Effects of Age, Sex, Prior Experience, and Intraspecific Food Variation on Diet Composition of a Tropical Folivore (Phasmatodea: Phasmatidae)

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ABSTRACT Recent attention in ecology has focused on factors that influence the foraging behavior of herbivores. We evaluated responses to different arrays of food plants exhibited by an abundant folivore within the tabonuco forest of Puerto Rico. Previous work indicates that the walkingstick *Lamponius portoricensis* Rehn forages on a limited array of plant species and selects habitats that contain high densities of *Piper treleaseanum* Britton & Wilson. We designed three separate experiments to evaluate (1) if walkingsticks of different ages or of different sex have different food preferences, (2) if previous exposure to only one food type affects subsequent diet composition, and (3) if walkingsticks distinguish among leaves of different quality from the same plant. Four plants [*Dendropanax arboreus* (L.) Decne & Planch, *Piper hispidum* Sw., *P. treleaseanum*, and *Urera baccifera* (L.) Gaud.] known to be forage for this insect were used in food choice experiments. Multivariate analyses revealed that, at different ages, males and females exhibit different patterns of consumption. Likewise, preexposure to only one food influences subsequent diet differently depending upon preexposure regime and sex. In addition, preferences are shown for different qualities of leaves within single forage species. In particular, lower (older) leaves of *P. treleaseanum* are preferred, whereas leaves of *D. arboreus* and *U. baccifera* are eaten indiscriminately. These results are consistent with the contention that herbivores forage within nutritional constraints. In addition, walkingsticks distinguish between plant species, recognize differences in leaf quality associated with age or position, and modify their diet to reflect past experience.

KEY WORDS herbivory, nutrient constraints, *Lamponius portoricensis*

THE CENTRAL THEME of classical optimal foraging theory (OFT) is that natural selection maximizes the rate of uptake of some critical currency (e.g., energy) (Pyke et al. 1977). As such, an organism should eat only those foods that confer the greatest net benefit, and the choice to consume particular foods should be based solely upon the relative abundances of foods of greater value. The theory assumes that a forager can rank foods according to net benefit and that less beneficial foods are consumed only if sufficiently compensated by an increase in encounter rate resulting from increased diet breadth. Food types included in the diet should be consumed in proportion to their encounter rates.

A continuing debate exists regarding the merits of studies conducted to test these predictions (Otte 1975, Fox 1981, Taghon 1981, Lacher et al. 1982, Stephens & Krebs 1986). In particular, Schluter (1981) stated that the energetic basis for OFT may be erroneous and contended that it is unrealistic to assume that a forager is able to assess relative abundances of foods or is capable of making optimal decisions based upon food ranking. Similarly, Belovsky (1984) considered the strict energetic optimization approach naive. Predictions made by OFT have been falsified by empirical studies in natural (Belovsky 1984 and references therein), seminatural (Lacher et al. 1982), and artificial conditions (Kaufman & Collier 1981). In general, only equivocal evidence supports the simplified classical approach. Stephens & Krebs (1986) considered numerous factors that cause foragers to behave contrary to classical predictions. The most commonly studied of these factors concerns nutrient constraints (e.g., Cates 1980, Strong et al. 1984, Vitousek 1985, Forno & Semple 1987, Willig & Lacher 1991).

Consumers often face conflicting demands regarding food choice, and herbivores must assess more variables to determine food selection than do other consumers (Stephens & Krebs 1986). Herbivore diets may comprise many foods because food quality of any one food type is rela-

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tively low (when compared with food quality for carnivores) and one food type rarely will provide all essential nutrients for survival (Pulliam 1975, Joern 1979, Milton 1979, Cates 1980, Taghon 1981, Belovsky 1984, Stephens & Krebs 1986). Similarly, the presence of toxic compounds can modify the value of foods that are otherwise nutrient rich (Strong 1988). Many herbivores acquire a balanced diet by consuming a variety of plant species.

Differences in quality of various parts of the same plant may be important determinants of food choice, and intraspecific patterns of resource allocation vary among plant taxa (Milton 1979). Herbivores may therefore feed in only one region of a plant. For instance, leaf miners feed and oviposit more often on apical leaflets than on older (lower) leaves on unexploited alfalfa hosts (Quiring & McNeil 1987). Old leaves generally contain higher fiber content and greater lignin concentrations than young leaves, and the former may become less palatable as a result of prior herbivore damage. For these reasons, Milton (1979) proposed that young leaves may be preferred over older ones.

Prior feeding experience may strongly influence subsequent ability to utilize some host plants (Karowe 1989). Some degree of induced preference exists as a consequence of habitat or oviposition site selection (Stanton 1982, Quiring & McNeil 1987, Papaj & Prokopy 1988). Food selection often is based upon larval experience or physiological specialization (Otte 1975, Redfearn & Pimm 1988, Karowe 1989). In addition, previous encounters with a food may constitute a measure of abundance or apparency, and this may be one of the most critical factors affecting food selection (Cates 1980).

Individual variation in diet composition may exist within a population (Cates 1980, Karowe 1989) or change through time as a function of age, sex, or morphology (Gustafsson 1988) of the consumer. Different nutrients or different proportions of nutrients may be required during different developmental stages. For example, most insects have complex life cycles, including metamorphosis with attendant niche shifts. If individuals of different ages have different nutrient requirements, then diet composition may be age-specific.

The order Phasmatodea (walkingsticks and leaf insects) contains >2,500 externally chewing folivorous species (Strong et al. 1984) that occur worldwide in both temperate and tropical regions. Most are nocturnal and often mimic plant parts or other organisms (e.g., scorpions [Bedford 1978]). Their fundamental survival strategy is crypsis, although they exhibit a variety of predator-avoidance behaviors. Many are polyphagous and show distinct feeding preferences. Walkingsticks reach sufficient numbers to damage forests severely in some regions

(Bedford 1978) and may be key agents in maintaining forest dynamics and ecosystem stability (Lowman 1984, Brokaw 1985, Collins et al. 1985, Schowalter 1985, Brown et al. 1987). Nonetheless, little basic research has been done concerning the biology and ecology of the Phasmatodea.

Lamponius portoricensis Rehn is nocturnal and the most abundant walkingstick in the Luquillo Experimental Forest (LEF) of Puerto Rico (Van Den Bussche et al. 1989, Willig & Camilo 1991). It occurs in high densities within light gaps throughout the tabonuco forest (Willig et al. 1986). It is an important species because of its abundance and longevity (Willig et al. 1986). Previous work with *L. portoricensis* revealed that individuals differ in food preference, that considerable daily variation exists in the composition of an individual's diet, and that diet composition depends on sex (Willig et al. 1986, Sandlin Smith 1989; M.R.W., unpublished data). A recent study regarding habitat selection (Willig et al. 1993) has shown that these walkingsticks differentially prefer habitats that contain high densities of *Piper treleaseanum* Britton & Wilson, a common light-gap shrub.

We were interested in learning how age or sex, previous exposure to only one food, or intraspecific food variation influence diet composition. Although phasmatids do not exhibit complex metamorphosis, they are paurometabolous and undergo between four and eight molts. Reproductive organs are present only in adults. Male and female walkingsticks may have different growth rates (Bedford 1978), and young individuals may have different diets that reflect either lack of experience (Price 1984), differences in morphology, or different nutritional requirements. As adults, walkingsticks experience additional reproductive constraints (especially females), and these constraints may require different nutrients. *L. portoricensis* is wingless, has limited mobility within a patch (Willig et al. 1986), and may not forage as if it is familiar with the food composition of the entire landscape (Stephens & Krebs 1986). Previous exposure to forage species within limited home ranges may provide the sole basis for resource evaluation. We evaluated if previous experience with only one food item influences subsequent diet composition. Plants frequently concentrate secondary defense compounds (e.g., tannins, phenols, alkaloids) within topmost (newest) shoots and leaves to protect them from herbivore damage (Strong et al. 1984, Salisbury & Ross 1985). Within an individual plant species, some leaves may be less suitable as food, and this variation may be detected by a forager. Thus, we assessed if differences in leaf quality affect food selection by *L. portoricensis*.

Materials and Methods

Collection and Maintenance. Specimens were captured from various light gaps near El Verde Field Station within the LEF. This forest is classified as Subtropical Wet Forest (Ewel & Whitmore 1973), is dominated by *Dacryodes excelsa* Vahl. (tabonuco), has been intensively studied (Gines et al. 1984), and is extensively described by Brown et al. (1983). Each walkingstick was marked with a unique symbol, and total length from tip of the head to end of the abdomen was measured to the nearest millimeter. Walkingsticks were acclimated to laboratory conditions in glass terraria before they were subjected to feeding trials. All terraria were maintained at ambient temperature and humidity; in addition, twigs were provided so that walkingsticks could climb and rest. Food in acclimation terraria was suspended from wire-mesh covers. Each walkingstick was placed individually into a 12.5 by 30.0 by 32.5 cm compartment within a terrarium during feeding trials and given a suite of food choices on each of 3 d.

All plants used in the food choice experiments occur naturally in light-gap areas of the forest and were collected from the same vicinity as were walkingsticks. Walkingsticks commonly are found foraging on four plant species in the forest (Willig et al. 1986): a midsuccessional canopy tree, *Dendropanax arboreus* (L.) Decne & Planch (Araliaceae); two species of shrub, *Piper hispidum* Sw. and *P. treleaseanum* (Piperaceae); and a woody shrub, *Urera baccifera* (L.) Gaud. (Urticaceae). Both species of *Piper* have similar physiognomic structure and are early successional colonists of light gaps. *D. arboreus*, when it occurs in light gaps, is a sapling. *U. baccifera* usually grows as a tall branch from prostrate stems in rocky outcroppings. Considerable intra- and inter-individual variation in leaf quality may exist within each of these four food types (Belovsky 1986). Leaves with extensive insect damage were not used, and no more than two leaves were taken from the same plant on any given night to ensure broad representation of available forage substrate in the laboratory experiments.

Feeding Trials. For each 3-d feeding trial, walkingsticks were given single 500-mg portions of leaves placed atop wire-mesh platforms early in the night. This amount of food is in excess of average nightly consumption for an individual adult (M.R.W., unpublished data). Individuals were only used in a single feeding trial. Leaf area was measured using a portable area meter (Model 3000, LI-COR, Lincoln, NE) in conjunction with a LI-COR LI-3050A transparent belt conveyor assembly (resolution: 1 mm^2; accuracy: ± 1% for 10-cm^2 samples) before each trial. Unconsumed leaf area was measured early the following morning while walkingsticks were inactive.

Experiment 1. Age- and Sex-Specific Variation. Based on head-to-abdomen length, nymphs were classified into three age categories (S1, 10–37 mm, $n = 24$; S2, 38–60 mm, $n = 24$; S3, 61–75 mm, $n = 24$). Classification as adults ($n = 24$) was based upon total length measurements (≥ 79 mm; Willig et al. 1986) or evidence of copulatory behavior. Adults and nymphs were presented with all four foods for at least three nights before use in food choice experiments. Feeding trials consisted of presenting individuals with equal masses (500 mg) of *D. arboreus*, *P. hispidum*, *P. treleaseanum*, and *U. baccifera* leaves on each of three consecutive nights. Individuals that did not eat during two consecutive days or that molted during a feeding trial were not used in the food choice experiments.

Experiment 2. Variation Due to Preexposure. The effects of limited preexposure to only one of the four food types on subsequent diet composition were evaluated separately for each food in a series of experiments. Control individuals were maintained in acclimation terraria and presented with all four foods for at least 10 nights before feeding trials. Individuals for each preexposure treatment (i.e., *D. arboreus* alone, *P. hispidum* alone, *P. treleaseanum* alone, or *U. baccifera* alone) were fed exclusively one of the four foods for 10 consecutive nights. For each preexposure or control treatment, eight adult males and eight adult females constituted the experimental population. One female died during the *D. arboreus* preexposure; as a result, only seven females were used in that experiment. Feeding trials consisted of presenting individuals with equal amounts (500 mg) of *D. arboreus*, *P. hispidum*, *P. treleaseanum*, and *U. baccifera* leaves for three consecutive nights. All members of a particular preexposure group were measured simultaneously. To maintain equal sample sizes for all treatments (i.e., a balanced statistical design), average consumption values for each plant species exhibited by the seven females in the *D. arboreus* preexposure group were substituted as these values for the dead female.

Experiment 3. Intraspecific Food Variation. Adults were fed all four foods for at least three nights before feeding trials. Eight males and eight females were used in each treatment group. A treatment consisted of presenting individuals with equal amounts (500 mg) of top, middle, and bottom leaves of one of the four foods for three consecutive nights. Top leaves were considered to be the first fully expanded leaves on any of the four plant species. Bottom leaves that were relatively undamaged were chosen as the lowest (or oldest) leaves. Middle leaves were those not satisfying these criteria.

Statistical Analyses. The original data represent the area of a 500-mg portion of leaf before (B) and after (A) feeding by a single walkingstick. However, in addition to area lost as a result of

Table 1. Annotated results for averaged univariate and multivariate repeated measures analysis of variance of proportional consumption data from an experiment showing age-specific variation in food choice (food is the within-subjects factor; sex and age are the between-subjects factors)

Source of variation	Averaged univariate approach					Multivariate approach	
	df	SS	MS	F	P	Wilks lambda	P
Food	3	8.46	2.82	39.31	<0.001	0.080	<0.001
Sex × food	3	0.32	0.11	1.51	0.213	0.948	0.200
Age × food	9	1.09	0.12	1.69	0.092	0.839	0.081
Sex × age × food	9	2.00	0.22	3.09	0.002	0.793	0.016
Within	264	18.93	0.07				

leaf consumption, A reflects area lost because of desiccation. We adjusted A for this confounding effect. Five additional sets of 500-mg leaf portions (for each type of leaf used in the experiment) were cut each night, placed in wire-mesh containers, and measured the next morning with those pieces that were offered to walkingsticks. The average proportion of area lost from these five sets of leaf portions and any 500-mg portions left undisturbed by walkingsticks represents the average leaf area lost by desiccation alone. This value, unique to each type of leaf for each night of a feeding trial, was subtracted from 1.00 to obtain a value (C) representing the average proportion of leaf remaining after desiccation. The quantity Y is the total mg of leaf (for each type of leaf in the experiment) eaten by a walkingstick on one night of a feeding trial and is given by

$$Y = [B - (A/C)]B^{-1}\,(500\,\text{mg}).$$

Thus, the quantity in brackets, the corrected value for A, represents the adjusted leaf area consumed by a walkingstick. Values for Y were calculated using unique Cs for daily leaf area measurements collected. The resulting values of Y for each leaf type offered over the 3 d were converted to 3 d percentage consumption data for each insect. These data were used in all subsequent analyses. By using percentage consumption data, variation in the quantities eaten because of size differences among individuals was eliminated, with the data standardized by adjusting consumption of each food by total daily consumption of all foods. Individuals occasionally did not forage on one of the three nights and this standardization over the 3 d circumvents the problem of treating zero consumption of four foods on a single night as indicative of equal preference. Also, this method does not require mean substitutions (which might misrepresent actual consumption of individuals) to maintain equal sample sizes.

In the foraging experiments, the data contain repeated, and thus nonindependent, measures for a given individual (e.g., food type and leaf position). Hence, repeated measures analysis of variance was performed using SPSS-X statistical software package (SPSS 1988). Tests for sphericity (to detect repeated measures heteroscedastic-

ity) were performed using the Mauchly sphericity test. Both averaged univariate and multivariate tests were performed by SPSS-X procedure MANOVA. Averaged univariate approaches to repeated measures analyses are sensitive to deviations from underlying assumptions. We therefore evaluated sphericity via the Mauchly sphericity test with $\alpha = 0.10$ to have greater power at detecting deviations that could confound interpretations of subsequent analyses.

Results

Only the multivariate analyses are meaningful because significant heteroscedasticity characterized the data (chi-square approximation of Mauchly sphericity test W: $P < 0.001$ for age-specific variation and preexposure experiments; $P = 0.075$ for the intraspecific variation experiment), and they form the basis for subsequent discussion. Nonetheless, averaged univariate results are in accord with multivariate results in all but one case.

Effects of Age- and Sex-Specific Variation. Multivariate tests showed a significant ($P = 0.016$) three-way interaction (sex by age by food), indicating that the sexes responded differently to the four food types during different times in their life cycle (Table 1). Regardless of the age or sex of walkingsticks, D. arboreus, P. hispidum, and U. baccifera each constituted at least 10% of the diet, whereas P. treleaseanum consistently represented a minor proportion, except in the diet of S3 males (Fig. 1), where it exceeded 10% and was equal to that of P. hispid um. Patterns of food consumption exhibited by males and females, as well as by different age groups, are complex. For example, the proportional representation of P. hispidum in the diet decreased with increasing age for males but remained relatively constant for females. Similarly, D. arboreus was a major dietary component (>25%) for all age and sex groups, except S1 males, for which it constituted <15% of the diet. In this last case, P. hispidum dominated, representing >50% of the diet.

Specific trends are more easily delineated by considering one food at a time. D. arboreus consumption patterns differed markedly between males and females. Percentage consumption by
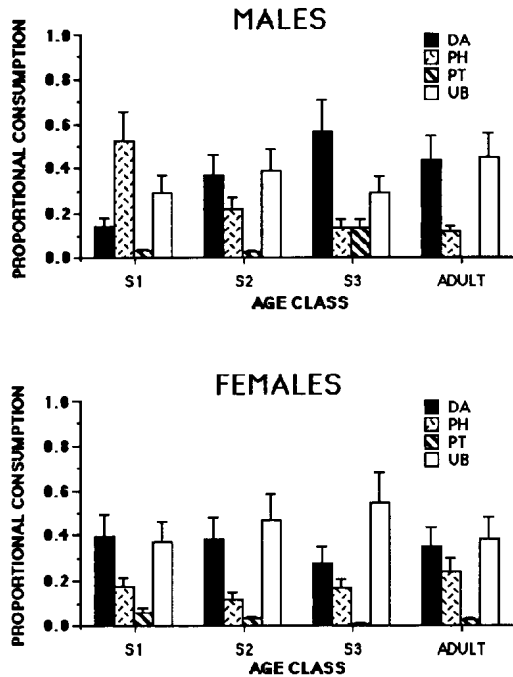
Fig. 1. Bar diagrams showing average proportional consumption by L. portoricensis of four foods offered during feeding trials for each age class and sex. Lines above each bar represent standard errors. DA, Dendropanax arboreus; PH, Piper hispidum; PT, P. treleaseanum; UB, Urera baccifera; S1, smallest size class of nymphs; S2, intermediate-sized nymphs; S3, largest nymphs; adult, adult walkingsticks. See text for exact lengths for size classes.
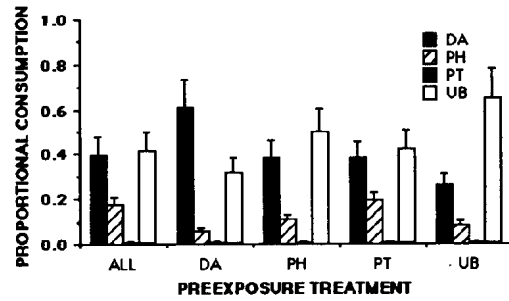

Fig. 2. Bar diagram showing average proportional consumption by adult L. portoricensis of four foods offered during feeding trials for each preexposure treatment. The sexes are combined to show only significant groups for the two-way interaction between preexposure and food. Lines above each bar represent standard errors. All, preexposure to all four foods (control); DA, Dendropanax arboreus; PH, Piper hispidum; PT, P. treleaseanum; UB, Urera baccifera.

males increased with age, whereas all age categories of females consumed relatively equal amounts of this food. Older males consumed less P. hispidum, but females ate the same amounts or, if anything, increased the proportion of P. hispidum in their diet as they aged. Patterns of P. treleaseanum consumption were comparable for all groups (except S3 males), with P. treleaseanum being the least preferred food; it did not contribute to the diet of adult males and figured only minimally in the diet of females. Urera baccifera consumption remained fairly constant for both sexes; however, the proportion of U. ac-

cifera in the diet was generally greater for females than for males. Consumption of U. baccifera predominated in the diet, especially for males, and it was more consistently favored than was D. arboreus. These results unequivocally demonstrate that food selection in L. portoricensis is affected by the walkingstick's age and that males and females differ in the manner in which food selection changes with age. Nonetheless, P. treleaseanum was the least consumed food for any age or sex class and was, therefore, the least preferred food (of those offered) of L. portoricensis.

Effects of Preexposure. The manner in which males and females modify their diet in response to different preexposure regimes is complex (Table 2) as indicated by two significant two-way interactions but a nonsignificant three-way interaction. Preexposure to one particular food type affected subsequent patterns of consumption in the same fashion for males and females, as indicated by the significant interaction between food and preexposure (Fig. 2). Compared with controls, preexposure to U. baccifera resulted in increased consumption of U. baccifera and decreased consumption of P. hispidum. Similarly, preexposure to D. arboreus resulted in decreased consumption of P. hispidum and an

Table 2. Annotated results for averaged univariate and multivariate repeated measures analysis of variance of proportional consumption data from an experiment showing effects of preexposure on food choice (food is the within-subjects factor; sex and preexposure are the between-subjects factors)

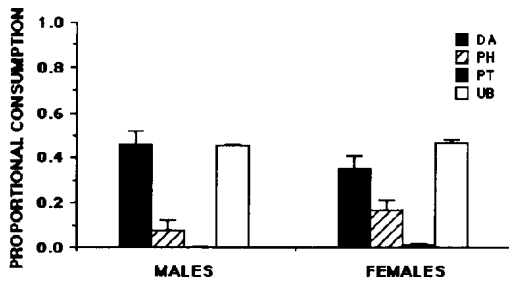| Source of variation	Average univariate approach					Multivariate approach	
	df	SS	MS	F	P	Wilks lambda	P
Food	3	11.55	3.85	115.77	<0.001	0.003	<0.001
Sex × food	3	0.43	0.14	4.35	0.005	0.750	<0.001
Preexposure × food	12	2.21	0.18	5.53	<0.001	0.584	<0.001
Sex × preexposure × food	12	0.77	0.06	1.93	0.032	0.795	0.190
Within	210	6.99	0.03				

Fig. 3. Bar diagram showing average proportional consumption by adult *L. portoricensis* of four foods offered during feeding trials for each preexposure treatment. The preexposure groups are combined to show only significant groups for the two-way interaction between sex and food. Lines above each bar represent standard errors. DA, *Dendropanax arboreus;* PH, *Piper hispidum;* PT, *P. treleaseanum;* UB, *Urera baccifera.*

Fig. 4. Bar diagram showing average proportional consumption by adult *L. portoricensis* of three leaf types offered during feeding trials. The sexes are combined to show only significant groups for the two-way interaction between species and position. Lines above each bar represent standard errors. DA, *Dendropanax arboreus;* PH, *Piper hispidum;* PT, *P. treleaseanum;* UB, *Urera baccifera.* Bottom, middle, and top refer to leaf position on a plant.

enhanced representation of *D. arboreus,* compared with the situation in the control group. Preexposure to either species of *Piper* did not strongly modify consumption patterns from that of the control.

Regardless of preexposure regime, the sexes differed in their proportional consumption of the four food types, as indicated by the significant sex by food interaction (Table 2). This sex-specific difference in consumption patterns most likely was associated with a greater consumption of *P. hispidum* and reduced consumption of *D. arboreus* by females as compared with males (Fig. 3). Relationships within the data are intricate; however, the observed consumption patterns clearly demonstrate that previous experience with only one food item influences subsequent food choices.

Effects of Intraspecific Variation in Food Quality. The significant species by position interaction in the analyses (Table 3) reveals that the degree to which presumptive intraspecific differences in plant quality affect consumption depends on the particular forage plant and that these effects are consistent in both males and females (i.e., no significant three-way interaction). In general (Fig. 4), both sexes indiscriminately consumed top, middle, and bottom leaves of *P. hispidum,* strongly preferred top leaves to middle or bottom leaves of *P. treleaseanum,* and
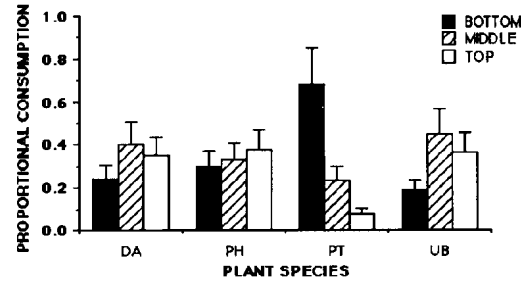
may have slightly avoided bottom leaves compared with top or middle leaves in the case of *D. arboreus* or *U. baccifera.* Results from this experiment show that *L. portoricensis* perceives and responds to differences (or their absence) in the quality of leaves representing different positions (ages) on forage plants and that this response is species-dependent.

Discussion

Stephens & Krebs (1986) considered special features of herbivores that make them unusual consumers, noting that they face problems regarding foraging strategies that others do not. In some cases, generalist herbivores have relatively complex diets to meet nutritional requirements (Belovsky 1984) while avoiding plant defenses. As a result, diets are characterized by partial consumption of a few or many plant species, even when abundances of foods should favor specialization according to the predictions of classical OFT (Lacher et al. 1982; Willig & Lacher 1991; M.R.W., unpublished data).

Our results consistently obviate the contention that *L. portoricensis* forages in a manner consistent with the predictions of OFT. Never were all four foods equally consumed. This was true when dietary choices were interspecific (experi-

Table 3. Annotated results for averaged univariate and multivariate repeated measures analysis of variance of proportional consumption data from an experiment showing variation in intraspecific food choice (leaf position is the within-subjects factor; sex and plant species are the between-subjects factors)

Source of variation	Averaged univariate approach					Multivariate approach	
	df	SS	MS	F	P	Wilks lambda	P
Position	2	0.16	0.08	2.00	0.141	0.919	0.099
Sex × position	2	0.07	0.03	0.85	0.432	0.959	0.320
Species × position	6	3.79	0.63	15.78	<0.001	0.299	<0.001
Sex × species × position	6	0.32	0.05	1.33	0.251	0.856	0.193
Within	112	4.49	0.04				

ments 1 and 2) or intraspecific (experiment 3), despite controlling for the effects of other factors such as sex and age (experiment 1), previous exposure (experiment 2) or plant species (experiment 3). Clearly, the failure of *L. portoricensis* to forage optimally (sensu OFT) here and elsewhere (M.R.W., unpublished data) is, at least in part, dictated by environmental or genetic factors beyond those considered herein. Nonetheless, our results are consistent with predictions based upon nutritional constraints and may be interpreted in light of a number of contemporary paradigms in ecology.

Foraging decisions may reflect sex-related constraints. Adult female walkingsticks are consistently larger than adult males (Willig et al. 1986), a pattern found commonly in phasmatids that may be explained by an additional instar in females (Bedford 1978). This instar might account for differences in abundance between females and males (in all studies with *L. portoricensis*, field-capture rate of females was lower than that for males [see Willig et al. 1986]) and for lower survivorship by females. Differences in life history between the sexes could select for dietary divergence such as that elucidated here. Most females in this experiment were laying eggs continually and thus were potentially functioning with nutritional requirements different from those of males. Females consistently included small amounts of *P. treleaseanum* in their diet, regardless of previous treatment (preexposure or acclimation), whereas males usually excluded this food from their diet. One likely explanation is that females are more nutrient-limited than males because of their relatively higher reproductive investment; they may obtain a portion of their nutritional requirement from *P. treleaseanum*.

The manner in which diet composition changes with age is different for males and females. Otte (1975) found that first and late instars of three species of *Schistocerca* (Orthoptera: Acrididae) exhibited differences in food preference; Blaney & Simmonds (1988) demonstrated that cues for food selection, and thus, food selection itself, changed between young and adult butterflies. Similarly, older individuals of the Indian walkingstick, *Carausius morosus* Stål, are more selective than are younger individuals (Cassidy 1978). The overall trend in female *L. portoricensis* is for the diet to remain broadly based throughout. Conversely, in males, *P. hispidum* is gradually eliminated from the diet, while *D. arboreus* and *U. baccifera* become dominant. Because adults move more than do nymphs (Willig et al. 1986), they may be better able to select only their preferred foods and exhibit a narrower diet. If nutritional requirements for walkingsticks change as they mature and are sex-specific, and if different nutrients are obtained from different plants (Otte 1975, Belovsky 1984,

Stephens & Krebs 1986), then the observed patterns of food consumption require no further explanation.

Preexposure for only a short time affects subsequent food consumption patterns in adult *L. portoricensis*. Others (Papaj & Prokopy 1988, Redfearn & Pimm 1988, Karowe 1989) have shown that variation in feeding habits of adults reflects previous events as a consequence of induced preferences or physiological specialization throughout an individual's lifetime. We did not address previous exposure from earliest instar to adult; thus, our results probably are not a product of physiological specialization during the preexposure time. However, an induced preference is exhibited by walkingsticks preexposed to either *D. arboreus* or *U. baccifera*.

Extrapolations to Foraging Ecology. The differences in leaf quality from a single plant species may be nutrient-related or may reflect changes resulting from prior leaf damage (Forno & Semple 1987), with older leaves likely to show signs of increased damage and lowered nutritional content. Although young leaves may be more nutritious, Cates (1980) remarked that young leaves of many species may have the highest concentrations of defense compounds and that leaves of early successional plants harbor fewer toxins than do comparable leaves of later successional plants. In addition, he proposed that individuals of mono- and oligophagous species should respond better to these toxins than should polyphagous species. Thus, polyphagous insects should prefer to eat leaves that have the lowest levels of defense compounds—specifically, older leaves on any plant, and leaves of early successional plant species. *L. portoricensis* seems to forage according to these considerations, although not entirely.

The production of defense compounds may be related to the successional stage of a plant. Early successional plants concentrate energetic efforts on rapid vegetative growth and early reproduction, devoting less energy to chemical protection (Cates & Orians 1975, Otte 1975). Mid and late-successional trees, when in light gaps, may be characterized by rapid growth and thus be more palatable as saplings because of lower concentrations of defense compounds (Baldwin & Schultz 1988). Cates (1980) found that polyphagous herbivores preferred mature leaf tissue and leaves of mid and late-successional plants. According to Cates' definition, *L. portoricensis* is a polyphagous species because it consumes foods from three or more plant families. *D. arboreus* and *U. baccifera* are characterized as midsuccessional plants (Perez 1988), and *P. hispidum* and *P. treleaseanum* are early successional plants (Brokaw 1985). Our results partially corroborate those of Cates: *L. portoricensis* distinctly prefers mature leaves of an early successional plant, *P. treleaseanum*, and does not discriminate among

leaves of midsuccessional species such as *D. arboreus* and *U. baccifera*. In contrast, *L. portoricensis* shows an overall preference for the midsuccessional species, *D. arboreus* and *U. baccifera*. These plants may contain substitutable currencies—foods that confer equivalent benefits (Stephens & Krebs 1986). Perhaps *D. arboreus* and *U. baccifera* are foods of equal value, are perceived as indistinguishable, or both offer unique dietary components required in roughly equivalent amounts. Moreover, the choice of which plant to consume may be related to properties such as masticability and fiber, nutrient, or toxin content. Both *P. hispidum* and *P. treleaseanum* have relatively thick leaves and may be less suitable for chewing, require an increased number of foraging bouts because of volumetric constraints, or require excessive handling time. It is likely that considerable variation in the nutritional quality exists among these plants. Future studies of relative nitrogen, phosphorus, tannin, lignin, cellulose, and carbon contents of these plants and assessments of the relative toxicity of secondary metabolites will serve to resolve these questions.

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