

Feeding preference of an aquatic gastropod, *Marisa cornuarietis*: effects of pre-exposure

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Abstract. We evaluated factors that influence food preference of the giant rams-horn snail *Marisa cornuarietis* for two aquatic macrophytes, *Vallisneria americana* and *Ludwigia repens*. The effects of pre-exposure and time-of-year on differences in consumption of plant species were determined by means of laboratory feeding trials. Snails had higher rates of ingestion in November 1991 than February 1992, but composition of diet was similar between dates. *Marisa cornuarietis* exhibited a distinct preference for *L. repens* following pre-exposure to both plants or to only *V. americana*. In contrast, pre-exposure to only *L. repens* resulted in equal consumption of both macrophytes. To gain insight to the factors producing these patterns of consumption, apparent digestibility (=ingestion - egestion) of plant materials was evaluated by additional feeding trials, and phytochemical characteristics of *L. repens* and *V. americana* were determined by laboratory analyses examining: 1) polar + nonpolar soluble (labile), 2) acid-soluble (=cellulose + hemicellulose), 3) acid insoluble (e.g., lignins), 4) total phenolics, and 5) ash contents. The consumption of *L. repens* in higher amounts may be due to the higher apparent digestibility of *L. repens* than *V. americana*. *L. repens* has a higher concentration of holocellulose, which appears to be readily digested. Plant phenolics and ash contents did not differ between plant species. *V. americana* is reported to have higher nutrient concentrations than *L. repens*, which may explain why *M. cornuarietis* consistently consumed *V. americana* even though the latter plant species has lower apparent digestibility than *L. repens*.

Key words: optimal foraging, diet selection, *Marisa cornuarietis*, aquatic gastropod.

Foraging behavior has long been a major focus of inquiry in ecology because the consequences of feeding are intimately related to fitness (see review by Pyke et al. 1977, Stephens and Krebs 1986). Classical models of diet optimization (Schoener 1971) predict that foraging behaviors maximizing the intake of energy within time constraints will be favored by natural selection. However, foraging may deviate from optima predicted on an energetic basis because of other physiological or environmental constraints (Pulliam 1975). For instance, diet choice of an herbivore may be constrained by nutrient requirements or digestive limitations (Owen-Smith and Novellie 1982). In fact, Vadas (1982) found that food preference of sea-urchins was not correlated with energy content of plants, but instead was correlated with the efficiency of digestion. Similarly, avoidance of plant toxins may constrain diet choice, as is well demonstrated for both terrestrial and aquatic herbivores (Freeland and Janzen 1974, Hay and Fenical 1988). For example, brown algal poly-

phenolics and tannic acid consistently deterred feeding by marine herbivores (Steinberg 1988). Clearly, plant chemistry, in terms of caloric content, nutritional quality, and toxin content, is important to food selection by herbivores (Boyd 1970, Hay and Fenical 1988, Newman et al. 1990).

The giant rams-horn snail, *Marisa cornuarietis* L. (Ampullariidae) is an excellent subject for studying the foraging behaviors of freshwater gastropods. *Marisa cornuarietis* is a large (40-60 mm diameter) discoidal prosobranch gastropod that recently was introduced from South America into the San Marcos and Comal Rivers of Central Texas (Jobin 1970, Neck 1984). This snail grazes voraciously on *Ludwigia repens* Forst. and *Vallisneria americana* Michx., dominant macrophytes in the Comal River (Horne et al. 1992). Aquatic macrophytes were considered to be minor components of the diet of herbivores (Hutchinson 1975, Gregory 1983) until recent studies documented that macrophytes are subject to substantial grazing losses (Sheldon 1987, Lodge 1991). This is not surprising, because many aquatic plants contain high concentrations of nitrogen, an essential nutrient for her-

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bivores (Mattson 1980). However, freshwater macrophytes generally have high water and ash contents that decrease the nutritional value on a per wet weight basis. High ash content also may interfere with digestion and absorption of nutrients (Muztar et al. 1978). Moreover, many aquatic macrophytes contain secondary compounds that could reduce grazing (Su et al. 1973, Ostrofsky and Zettler 1986), including tannins that may decrease the assimilation of plant nutrients (Feeny 1976) and negatively affect the growth and survival of herbivores (Manuwoto and Scriber 1986).

Little is known about the chemistry of *Ludwigia repens*, an important dietary constituent of the giant rams-horn snail in the Comal River. Terry and Tanner (1986) estimated nitrogen and phosphorus contents of *L. repens* at 1.7% and 0.4% of dry mass, respectively, which are lower than reported values for nitrogen (1.7–4.07%) and phosphorus (0.16–0.62%) in *Vallisneria americana* (Riemer and Toth 1969, Muztar et al. 1978). In addition, *V. americana* contains several secondary compounds that may affect herbivore grazing, including alkaloids, steroids, tannins, and saponins (Su et al. 1973, Ostrofsky and Zettler 1986, Cheng and Riemer 1989).

The goal of this study was to examine the diet choice of *M. cornuarietis* under laboratory conditions. Specific objectives were to determine: 1) if this snail exhibits food preference for *L. repens* or *V. americana*, 2) if pre-exposure to either plant modifies subsequent diet composition, and 3) if plant chemistry (i.e., fiber, ash, or tannin contents) is related to patterns of ingestion.

Methods

Adult snails (>30 mm shell diameter) and macrophytes were collected from the Comal River near San Marcos, Texas. Animals were collected in autumn, 1991, numbered uniquely, maintained at 20°C in aerated 80-L aquaria, and offered a mixture of *Ludwigia repens* (Lr) and *Vallisneria americana* (Va) for consumption. Leaves and stems were clipped from submergent plants every two weeks, placed in aerated aquaria at 20°C, and turned daily. Previous experience showed that plants maintained in such a manner remain in good condition for about two–three weeks, but begin to decay after three weeks. Water in all aquaria was changed weekly

and the laboratory was illuminated for 12 h per day.

Food preference and the effects of pre-exposure on consumption

The effects of pre-exposure on subsequent diet selection by *M. cornuarietis* were evaluated with two sets of feeding trials; the first set was conducted in November 1991 and a second set in February 1992. At both times, each trial consisted of three treatments, determined by the combination of plant species used for pre-exposure. In the control treatment, 4–6 snails were randomly selected from those obtained from the field (see above), and each snail was placed in a separate 4-L aquarium and pre-exposed to both Lr and Va. In the other two treatments, pre-exposure was restricted to a single food type, Lr or Va. In all cases, the pre-exposure period comprised four consecutive days. The response period included the four days immediately following pre-exposure, at which time equal quantities (~0.5 g wet mass, blotted to remove excess water) of Lr and Va were offered simultaneously to each snail. Mean daily food ingestion was measured as milligrams dry mass of Lr or Va eaten per day, with plant material replaced each day. Food preference was evaluated by comparing the quantities of Lr and Va ingested. A total of 18 snails were examined in November ($n_1 = 18$) and 16 snails in February ($n_2 = 16$).

Phytochemical analyses

Solubles, holocellulose, and lignin.—The carbon chemistry of Lr and Va were determined according to Moorhead and Reynolds (1993). Within one week of collecting leaves of Lr and Va from submergent plants growing in the Comal River, the leaves were cleaned of debris, and gently washed by hand with a soft brush under flowing water to remove epiphytic growth. Six samples of each plant species were oven-dried at 60°C to constant mass. Dried samples were ground to pass through a USDA standard #40 mesh screen size (~300 μ m grid) and 0.25 g of each dried sample was used for chemical analysis. Each sample was transferred to a 50-mL centrifuge tube, to which was added 15 mL of distilled water. Samples were then placed in a sonicating water bath at 60°C for 30 min. Following sonication, the samples were centri-

fuged for 20 min at 15,000 rpm to facilitate separation of soluble from insoluble materials. The supernatant was removed and this procedure was repeated three times. The nonpolar soluble fraction of each sample was extracted with ethanol in the same manner. After polar and nonpolar solubles were extracted, the samples were dried at 60°C for 24 h and the residues (consisting of fiber) were weighed. Total soluble content was estimated as the difference between initial sample mass and residue mass after extraction.

Cellulose and hemicellulose fractions (=holocellulose) were hydrolyzed by sulfuric acid digestion (Effland 1977). Following ethanol extraction, the residues were placed in separate 125-mL flasks; 2 mL 72% sulfuric acid was added to each, and flasks were incubated at 30°C for 1 h. Distilled water (56 mL) was added to each flask, and the resulting mixture was autoclaved for 1 h at 120°C. The samples then were suction filtered through 1- μ m membrane filters, and oven-dried overnight at 60°C. The remaining material (consisting primarily of lignins) was weighed and holocellulose content was estimated as the difference between residue mass after extraction of solubles and residue mass after acid digestion.

Dry mass and ash.—Five plants of each species were dried at 60°C for 48 h to obtain a dry mass to wet mass ratio that subsequently was used to convert all data measurements to dry mass. Dried samples were placed in pre-weighed crucibles and ashed in a muffle furnace at 500°C for 6 h to determine ash content.

Soluble polyphenols (total phenolics).—Crude tannin extracts were prepared from dried leaves of Lr and Va, using the method of Schultz et al. (1981), slightly modified. For each species, six replicates of 0.1 g were placed in centrifuge tubes; 3.5 mL methanol-water solution (1:1, by volume) was added to each, and the tubes were placed in a water bath at 77–80°C for 1 h. After extraction, all samples were centrifuged for 20 min at 15,000 rpm to facilitate separation of soluble from insoluble materials, and the supernatant was collected.

The total content of phenolic compounds in sample extracts was measured by the Folin-Denis technique (Swain and Hillis 1959, Schultz et al. 1981), using tannic acid as a standard. One mL of sample extract was added to 1 mL of Folin-Denis reagent; after 3 min, 1 mL of 2N NaHCO₃

was added as a fixative. After 60 min, absorbance was read at 725 nm against a blank of equal parts distilled water, Folin-Denis reagent, and NaHCO₃. The results then were compared to absorbance values obtained for standard solutions of tannic acid ranging between 0.01 and 0.1 mg/mL.

Efficiency of dietary use.—A nutritional index, "approximate digestibility" (AD), was used to assess host plant use (Calow and Calow 1975):

$$AD = [(I - F \times 100)/I] \quad (1)$$

where I is milligrams (dry mass) of food ingested, and F is milligrams (dry mass) of feces produced. AD was calculated separately for Lr and Va, using the following procedure. Six-seven snails were starved for 3d; then each was transferred to a 2-L separate container (10 cm diameter), and subsequently fed a pre-weighed quantity of one plant species until satiated. Remaining plant materials were removed from the containers and the total amount of food ingested (I) by each snail was estimated as the reduction in dry mass of plant matter. For each snail, feces then were collected daily by suction filtering the water in containers through 1- μ m membrane filters. The filters were oven-dried at 60°C to determine the total mass of feces (F) produced over four days (no feces were observed after four days).

Statistical analyses

Consumption of Va is not independent of consumption of Lr for a particular snail, necessitating a statistical approach similar to that of a paired *t*-test, rather than a simple *t*-test or one-way analysis of variance (ANOVA), to detect treatment effects on diet composition. Had no treatment factors (pre-exposure regime or time) been employed in our research, a univariate paired *t*-test appropriately would evaluate the existence of preference for Lr or Va. However, our experiments were specifically designed to assess the effects of both pre-exposure treatment (Lr and Va together, Va only, or Lr only) and time (November or February) on subsequent consumption of Lr and Va, so we conducted two-way ANOVA with repeated measures (see also SPSS 1988, Sandlin and Willig 1993). The repeated measures ANOVA and subsequent pairwise comparisons of the effects of pre-exposure regime on preference were performed

TABLE 1. The results of repeated measures ANOVA to detect the effects of pre-exposure and time on the differences between consumption of *Ludwigia repens* (Lr) and *Vallisneria americana* (Va). df = degrees of freedom, MS = mean square, F = F -statistic, p = significance of two-tailed test.

| Source | df | MS | F | p |
|---------------------------|----|--------|-------|--------|
| Between-subject effects | | | | |
| Time (T) | 1 | 270.23 | 18.33 | <0.001 |
| Pre-exposure (E) | 2 | 83.07 | 5.64 | 0.009 |
| T × E | 2 | 24.08 | 1.63 | 0.213 |
| Within | 28 | 14.74 | | |
| Within-subject effects | | | | |
| Consumption (C) | 1 | 557.58 | 29.38 | <0.001 |
| C × T | 1 | 161.13 | 8.49 | 0.007 |
| C × E | 2 | 170.64 | 8.99 | 0.001 |
| C × T × E | 2 | 48.73 | 2.57 | 0.095 |
| Within | 28 | 18.98 | | |
| Pairwise comparisons of E | | | | |
| (Lr + Va) vs. (Va) | 1 | 10.20 | 0.69 | 0.413 |
| (Lr + Va) vs. (Lr) | 1 | 121.82 | 8.26 | 0.008 |
| (Va) vs. (Lr) | 1 | 52.73 | 3.58 | 0.069 |
| Within | 28 | 14.74 | | |

using SPSS-X Program MANOVA (SPSS 1988). Interspecific differences in phytochemistry and digestibility (% dry weight, % lignin, % holocellulose, % ash, % tannin, and % digestibility) between Lr and Va were analyzed with t -tests.

Results

Food preference and ingestion patterns

Marisa cornuarietis does exhibit preference in the selection of food types. Based upon within-subject factors in the repeated measures ANOVA (e.g., ingestion of Lr and Va by the same individual), significant differences in consumption existed between Lr and Va, confirming preference in food choice (Table 1). Moreover, the consumption pattern (i.e., amounts of Lr and Va ingested) was affected consistently by time as well as by pre-exposure (significant two-way interactions of time by ingestion and pre-exposure by ingestion in the absence of a three-way interaction). Snails ate absolutely more plant material during the November trials than they did in February, but the relative amounts of Lr and Va eaten were consistent within each pre-exposure treatment (Fig. 1). Relative inges-

tion of Lr was greater than that of Va in the control group and in the Va pre-exposure group, whereas Lr and Va were preferred equally when snails were pre-exposed only to Lr. A posteriori tests confirmed that pre-exposure to Va or to both Lr and Va (control) affected ingestion patterns in a similar way, whereas pre-exposure to Lr resulted in a different pattern.

Phytochemical analyses

Va contained significantly less holocellulose and lignin than did Lr, and based upon approximate digestibility, Lr can be digested almost twice as efficiently as can Va (Table 2). Although ash content of the plant species was similar, a t -test revealed differences approaching significance. In contrast, the difference between Lr and Va in dry mass to wet mass ratio and in total phenolics (as a percentage of dry mass) was not significant.

Discussion

A fundamental assumption of optimal foraging theory is that all other factors being equal, a food type, if included in the diet, is eaten in proportion to its "availability". This occurs because organisms are assumed to be able to fulfill all other nutrient requirements while maximiz-

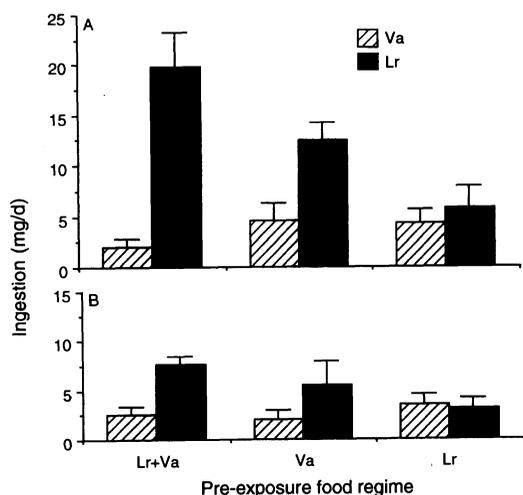


FIG. 1. Mean (± 1 SE) ingestion of Lr and Va by an individual *M. cornuarietis* following pre-exposure regimes (Lr = *Ludwigia repens*, Va = *Vallisneria americana*); A.—November, B.—February.

ing the acquisition of some critical limiting resource, such as energy. Nonetheless, it is well known that nutrient constraints can alter foraging behavior and diet composition, especially in folivores. Clearly, chemical attributes of plants affect foraging by herbivores; consequently we compared chemical features of Lr and Va in an effort to uncover the factors underlying food preferences of *M. cornuarietis*. In particular, we wish to understand: 1) why Lr generally was preferred over Va, and 2) why Va was consumed at all.

The fiber content (=holocellulose + lignin) of Lr significantly exceeded that of Va, and high concentrations of fiber can reduce the digestibility of plant material. However, both Lr and Va contained less than 55% fiber, the critical level reported to limit voluntary intake or lower dry matter digestibility (Ingalls et al. 1965). In our study, Lr was preferred under control conditions, Lr contained 30% more holocellulose than did Va, and the digestibility of Lr was almost twice that of Va (Fig. 1). Since gastropods exhibit cellulase activity (Calow and Calow 1975), *M. cornuarietis* may be able to derive more energy from plants like Lr, which have high cellulose content, than those containing less cellulose (e.g., Va). Preference for Lr would be consistent with a foraging strategy that tends to emphasize energy acquisition.

In the present study, *M. cornuarietis* generally ingested more Lr, but consistently exhibited partial preference (proportional ingestion less than proportional availability) for Va when both Lr and Va were offered in equal abundance. This suggests that diet composition was determined by more than one factor. Our observations are consistent with the presence of nutrient constraints on feeding behavior, as has been demonstrated for other herbivores (Pulliam 1975, Belovsky 1978, Willig and Lacher 1991, Sandlin and Willig 1993). Aquatic herbivores may prefer macrophytes with high protein ratios (Mattson 1980, Lodge 1991) and Va is reported to have higher concentrations of nitrogen and phosphorus than does Lr (Riemer and Toth 1969, Terry and Tanner 1986). The partial inclusion of Va in the diet of *M. cornuarietis* may result from the existence of nutritional needs exceeding those that can be met by consuming Lr, in spite of the apparently higher energy content of Lr.

All of the essential nutritional requirements

TABLE 2. Mean values (standard errors) for the chemical composition of *Ludwigia repens* (Lr) and *Valisneria americana* (Va), as per cent of dry weight, and results of *t*-tests evaluating differences in chemistry between plant species. All values were arcsin transformed for statistical analyses; *p* values for two-tailed tests.

| Variable | Lr (%) | Va (%) | <i>p</i> |
|-----------------|--------------|--------------|----------|
| Cellulose | 44.10 (1.20) | 29.5 (0.70) | <0.001 |
| Lignin | 8.40 (0.50) | 5.80 (0.40) | 0.001 |
| Ash | 9.26 (1.03) | 11.78 (0.56) | 0.063 |
| Dry weight | 9.91 (0.45) | 8.72 (0.80) | 0.231 |
| Digestibility | 52.23 (3.40) | 25.62 (3.00) | <0.001 |
| Total phenolics | 0.25 (0.03) | 0.29 (0.02) | 0.280 |

of an organism must generally be supplied by the composite diet of that organism. For this reason, foraging behavior may demonstrate both a clear preference and persistent partial preferences, as we observed for *M. cornuarietis*. We hypothesize that *M. cornuarietis* met the bulk of its energy needs in this study by the ingestion of the preferred Lr and yet required a minimum quantity of Va to supply other nutrients. This hypothesis is consistent with the demonstrated higher digestibility of Lr, and reported higher N and P contents of Va. Furthermore, the responses of *M. cornuarietis* to the various pre-exposure regimes are consistent with this supposition. Given that animals are generally more efficient at storing excess energy than in sequestering nutrients, such as N and P (e.g., Hill and Wyse 1989), pre-exposure to a food type containing high nutrient content would not be expected to have much impact on subsequent food choice. In our study, food choice following pre-exposure to only Va did not differ from food choice of the control group. In contrast, food choice following pre-exposure to a food type containing much available energy but few other nutrients should favor an increase in the subsequent consumption of nutrient-rich foods. When *M. cornuarietis* was pre-exposed to only Lr, subsequent foraging showed no difference between ingestion rates for Lr and Va, i.e., the amount of Va eaten increased relative to the quantity of Lr.

Other factors may affect foraging patterns of herbivores as well. For example, the high ash content of aquatic plants (in comparison with most terrestrial plants) reduces the concentra-

tion of organic matter, and may interfere with digestion and absorption of energy-contributing compounds. Differences in ash content of Lr and Va approach significance, and may have contributed to the lower consumption of Va by *M. cornuarietis*. Also, feeding preference of aquatic herbivores is sometimes related to the avoidance of plant defenses (Newman et al. 1990, Lodge 1991, Newman 1991, Newman et al. 1992). However, no significant difference was demonstrated between the total phenolics (tannin) content of Lr and Va. In addition, neither of the plant species had high quantities of phenolics, suggesting that both plants can be tolerated in large amounts (Steinberg 1988). Presence of other secondary compounds (e.g., alkaloids, steroids, and saponins) may be responsible for lower consumption of Va (Ostrofsky and Zettler 1986); unfortunately, comparable data are not available for Lr, so such views are conjectural.

In conclusion, preference patterns in *M. cornuarietis* may be a result of higher digestibility or higher holocellulose content of Lr compared with that of Va, but not a result of the avoidance of plant phenolics. Partial preference of Va is consistent with the hypothesis that *M. cornuarietis* forages under nutrient constraints. If *M. cornuarietis* forages optimally with respect to both energy and nutrients, it may balance the high energy supply of Lr with high nutrient content of Va. This leads to foraging patterns that demonstrate both a clear preference for one plant (Lr) and a consistent, partial preference for the other plant (Va). Seemingly complex changes in foraging pattern following different pre-exposure regimes may result from the differential capacities of organisms to store nutritional requirements.

Acknowledgements

This work contributed to the partial completion of Master of Science degree requirements for Ms. Özlen K. Grantham at Texas Tech University. We wish to thank J. M. Burns, M. K. Rylander, and T. L. Arsuffi for providing critical input and reviewing the manuscript. Also, we would like to thank M. Skalberg and T. L. Arsuffi for assistance with field collections and for sharing unpublished data.

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Received: 17 March 1993

Accepted: 1 September 1993