chemical Company), a sesquiterpene lactone, was also tested because *Iva frutescens* contains this class of compounds.

## Results

### Plant species selection by geese

Based on the number of feeding observations in May and June, Canada geese fed primarily on grasses, a rush, the submerged angiosperm, *Zostera marina*, and the green alga *Enteromorpha* spp. (Table 1). *Triglochin maritima* and *Iva frutescens* were eaten to a lesser extent. *Limonium carolinianum*, *Solidago sempervirens*, *Salicornia bigelovii*, *Sa. europaea*, and *Fucus vesiculosis* were avoided completely even in areas where other species were heavily grazed.

Feeding preference tests with captive geese confirmed the unpalatability of *L. carolinianum*, *So. sempervirens*, and *Sa. bigelovii* (Table 1). Both *L. carolinianum* and *So. sempervirens* were virtually ignored by captive geese just as they had been by wild geese. After an initial sampling period of several min with either of these two plants, the geese fed exclusively on *Sp. alterniflora* for the remainder of the experiment. We noted that when *L. carolinianum* and *So. sempervirens* were presented to the geese alone without the alternative choice of *Sp. alterniflora*, the geese would not feed on these plants after a short sampling period.

*Sa. europaea*, although not eaten by wild geese in May and June, was found to be of limited palatability to captives (Table 1). Captives ignored this plant in favor of *Sp. alterniflora* but ate it if it was offered along with *Sa. bigelovii* in the two choice experiments (Table 1, bottom), or if it was the only plant offered to them. In contrast, *Sa. bigelovii*, which has an obvious pungent odor, was completely avoided in the feeding trials (Table 1).

### Correlation of plant chemistry and feeding choices

Plants that were rarely or never eaten by geese were relatively high in total soluble phenolic content (Table 2). Using plant constituents from Table 2 as independent variables and number of feeding observations as the dependent variable, multiple regression analysis showed that phenolics had

Table 1. Feeding selection by wild and captive Canada geese on plants commonly occurring in the West Falmouth Harbor area. Selection by wild geese is expressed both as the number of feeding observations on each plant during surveys in May and June and as the ratio of the number of feeding observations for each plant relative to tall *S. alterniflora*. Selection by captive geese is expressed as the ratio of each plant eaten to the amount of tall *S. alterniflora* eaten in two choice experiments. Standard errors are in parentheses. In one set of feeding trials, feeding on *Sa. bigelovii* and *Sa. europaea* was compared

| Plant | Wild geese # observations | Wild geese selection ratio | Captive geese selection ratio |
|---|---|---|---|
| *Zostera marina* | 413 | 1.44 | 0.41 (0.15) |
| tall *Spartina alterniflora* | 286 | 1.00 | 1.00 |
| *Poa pratensis* | 235 | 0.82 | n.d. |
| *Enteromorpha* spp. | 142 | 0.50 | n.d. |
| *Juncus Gerardi* | 138 | 0.48 | 1.39 (1.33) |
| short *Spartina alterniflora* | 135 | 0.47 | 0.58 (0.20) |
| *Spartina patens* | 131 | 0.46 | 0.24 (0.04) |
| *Triglochin maritima* | 56 | 0.20 | 0.15 (0.07) |
| *Iva frutescens* | 16 | 0.06 | n.d. |
| *Phragmites communis* | 1 | <0.01 | n.d. |
| *Fucus vesiculosis* | 0 | 0 | n.d. |
| *Limonium carolinianum* | 0 | 0 | 0.03 (0.01) |
| *Salicornia bigelovii* | 0 | 0 | see below |
| *Salicornia europaea* | 0 | 0 | 0.004 (0.004) |
| *Solidago sempervirens* | 0 | 0 | 0.03 (0.01) |
| | | | ratio with Sa. europaea |
| *Salicornia bigelovii* | | | 0.04 (0.01) |

n.d. = not done

a significant negative relationship with feeding observations and explained more of the variation in feeding selection (33%) than any other constituent (Table 3). Soluble carbohydrates, which were positively correlated with feeding, explained an additional 14% of the variation in feeding selection after controlling for phenolics (Table 3). No other variable met the 0.15 significance level for entry into the regression model. No significant relationship was found between feeding selection and nitrogenous nutrients, even when soluble proteins and soluble free amino acids were substituted for total nitrogen as independent variables.

In characterizing the chemical nature of the phenolic compounds in uneaten plants, we found that *L. carolinianum* and *So. sempervirens* plus the brown alga *F. vesiculosis* had over 2% tannin acid equivalents as determined by an astringency test (Table 4). Lower levels of astringency were found in *I. frutescens* and *Phragmites communis* (Table 4), both of which were eaten less than 16 times by geese (Table 1). *L. carolinianum* gave positive results in tests for condensed tannins and gallotannins (Table 4). The cause of the astringency in *So. sempervirens*, *I. frutescens*, and *Ph. communis* was unclear since they did not contain any identifiable condensed or hydrolyzable tannins. Gas-liquid and paper chromatography of *So. sempervirens* showed that its high phenolic content consisted mostly of phenolic acid esters, of which about half were chlorogenic and isochlorogenic acids and the remainder *p*-coumaric and ferulic acids.

**Table 2.** Chemical analysis of leaves of plants from West Falmouth Harbor area. Leaves collected within 10 days of June 1. Values expressed as % dry wt. except for water content which is expressed as % fresh wt

| Plant | Soluble Pheno- lics | Total N | Ampro | Soluble Carbo- hydra- tes | Fiber | Ash | Wa- ter |
|---|---|---|---|---|---|---|---|
| *Zostera marina* | 0.37 | 1.24 | 0.88 | 11.90 | 30.4 | 34.6 | 81.5 |
| tall *Spartina alterniflora* | 1.09 | 2.68 | 2.20 | 2.45 | 33.1 | 12.9 | 78.0 |
| *Poa pratensis* | 1.50 | 2.38 | 2.80 | 4.83 | 60.6 | 11.6 | 70.6 |
| *Entero- morpha* spp. | 0.07 | 4.28 | 1.09 | 2.10 | 13.2 | 54.5 | 90.0 |
| *Juncus Gerardi* | 2.36 | 2.30 | 3.46 | 8.10 | 29.8 | 9.0 | 69.8 |
| short *Spartina alterniflora* | 2.10 | 2.60 | 4.08 | 2.20 | 32.5 | 9.5 | 80.7 |
| *Spartina patens* | 1.64 | 2.46 | 1.66 | 7.90 | 46.6 | 11.8 | 69.3 |
| *Triglochin maritima* | 3.19 | 3.83 | 8.66 | 5.40 | 19.9 | 15.3 | 80.4 |
| *Iva frutescens* | 6.44 | 4.70 | 14.00 | 5.56 | 28.3 | 22.8 | 85.8 |
| *Phragmites communis* | 1.57 | 2.88 | 3.05 | 5.44 | 55.0 | 5.4 | 69.1 |
| *Fucus vesiculosus* | 3.35 | 1.28 | 2.76 | 1.05 | 29.6 | 27.1 | 76.8 |
| *Limonium carolinianum* | 9.44 | 4.37 | 2.23 | 5.60 | 29.4 | 15.1 | 77.8 |
| *Salicornia bigelovii* | 2.80 | 1.40 | 2.15 | 2.04 | 26.6 | 42.5 | 90.2 |
| *Salicornia europaea* | 1.80 | 1.54 | 1.95 | 5.88 | 19.2 | 46.1 | 91.5 |
| *Solidago sempervirens* | 5.44 | 2.95 | 6.57 | 6.30 | 27.3 | 14.2 | 85.4 |

total N = total nitrogen; ampro = soluble proteins plus free amino acids; Plants listed in order of preferences of wild geese (Table 1)

**Table 3.** Stepwise multiple regression analysis of feeding selection by geese in relation to the chemical content of marsh plants. The number of feeding observations (from Table 1) was the dependent variable and the constituents listed in Table 2 were the independent variables. The variable "soluble protein plus free amino acids" (ampro) was not used in this analysis because it is closely related to total nitrogen content. The stepwise program of the Statistical Analysis System was used

| Step num- ber | Variable entered | Regres- sion coeffi- cient | $R^2$ | Increase in $R^2$ | Prob > F |
|---|---|---|---|---|---|
| 1 | phenolics | −29.0 | 0.33 | 0.33 | 0.026 |
| 2 | carbo- hydrates | 16.5 | 0.47 | 0.14 | 0.023 |

**Table 4.** Phenolic constituents from the leaves of some relatively unpalatable plants collected within 10 days of June 1. All values are in % dry weight. Astringency is in tannic acid equivalents. Proanthocyanins indicate the presence of condensed tannins

| Plant | Astrin- gency | Pro- antho- cyanins | Gallo- tannins | Phenolic acids and flavonoids |
|---|---|---|---|---|
| *Fucus vesiculosis* | 10.5 | 0 | | phloroglucinol |
| *Iva frutescens* | 1.3 | 0 | | not done |
| *Limonium carolinianum* | 10.1 | 6.28 | 6.48 | myricetin |
| *Phragmites communis* | 1.6 | 0 | | not done |
| *Salicornia europaea* | 0 | 0 | | chlorogenic acid p-coumaric acid ferulic acid |
| *Solidago sempervirens* | 3.8 | 0 | | chlorogenic acid isochlorogenic acid p-coumaric acid ferulic acid |

**Table 5.** Inhibitory effects of petroleum and methanol extracts of unpalatable marsh plants. Geese were presented with a choice between extracts of an unpalatable plant or a palatable control plant. Both extracts were added to *P. pratensis*. Extracts of *Sp. alterniflora* were used as the palatable control except in the experiment with *Sa. bigelovii* when *Sa. europaea* extracts were used. Percent inhibition calculated by subtracting the ratio of the percent of the unpalatable to the percent of the control extract eaten from 1. Standard errors are in parentheses

| Unpalatable plant extract added | Solvent used in extract | % con- trol extract eaten | %un- pal. extract eaten | % inhi- bition | G test |
|---|---|---|---|---|---|
| *L. caro- linianum* | petroleum | 45.0 | 55.0 | 0 (23.6) | NS |
| | methanol | 65.0 | 35.0 | 40.8 (21.3) | *** |
| *Sa. europaea* | petroleum | 56.9 | 43.1 | 12.1 (24.7) | NS |
| | methanol | 66.1 | 33.9 | 46.7 (18.0) | *** |
| *So. semper- virens* | petroleum | 57.5 | 42.5 | 24.7 (15.9) | NS |
| | methanol | 68.2 | 31.8 | 52.7 (9.9) | *** |
| *Sa. bigelovii* | petroleum | 73.3 | 26.7 | 61.5 (7.8) | *** |
| | methanol | 50.7 | 49.3 | 2.7 (4.3) | NS |

*** = $p < 0.005$, NS = not significant, heterogeneity G test (Sokal and Rohlf 1975)

### Responses of captive geese to plant extracts and isolated compounds

Aqueous methanol extracts of three relatively unpalatable plants, *L. carolinianum*, *So. sempervirens*, and *Sa. europaea*, all inhibited feeding by geese by about 50% when compared to the aqueous methanol extract of the palatable plant, *Sp. alterniflora* (Table 5). In contrast, petroleum ether extracts of *L. carolinianum* and *Sa. europaea* did not inhibit feeding by geese relative to that of *Sp. alterniflora* (Table 5). The petroleum ether extract of *So. sempervirens* caused
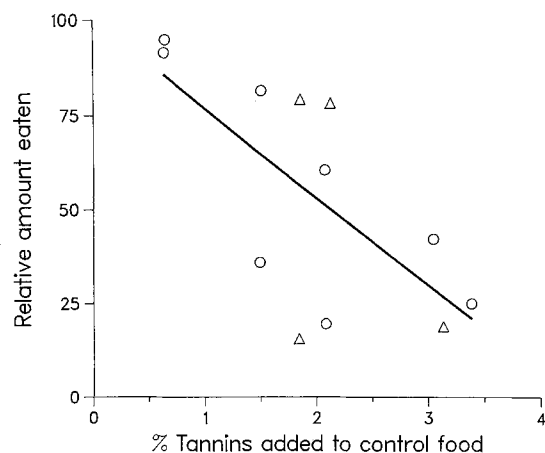
**Fig. 1.** Inhibition of feeding by geese caused by the addition of tannins to a palatable plant. Tannic acid or quebracho tannin (a condensed tannin) added to *Poa pratensis* as described in Materials and methods and then fed to captive Canada geese. Data expressed as the percent of the tannin impregnated grass eaten compared to a control of *P. pratensis* impregnated only with 80% methanol. o tannic acid, △ quebracho tannin

**Table 6.** Effect of phenolic acids and a sesquiterpene lactone added to *P. pratensis* and then fed to geese. Control grass was treated with solvent alone. Percent inhibition calculated as in Table 5. Standard errors in parentheses. G test symbols as in Table 5

| Compounds | Concentration by dry weight | % inhibition of feeding | G test |
|---|---|---|---|
| ferulic acid alone | 1% | 20.1 (1.8) | NS |
| ferulic acid + p-coumaric acid | 1% 1.5% | 17.7 (4.1) | NS |
| ferulic acid + p-coumaric acid + chlorogenic acid | 1% 1.5% 2.5% | 38.8 (17.4) | *** |
| p-coumaric acid alone | 1% | 2.0 (27.1) | NS |
| chlorogenic acid alone | 2.5% | 20.8 (11.7) | NS |
| helenin alone | 1% | 1.8 (6.1) | NS |

some reduction in feeding but the results were not statistically significant.

In the case of another unpalatable plant, *Sa. bigelovii*, the petroleum ether extract did inhibit feeding by 50% compared to the petroleum ether extract of its congener, *Sa. europaea* (Table 5). The aqueous methanol extracts of these two plants showed no significant differences.

Both hydrolyzable and condensed tannins (which are present in *L. carolinianum*) inhibited feeding from 30 to 75% above a threshold concentration of about 2% tannin (Fig. 1). Phenolic acids at their approximate concentrations in *So. sempervirens* generally caused less than 25% feeding inhibition, and this inhibition was statistically significant only when all three phenolic acids were present (Table 6). The sesquiterpene lactone helenin at 1% by dry weight had no effect on feeding by captive geese (Table 6).

In none of the feeding tests in which we added plant extracts or secondary metabolites to the food did we see as much rejection of the food as when the unpalatable plant

itself was presented to the geese (Table 1 vs Fig. 1 and Tables 5 and 6). Thus the whole plant is more distasteful to the geese than any of its isolated chemical extracts.

## Discussion

### Importance of secondary metabolites in feeding selection by geese

Our results support the hypothesis that the content of secondary plant metabolites rather than nutrients or digestibility is the best predictor of which marsh plants are most preferred by Canada geese. Geese tended to select plants low in soluble phenolic compounds and definitely avoided high phenolic plants. The geese were not simply selecting low phenolic plants such as *Sp. alterniflora* and *Z. marina* because these plants were more abundant than high phenolic plants in this coastal habitat. High phenolic plants and their extracts were also actively rejected by captive Canada geese in feeding preference trials.

Some species of marsh plants characterized by the presence of certain secondary metabolites were particularly unpalatable to geese. The unpalatability of *Limonium carolinianum* could be attributed to the presence of tannins, since the tannin-containing aqueous methanol extract of this plant inhibited feeding by geese (Table 5). In addition, the concentration of tannins in *L. carolinianum* (about 10% by dry weight) was much higher than the threshold concentration (about 2% tannin) required to inhibit feeding in experiments in which tannic acid or a condensed tannin were added to food (Table 6). This 2% threshold concentration is in accordance with the generalization of Feeny (1975) that a plant needs at least 2% dry weight of tannins to deter herbivores.

*Solidago sempervirens* was another uneaten, astringent plant, but it lacked typical condensed or hydrolyzable tannins. The phenolic acids present in this plant were not nearly as repellent as tannins and did not completely account for its unpalatability to geese. Diterpenoids are commonly found in *Solidago* spp. and may contribute to the unpalatability of *So. sempervirens* (Hegnauer 1977). Rhoades (1977) has suggested that a combination of low molecular weight phenolic and terpenoid compounds can function as protein precipitators, and thus explain the astringency of plants like *So. sempervirens* (and *I. frutescens*) that lack polyphenols. Our preliminary attempts to precipitate hemoglobin with the combination of the major phenolic acids of *So. sempervirens* plus polyphenol oxidase have thus far been unsuccessful.

*Salicornia bigelovii* was completely rejected by geese and was obviously less palatable than its congener, *Sa. europaea*. Although low in phenolics compared to other uneaten plants, *Sa. bigelovii* contained a lipid soluble deterrent (Table 5), possibly a terpenoid, which may be responsible for the pungent odor of this plant.

Despite the obvious repellent effect on geese of some plant compounds, there were two examples of geese showing tolerance to deterrents. Arrowgrass, *T. maritima*, which is cyanogenic and highly poisonous to sheep (Muenscher 1939), was occasionally eaten by geese in our study and is often heavily consumed during migration (Thomas and Prevatt 1980). Geese were also not repelled by 1% helenin, a sesquiterpene lactone such as those found in the marsh elder *I. frutescens* (Seaman 1982). In contrast, Picman et al.

(1982) found that only 0.05% helennin added to food inhibited feeding by tundra red back voles (*Clethrionomys rutilis*). At 1% or greater helenin concentrations, the voles refused to eat and starved. Thus geese can tolerate some plant compounds that herbivorous mammals must avoid.

Isolated plant extracts or pure secondary substances were never rejected as strongly as the unpalatable plant itself. Geese probably learn to associate distasteful compounds with other cues such as the texture and water content of the particular plant. Any synergistic effects of constituents in the intact plants may also have been eliminated when these constituents were fractioned.

*Hierarchies of feeding cues*

Our results indicate that selection of different species of marsh plants by Canada geese was largely determined by the content of plant defense compounds. Owen (1980) proposed that the most important basis for food choices is the digestible caloric content of the plant, however he did not look at the chemical defenses of plants against grazers. Although our multiple regression analysis indicated that 14% of the variation in feeding choices could be explained by soluble carbohydrates after phenolics were controlled, our results contradict his idea, in that (1) plants that were highest in soluble carbohydrates were not the most preferred species because they were frequently also high phenolics (Table 2), and (2) the higher fiber (and therefore presumably less digestible grasses) were generally favored over the low fiber succulent forbs, because the succulents such as *L. carolinianum*, *So. sempervirens*, and *Salicornia* spp. were protected by defensive secondary metabolites.

These contrasting observations on the feeding cues used by geese can be reconciled by considering that palatability is determined by a hierarchy of cues. For a plant species to be a dietary staple for geese, it must first of all be relatively low in deterrent secondary metabolites or other types of plant defenses. Acceptable plant species can be further discriminated by a second cue, nutrient content. Occasionally eaten plants like *T. maritima* and *I. frutescens* are intermediate between dietary staples and rarely eaten plants in levels of defensive chemicals. Geese are likely to detect the chemical deterrents in these plants and to eat them only if the plants contain either a large amount of nutrients or an essential micronutrient lacking in dietary staples. *T. maritima* and *I. frutescens*, for example, are both higher in total nitrogen than any plant eaten more often except *Enteromorpha* spp. Geese are also likely to tolerate at least low levels of the deterrents in these plants. Rarely eaten plants, however, are high enough in defensive chemicals to be completely unpalatable or toxic and are avoided even if high in nutrients. In summary the lower a plant species is in deterrent secondary metabolites, the more important nutrients become as feeding cues to geese.

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