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TESTING MODELS OF OPTIMAL DIET ASSEMBLY BY THE GENERALIST HERBIVOROUS LIZARD *CNEMIDOPHORUS MURINUS*¹

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Abstract. The diet of the predominantly herbivorous Bonaire Island whiptail lizard (Teiidae: *Cnemidophorus murinus*) was examined to assess three models of diet selection by generalist herbivores. These models were: single-nutrient maximizing, toxin avoiding, and nutritional wisdom. At three sites we gathered data on the diet of the lizard over a full year (both wet and dry seasons), on the relative abundance of all plant food types available to the lizards during that period, and on the nutritional composition of each plant type. Thirteen nutritional variables were measured, including content of energy, protein, minerals, water, and potentially toxic plant secondary compounds, and digestibility of protein.

The lizards were generalist feeders, consuming a wide variety of flowers, fruits, leaves, nectar, and some animal material. Most stomachs contained more than one food type, suggesting *C. murinus* typically samples several kinds of plant materials each day. The lizards were selective with regard to foods eaten; most foods were not taken in proportion to their availability in the environment. Potential plant foods varied in nutritional quality, but no one nutrient was correlated with dietary preferences. Multivariate analysis revealed that preference or avoidance of a potential food type could be predicted by a combination of nutritional properties, but these differed among sites. Despite differing plant assemblages at each site, annual intake of nutrients by the lizards was similar among sites. The results best support the nutritional wisdom hypothesis; the Bonaire whiptail lizard may assemble its diet to obtain the proper balance of required nutrients, while avoiding dangerous levels of plant secondary compounds.

Key words: Bonaire Island; *Cnemidophorus murinus*; food preferences; generalist herbivores; herbivory; nutritional wisdom; optimal diets; plant toxins; tropical lizards.

INTRODUCTION

The theory of optimal diets usually regards energy as the currency to be maximized during an animal's selection of foods, and assumes that fitness of foraging animals is proportional to energy profit (Stephens and Krebs 1986). Organisms obviously do not consist only of energy, but this simplification in the theory is tolerable if concentrations of all vital nutrients in food items are positively correlated. Food types can then be ranked from low to high quality based on the availability of a single nutrient. This appears to be the case for animal foods because foods drawn from different species of animals are fairly uniform in their nutritional content, with each different food item (different species) possessing approximately the necessary requirements of its consumer (Needham 1964). The classical theory of optimal diets, therefore, focuses on zoophagous animals. In fact, the authors of the founding paper on optimal diets (MacArthur and Pianka 1966) considered insectivorous birds and lizards as their

model organisms (E. R. Pianka, *personal communication*).

In contrast, classical optimal diet models may not apply to herbivores. Plant foods are far more variable in their overall nutritional quality among species than are animal food types. The ratios of energy, protein, water, minerals, and toxins typically vary substantially among species of plants and different tissue types (leaves, flowers, fruit) on the same plant (Needham 1964, Maynard and Loosli 1969). For example, fruits may be high in easily digested sugars, but low in protein; some leaves may be relatively low in available energy content, but high in protein. So, for herbivores, no single nutrient can be used as an indication of the overall quality of any food type. In addition, many plants contain toxic compounds that render them impossible or very expensive to process (Freeland and Janzen 1974). Such plants may be unavailable for consumption by a herbivore, even if they contain needed positive nutrients.

Small herbivores, such as insects, that remain on a single plant during their feeding life, possess specialized digestive adaptations to extract or synthesize all needed nutrients from their host plant. Because of the large surface area of their gut compared to their mass, they

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can process large quantities of food to obtain rare nutrients. In contrast, large herbivores have relatively small guts, typically are more mobile, and have a more generalized diet (Westoby 1978). These facts argue that the rules for efficient foraging by generalist herbivores must be more complex than those used by specialist herbivores or zoophagous animals.

Three models have been presented to explain the assembly of generalist herbivore diets: single-nutrient maximizing, toxin avoiding, and nutritional wisdom (reviewed by Milton 1979, Schoener 1986, Stephens and Krebs 1986). We examine these models with a study of the diet of a small herbivorous lizard, the Bonaire Island whiptail, *Cnemidophorus murinus* (Teiidae). This lizard is a generalized herbivore and occurs in large numbers in the dry, vegetatively simple habitats of Bonaire, Netherlands Antilles. We gathered data on the natural diet of the Bonaire whiptail over a full year, the relative abundance of all plant food types available to the lizards during that period, and the nutritional composition of each plant type. Our goal was to determine which general model of diet selection best matches the feeding behavior of these lizards. The results provide the most detailed data and analysis of the diet of any herbivorous reptile and a rare opportunity to test simultaneously the available hypotheses on diet assembly by a generalized vertebrate herbivore.

MODELS AND PREDICTIONS

Single-nutrient maximizing.—Generalized herbivores select foods simply to maximize the intake of one nutrient (i.e., energy or protein) while being constrained by one or a few other simple nutritional requirements (avoidance of toxins, or obtaining sufficient sodium, for example) (Belovsky 1978, 1984, 1986, Stephens and Krebs 1986). This model requires that plants might vary in nutritive value, but items high in one nutrient tend to be high in most others (Arnold 1981). There should be strong preference for food types rich in some important nutrient (energy or protein). Linear programming would allow a predictive analysis that includes simple nutritional constraints. This single-nutrient maximization model presents predictions similar to those of classical optimal diet models, including preferences based on a single nutrient and expanding dietary diversity as preferred food types decrease in abundance. Sampling of newly available food types to determine if they are superior to the currently preferred best food would be expected, but the overall dietary diversity should still be very low. That is, during any single day's foraging, the preponderance of the diet should consist of the current best food type.

Toxin avoiding.—This model stresses the importance of plant secondary compounds as a dietary constraint (Freeland and Janzen 1974). The model predicts regular sampling of food types as they become available, but new foods should be taken in very small

quantities; hence, dietary diversity could be fairly low. Food preference should be strongly correlated with the presence or absence of plant toxins. Presence of "negative" nutrients of plant toxins would be the primary factor shaping a herbivore's diet, far more important than the "positive" nutrients of protein, minerals, or energy-rich compounds.

Nutritional wisdom.—This hypothesis assumes that different plant food types vary in the ratio of nutrients present. Thus, the dietary unit of a large generalized herbivore is not a food item or meal, but a cluster of meals, and the diet is assembled to assure a proper mix of nutrients while avoiding dangerous levels of toxic compounds (Westoby 1974, 1978). Some food types may be similar in their nutritional composition and are treated as alternatives in the diet, some others may be complementary if their nutrients interact, and others may be taken in threshold amounts to meet a dietary requirement or constraint.

This model predicts that generalist herbivores should sample food items to update continuously their information about potential resources if plant types appear and drop out of the environment over time. Although the forager should prefer some foods over others, the proportion of a preferred food item in the diet should never reach unity, regardless of its abundance (there are no single foods that can meet all nutritional needs). The generalist must obtain all essential nutrients from a variety of plant types, so no one nutrient should be highly correlated with food preferences. Dietary diversity should be broad. Diet preferences may change abruptly over time as plant types appear in the environment (for example, when flowers or fruit of different species appear), and differ over space in different floral communities. Last, the overall nutritional intake of the herbivore populations in different locations should be similar, despite differing floral communities in those environments. This last prediction makes the reasonable assumption that the nutritional requirements are the same for all populations of the herbivore and the animals will seek out the same nutritional balance at sites with differing kinds of potential foods.

These models clearly represent differences in emphasis, rather than exclusive hypotheses. As more and more nutritional requirements and constraints are added to the single-nutrient maximization model, it approaches the nutritional wisdom image. The toxin-avoiding model simply emphasizes the constraint of plant secondary compounds over other nutritional needs. Nonetheless, different predictions emerge, depending on the dietary elements being stressed. The single-nutrient maximizing and toxin-avoiding models predict fairly simple correlations between some nutrients or toxin and diet preferences that would be consistent over time and space, whereas the nutritional wisdom model argues for multiple nutrients being balanced and differences among sites and times in multiple correlations of nutrients and diet preferences.

Sampling is expected under all of the hypotheses, but dietary diversity should be greatest under the nutritional wisdom model because of both extensive sampling and the need to take a mixture of nutrients. During periods when the environment is less productive of potential foods (dry season, for example), the single-nutrient maximizing hypothesis predicts increasing diversity of foods taken, whereas this is not necessarily expected under the other two hypotheses. Under the toxin-avoiding model, a particular toxin avoided in one location should be avoided by animals at other sites, but the nutritional wisdom model predicts that toleration of toxins in some places may be necessary to obtain some rare positive nutrient.

Each model has its advocates who have presented data supporting a favored view (see *Discussion*). Researchers unfortunately have usually attempted to test only one of these competing hypotheses (for example, Schall and Ressel 1991), and rarely gather all necessary data to distinguish among the views (but see Milton 1979 for a model study).

STUDY SITES AND METHODS

Study areas

The study was conducted on the Caribbean island of Bonaire in the Netherlands Antilles. Bonaire is a small (250 km²) xeric island, located ≈74 km off the northern Venezuela coast. Various aspects of the island's natural history have been described in a series of technical and semitechnical works sponsored by Stichting Nationale Parken (STINAPA), the local parks and environmental research organization (examples are Boyer 1984 and STINAPA 1977). Temperatures vary little during the year (mean daily temperature [± 1 SD] = 27.4 \pm 0.5°C; Netherlands Antilles Meteorological Service data). In contrast, rainfall is strongly seasonal, but also quite variable among years. The rainy season typically extends from September through December. The endemic whiptail lizard (*Cnemidophorus murinus*) is probably the most abundant terrestrial vertebrate, and is found in nearly every habitat on the island. We chose to study this species because preliminary data demonstrated that the Bonaire whiptail is a generalist feeder, with a predominantly herbivorous diet.

We selected three study sites. Each had plant species unique to that study area, but also had species of plants in common with at least one of the other sites. The "Karpata" site was situated on the southern coast, ≈50–150 m from the sea. The substrate in this area is fossil coral flat, and the vegetation consists primarily of shrubs and small trees 0.5–3.0 m tall. The "Playa Frans" site was on the western coast, ≈160–300 m inland. The substrate is diabase soil, a weathering of a shallow intrusion of magma composed primarily of fine-grained lava that is ≈50% SiO₂ (STINAPA 1977). The vegetation at Playa Frans is generally taller than at Karpata, most trees being 2–3 m, with few shrubs under 1 m.

Cacti are also more abundant than at Karpata. The "Onima" site was on the northern coast, 0.5 km from the shoreline. The substrate is a mixture of limestone and diabase soil. The vegetation is primarily candle cactus, *Cereus repandus* and *Lemaireocereus griseus* (8–10 m high), with some shrub-like trees and vines. A fourth site had to be abandoned during the project because construction of a large building disrupted the area. However, miscellaneous observations on the lizards from this and other sites are occasionally referenced here.

Plant abundance

At each site the relative abundance of all plant species was determined by counting and measuring the volume of every individual plant on a measured portion of the site. Linear dimensions of each plant were measured with a tape, then volume estimated as if each plant were one to several rectangular boxes. A shortcoming of this method is that it did not account for plants with the same volume but different biomass, i.e., plants with densely arranged leaves vs. those with sparsely distributed leaves. Fortunately, most species on the island possessed similar leaf densities. Results were converted to volume of each species of plant per square metre of habitat. The plant volume measures were used as an estimate of leaf abundance. The areas and number of individual plants sampled were 469 m² and 439 individuals at Karpata, 190 m² and 228 individuals at Playa Frans, and 164 m² and 407 individuals at Onima.

The abundance of flowers and fruit varied greatly over time, so estimates of these were made every 10 d. For convenience, only the method of measurement of fruit abundance is discussed here; however, flower abundances were sampled in the same manner. The percent of each species in fruit was determined by examining a random sample of 20–40 plants (depending on their abundance) and recording the number in fruit. For small plants, or plants with a small number of fruits, the total number of fruits per plant were counted. For large plants, or plants with many fruits, the fruits on a portion of the plant were counted and multiplied by the number of such portions on the complete plant. These counts were made on at least eight plants in fruit. At least 10 fruits of each species were weighed. From these data we calculated estimates of total number of fruits and biomass of fruits of each species, which was converted into an estimate of biomass of each fruit type per square metre of habitat.

Measurement of nutrients and potential toxins

For each species of plant, 13 nutritional variables were measured for leaves, unripe and ripe fruit, and flowers. These nutritional variables were: (1) energy content per unit dry mass (adiabatic calorimetry using standard techniques); (2) water content (drying in an oven at 40°C until constant mass was reached in ≈1

wk); (3) protein acid digestibility (PAD) (treating 0.5 g samples for 48 h in 50 mL of 0.1 mol/L HCl containing 0.1 g pepsin, Terry and Tilley 1964); (4) nitrogen content (standard Kjeldahl procedure). Minerals were measured with dried plant samples in nitric-perchloric wet oxidase digests (Johnson and Ulrich 1959). These included: (5) calcium and (6) magnesium (atomic absorption spectrophotometry, Varian Techtron 1972); (7) potassium (flame emission, Varian Techtron 1972); (8) phosphorus (vanadate-molybdate yellow color development, Chapman and Pratt 1961); (9) sulfur (turbidimetric method of Tabatabai and Bremner 1970). Several potentially toxic plant secondary compounds were measured: (10) cyanide (picrate colorimetric method of Williams 1979), (11) phenols (p-nitroaniline spot test described by Schall and Ressel 1991); (12) alkaloids (bismuth nitrate-potassium iodide spot test of Schall and Ressel 1991); and (13) saponin (shaking 1 g of crushed plant material in 10 mL of water for 2 min, then measuring the column of foam after 2 min). Quantitative results were available for most of these measures. The spot tests for alkaloids and phenols, however, were scored as 0 for none detected to 3 (phenols) or 4 (alkaloids) for the greatest color change.

We did not compare the energy content of young vs. old leaves, but instead limited sampling to only mature leaves of each species. This decision was based on our inability to obtain newly erupted leaves for each species and time constraints in conducting the bomb calorimetry analysis. We believe using only mature leaves does not seriously compromise our data analysis. Actual digestibility of energy content by iguanas (*Iguana iguana*) for leaves of 14 of the species on our study site (data provided by W. Lichtenbelt) showed that young leaves contain significantly more digestible energy than mature leaves for 11 of the 14 species, but a strong correlation existed between available energy in young vs. mature leaves among the 14 species (Spearman rank correlation $r_s = 0.99$, $P < .01$). Thus, the ranking in available energy content among species is the same for either young or old leaves. No species ranking high in digestible energy for young leaves ranked low for mature leaves.

Diet of the Bonaire whiptail

Lizards were collected by shooting with a .22 caliber (5.6 mm) airgun during the height of their daily activity between 0900 and 1300. Ten lizards were sampled from each site every 10 d over a complete year from late August 1986 to late August 1987. Permission to collect lizards was granted by the appropriate island agencies. Bonaire whiptails are extremely abundant animals, so collection of such a large sample was possible without serious damage to the population. Population density of the lizards was estimated with counts made during standard walks through each site every 10 d, demonstrating no systematic decline in the population

size on our sites. In addition, collected lizards were used in simultaneous studies on reproduction, fat cycles, and thermoregulation (M. D. Dearing and J. J. Schall, *unpublished manuscript*).

Collected lizards were brought into the laboratory within a few hours. The stomachs were removed and the volume of each stomach estimated to the nearest 0.1 mL by using water displacement in a graduated cylinder. The water displacement of the empty stomach was then subtracted from the estimate of the full stomach to obtain the volume of the stomach contents. As lizards do not masticate their food, the contents of stomachs were reasonably intact and could be identified by examination under a dissecting microscope. Some leaf fragments, however, had to be identified by stoma shape or other cell characteristics under a compound microscope. Items appearing in the stomachs were identified by comparison with plant materials collected in the field at each site. Percent volume of each food type was determined by arranging the foods into piles of equal heights in a petri dish glued to graph paper. The area of each clump \times height provided an estimate of its volume. Volumes were then converted into percentages of total stomach contents.

Diet preferences

Preferences for each food type were determined by calculating the "electivity" values defined by Ivlev (1961):

$$\text{Electivity} = [r(i) - p(i)]/[r(i) + p(i)],$$

where $r(i)$ is the proportion of food type i in the diet and $p(i)$ is the proportion of food type i in the environment. The result is a metric ranging from -1 (food considered strongly avoided) to 0 (food taken in its proportion in the environment) to $+1$ (food considered strongly preferred) (Lechowicz 1982). The preference values for flowers and fruits were calculated independently from those for leaves. This was because leaves were always far more abundant than flowers and fruit; combining all abundance data would have obscured differences in preference values among flower/fruit types. Preferences were calculated for each sample period (every 10 d), for each month combining data, seasonally (wet vs. dry season), and for the entire year. We report here only analysis using seasonal and annual preferences because qualitative results for sample and monthly preferences were similar to the seasonal analysis.

RESULTS

Flora of study sites and nutritional quality of plants

From 9 to 16 plant species occurred on the sites, but as is typical for xeric habitats in the Caribbean (Schall and Ressel 1991), only a few species were abundant at any one site (Table 1). Most species are common com-

TABLE 1. Plant species present and types of foods eaten by the Bonaire whiptail lizards (*Cnemidophorus murinus*) at three sites.* N = the number of stomachs sampled for each site.

Plant species or food type	Site			Plant species or food type	Site		
	Kar-pata (N = 363)	Playa Frans (N = 368)	Onima (N = 371)		Kar-pata (N = 363)	Playa Frans (N = 368)	Onima (N = 371)
Anacardiaceae				Percentage by volume			
<i>Metopium brownei</i>	[10.0]	[...]	[...]	<i>Prosopis juliflora</i>	[...]	[48.8]	[68.0]
<i>Metastelma boldinghii</i>	[...]	<0.1	[...]	leaves	...	0.1	1.3
leaves	...	0.1	...	fruit	...	0.1	0.8
Cactaceae				Percentage by volume			
<i>Cereus repandus</i>	[0.5]	<0.1	[0.1]	<i>Passifloraceae</i>			
flowers	0.3	0.5	3.0	<i>Passiflora foetida</i>	<0.1	<0.1	<0.1
fruit	0.5	0.7	0	flowers	0.3	1.0	0
<i>Lemnaireocereus griseus</i>	[...]	[0.4]	[21.0]	leaves	0	0.8	<0.1
flowers	...	2.8	8.6	<i>Passiflora suberosa</i>	<0.1	<0.1	[3.6]
<i>Melocactus</i> sp.	<0.1	[...]	[0.1]	flowers	0	<0.1	0.7
flowers	0	...	1.3	ripe fruit	0	0	3.7
fruit	0.6	...	1.3	unripe fruit	0	0	1.0
<i>Opuntia wentiana</i>	[0.2]	<0.1	[1.0]	leaves	0.4	<0.1	25.1
Capparaceae				Polygonaceae			
<i>Capparis cyanophallophora</i>	[14.3]	[18.0]	<0.1	<i>Coccoloba swartzii</i>	[1.0]	[...]	[...]
flowers	4.0	11.7	<0.1	fruit	0.6
fruit	0.6	10.2	<0.1	Rubiaceae			
leaves	<0.1	1.5	<0.1	<i>Erithalis fruticosa</i>	[16.5]	[...]	[...]
Cucurbitaceae				flowers			
<i>Doyera emetocathartica</i>	[...]	[...]	[5.0]	ripe fruit	9.1
flowers	4.0	unripe fruit	24.0
fruit	1.9	dried fruit	3.2
leaves	4.7	leaves	5.7
Euphorbiaceae				<i>Randia aculeata</i>			
<i>Croton flavens</i>	[0.5]	[3.6]	[0.5]	leaves	[...]	<0.1	[...]
flowers	0	0	0.8	<i>Ernodia litoralis</i>	[2.8]	[...]	[...]
<i>Euphorbia thymifolia</i>	<0.1	[...]	<0.1	flowers	5.2
leaves	<0.1	0	0.9	fruit	8.6
<i>Jatropha gossypifolia</i>	[0.1]	[...]	[2.0]	Sterculiaceae			
flowers	<0.1	...	0	<i>Melochia tomentosa</i>	[...]	<0.1	[...]
<i>Phyllanthus botryanthus</i>	[3.3]	[1.1]	[...]	flowers	...	0.3	...
leaves	<0.1	2.8	...	leaves	...	<0.1	...
Fabaceae				Verbenaceae			
<i>Caesalpinia coriaria</i>	[43.7]	[12.7]	[...]	<i>Lantana canescens</i>	<0.1	<0.1	...
flowers	<0.1	0.1	...	flowers	0.3	0	...
leaves	0	0.1	...	leaves	<0.1	0.4	...
Flacourtiaceae				Grass leaves			
<i>Casearia tremula</i>	<0.1	[6.4]	<0.1	Fungi	1.0	0.8	1.3
flowers	0.3	0.2	0.2	Unknown plants	0.1	0	<0.1
fruit	0	5.2	0	Insects	3.1	6.5	4.7
leaves	0.1	0.2	0	Snails	12.5	15.2	11.0
Liliaceae				Other animal matter			
<i>Aloe vera</i>	<0.1	[2.9]	[...]	Feces	3.0	0.2	0.2
flowers	0.1	1.0	...	Sticks	0.8	0.2	0.3
leaves	0	0.2	...	Pebbles	4.1	5.8	6.4
Mimosaceae				Sticks			
<i>Acacia tortuosa</i>	[6.5]	[5.0]	<0.1	Pebbles	1.2	0.1	0.5
flowers	1.4	4.3	0.2	Unknown	<0.1	0.4	<0.1
leaves	<0.1	<0.1	0	Total plant material	2.2	3.7	3.2
				Total animal material	76	74	78
					16	16	11

* Percentage abundance of plants in the environment at each site [shown in brackets] estimated by volume of entire plants; ellipses within brackets indicate that the plant was absent from that site. Percentages of food types are from contents of stomachs examined over the course of a year.

ponents of the flora of dry Caribbean basin habitats (Broeders 1964, Stoffers 1966). Several plant types were excluded from subsequent analysis because it was mechanically impossible for the lizards to consume these items because of their size or very hard texture (some

of these we found difficult to open even using a knife). These were: *Lemnaireocereus griseus* fruit, *Capparis cyanophallophora* unripe fruit, *Caesalpinia coriaria* fruit, *Casearia tremula* unripe fruit, *Acacia tortuosa* fruit, *Prosopis juliflora* fruit, and *Cereus repandus* fruits (al-

though this fruit was occasionally available to the lizards if opened first by a bird or broken in a fall).

Analyses for nutritional-quality variables demonstrate substantial variation among potential food types in their nutritional quality. For example, energy content per unit dry mass of potential food types ranged from 14.3 to 27.7 kJ/g, and nitrogen content varied from 0.47 to 3.93% of dry mass. The PAD estimate of protein digestibility ranged from 37.8 to 78.0%. Almost all plant types contained potentially toxic materials. Nutritional quality did not differ systematically among tissue type (fruit, flowers, and leaves) (Kruskal-Wallis tests; $P < .05$, except for potassium and calcium when $P < .05$). Another analysis examined correlations among nutritional variables. Only 16 of 78 correlations were significant ($P < .05$), and only 4 of these were fairly tight relationships ($r_s > 0.50$). The minerals were more often correlated (6 of 10), but again these relationships were weak (0.35–0.55). Energy was significantly correlated with only one other nutritional variable, potassium. For each nutritional property, the potential food types were ordered from high to low, with the plant type with highest amount of a nutrient or lowest of a potential toxin ranked as 1. No pattern emerged; that is, no one or few plant types were of overall high nutritional quality. When ranks for all nutrients were summed, there was rather little variation among species (rank = 104.3 ± 23.1 [mean \pm 1 SD]). Thus, the data and analysis demonstrate significant variation in the ratios of essential nutrients and toxins within plants.

Foods in the Bonaire whiptail lizard's diet

Fully 94–97% of the stomach contents (depending on site) could be identified to species and tissue type. The Bonaire whiptail lizard consumed a broad variety of food types during the year. A total of ≈ 60 different types of food were found in the stomachs, but this number is conservative because all insects found were combined into one category. The degree of herbivory of *Cnemidophorus murinus* can be illustrated by the number of plant types in its diet as well as the percent volume of plant materials in its diet. For all sites combined over the entire year, 50 different types of plant material were consumed, ranging from 22 to 24 different types at each site. This plant material accounted for the vast majority of foods eaten (Table 1).

Table 1 presents combined data for stomach contents for the lizards at three sites. The lizards ate flowers, including buds, leaves, fruit, and sticks. Most of the flowers eaten were small (< 1 cm) as were most of the fruits (< 1 cm). However, the flowers and fruits that the lizards frequently ate did not differ from those infrequently or not eaten based on visual characteristics such as color, size, or shape. The leaves that were most commonly eaten were usually those that were not very tough (*Passiflora suberosa* and *Phyllanthus botryanthus*). There were, however, leaves that were not eaten

that seemed as tender (*Casearia tremula*) as those eaten. *C. murinus* also consumes nectar; we have seen lizards harvesting nectar from the flowers of *Aloe vera*.

The kinds of animal foods found in the whiptail's stomachs included insects, spiders, lizards, hermit crabs, and snails. Lepidopteran larvae were the most commonly taken insects, followed by beetles, moths, wasps, and ants. At each of the sites, the lizards feed on feces, some from *C. murinus*, judging from the shape and size, some from other lizards (contained much insect material), and some goat droppings.

The lizards did not appear to specialize on a particular plant tissue type because at each site they ate different proportions of flowers, leaves, and fruit (Fig. 1). Although many individual lizard stomachs contained only one or two types of food, most animals had taken a variety of food types (Fig. 2 top). In some cases, one food type dominated the stomach contents, but in many others there were more even proportions of foods taken (Fig. 2 bottom). Overall at the three sites, 75% of food types taken by the lizards made up only 2% or less of the diet by volume. These results demonstrate the lizards do not specialize on one superior food type and typically take a variety of foods during any feeding period. The diversity of plant types eaten did not differ between seasons (Mann-Whitney U test, $P > .05$).

Diet selection by C. murinus

The lizards showed pronounced preferences for some kinds of plant materials and avoided others regardless of the plant types' relative abundances. These results were consistent at all sites. Fig. 3 shows representative results for four plant types. These figures show that the flowers of *Doyera emetocathartica* and *Ernodia littoralis* were taken in a much greater proportion than their occurrence in the environment. Both of these flowers are small and cryptic, and in the case of *D. emetocathartica*, a vine entangled through *Prosopis* trees, occurs in difficult to reach places. The ripe fruits of *Eri-thalis fruticosa* were always commonly eaten, but their relative abundance in the diet fell when the fruits became very abundant. Flowers of *Prosopis juliflora* are conspicuous and frequently abundant, but were rarely eaten.

The food preference measures also demonstrated that the lizards were selective feeders. To eliminate any bias from the sensitivity of the index for rare food types, preference values were not used for potential food types that were rare in both the environment and the diet ($< 2\%$) (Lechowicz 1982). For the remaining value averaged over the entire year, most fell at either end of the scale, with few in the neutral range (annual preference values in Fig. 4 and seasonal values in Table 2). The exact value of the diet preference index often differed over time, and drastic changes were occasionally seen (Table 2). Nine of 52 pairs of preferences changed sign between seasons, but only three of these changes were substantial, that is, when the values had

different signs and were ≤ -0.3 and > 0.3 . Value changes within the -0.3 to 0.3 range can occur with only small changes in abundance in the diet or environment (Lechowicz 1982).

Food preference values and nutritional quality of plants

Potential food types are grouped as "Preferred" if the preference measure was > 0 and "Avoided" if the value was < 0 . Table 3 presents mean values and results of Wilcoxon rank tests on the nutritional quality variables for Preferred and Avoided foods. Of 39 comparisons made, only 4 were significant. Two Type I errors are expected from 39 comparisons at the $P < .05$ significance level, not much different from the 4 significant differences found. Perhaps the results for energy content of Preferred vs. Avoided potential foods are in error because we measured only total energy content, without knowledge of the availability to the lizards of energy chemically bound in cellulose. To test for this, we examined data for fruits that are generally low in fiber. The Spearman rank correlations between energy content and either percent in diet or preference values were not significant ($P \gg .05$). We conclude, therefore, that Preferred and Avoided plant types did not differ in nutritional quality measures using univariate analysis.

Clearly the Bonaire whiptail lizard discriminates among potential food types, but no single nutritional property of the potential food accounts for the structure of the lizard's diet. Therefore, we next consider multivariate analysis of the data to determine if two or more nutritional properties interact in structuring the lizard's food preferences. A discriminant analysis was first performed to determine which variables are best discriminators between the Preferred and Avoided

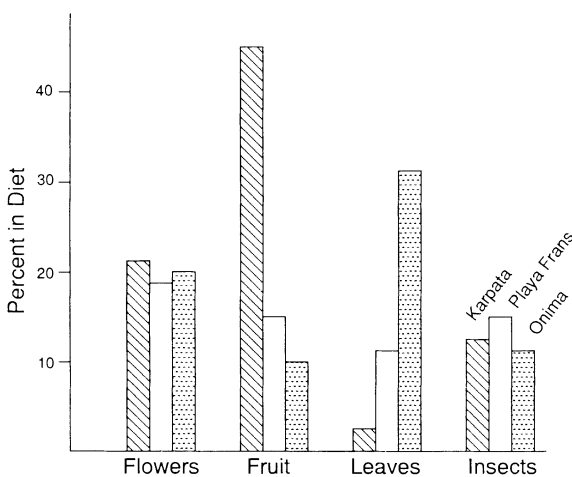


FIG. 1. Percent in diet, by volume, of different plant tissue types and insects consumed by the Bonaire Island whiptail lizard (*Cnemidophorus murinus*) over 1 yr for three sample sites: Karpata, Playa Frans, and Onima.

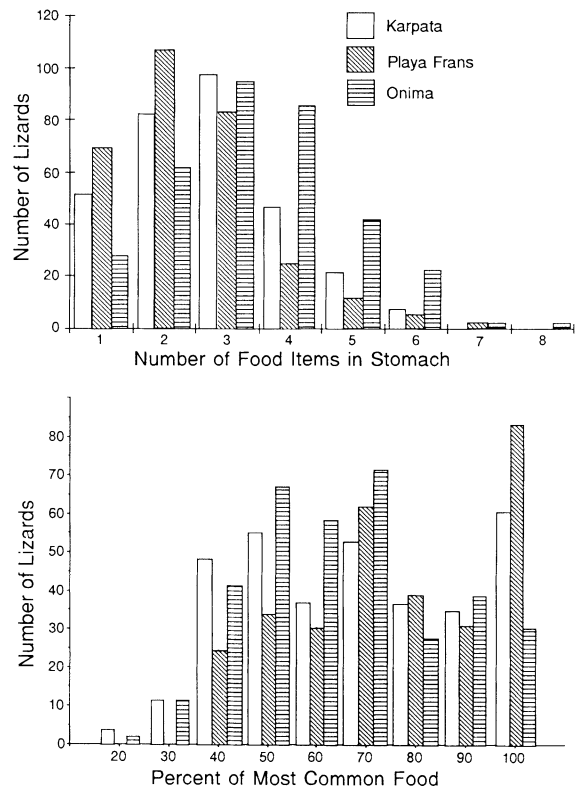


FIG. 2. (Above) Number of plant food types found in stomachs of Bonaire Island whiptail lizards (*Cnemidophorus murinus*). (Below) Percent by volume of the most common food type in individual stomachs of the Bonaire whiptail lizard. Upper figure indicates the lizards often feed on a variety of food types each day. However, this could be a result of sampling; in this case, one food would predominate, with the others appearing in very small quantities. The lower figure demonstrates this is not true. For many lizards the most common food type in the stomach made up only a small percentage of the total stomach contents, indicating dietary diversity was broad.

groups. The nutritional variables useful in discriminating between Preferred and Avoided plant materials differed among the three sites (Table 4). Moreover, no one group of variables (toxins, minerals, or macronutrients) were the best discriminating variables. The signs of the loading values in the discriminant analyses indicate selection (positive loading value) or aversion (negative value) for the nutritional variable. These also differed among sites (Table 4). For example, nitrogen scores positive at Karpata, but negative at Playa Frans.

A discriminant analysis was then used to determine the probability of correctly classifying potential food types into the Preferred or Avoided classes, based on the discriminant equation. Table 5 shows that the resulting classification was far better than random, with only 5 of 46 classifications being in error. All of these five misclassifications resulted in a plant type predicted to be preferred actually being avoided by the lizards.

TABLE 2. Preference values (= electivities) of potential foods items in the habitat of the Bonaire whiptail lizard (*Cnemidophorus murinus*) in the wet and dry season at different sites. Sign changes between the seasons are indicated in bold type.

Plant species	Site					
	Karpata		Playa Frans		Onima	
	Dry	Wet	Dry	Wet	Dry	Wet
<i>Metopium brownei</i>						
fruit	-1.00	-1.00				
<i>Metastelma boldinghii</i>						
leaves	0.06	0.28				
<i>Cereus repandus</i>						
flowers	-0.76	-1.00	-0.85	-0.82	-0.39	-0.31
fruit	-1.00	-1.00	-0.92	-0.98	-0.90	-0.60
<i>Lemaireocereus griseus</i>						
flowers					-0.27	
<i>Melocactus</i> sp.						
flowers					0.99	
fruit					0.99	
<i>Capparis cyanophallophora</i>						
flowers	0.73	-0.23		0.98		
fruit	1.00	-0.21		0.48		
leaves	-1.00	-0.97	-0.91	-0.83		
<i>Doyera emetocatharticus</i>						
flowers					1.00	0.95
fruit					-0.23	0.64
leaves					-0.52	0.02
<i>Croton flavens</i>						
flowers				-1.00	1.00	
fruit				-1.00		-1.00
leaves			-1.00	-1.00	-1.00	-1.00
<i>Jatropha gossypifolia</i>						
flower	-0.60	-1.00			-0.40	-0.58
leaves	-1.00	-1.00			-1.00	-1.00
<i>Phyllanthus botryanthus</i>						
leaves	-1.00	-1.00	-0.05	-0.05		
<i>Caesalpinia coriaria</i>						
flowers	-1.00	-1.00	-0.80	-0.68		
leaves	-1.00	-0.99	-0.97	-0.99		
<i>Casearia tremula</i>						
flowers			1.00			
ripe fruit				0.89		
leaves			-0.91	-1.00		
<i>Acacia tortuosa</i>						
flowers	0.20	-0.64	0.36	-0.21		
leaves	-1.00	-1.00	-0.94	-0.98		
<i>Prosopis juliflora</i>						
leaves	-1.00	-1.00	-0.99	-1.00	-0.95	0.97*
flowers	-1.00	-1.00	-0.74	-0.60	-0.27	0.15
<i>Passiflora suberosa</i>						
leaves					0.78	0.39
flowers					0.50	0.60
fruit					-0.34	0.55*
unripe fruit					0.20	0.57
<i>Coccoloba swartzii</i>						
fruit	-1.00					
<i>Erithalis fruticosa</i>						
ripe fruit	0.71	0.88				
unripe fruit	-0.49	-0.58				
flowers	-0.16	0.08				
leaves	-0.92	-0.93				
dried fruit	0.92	-1.00*				

TABLE 2. Continued.

Plant species	Site					
	Karpata		Playa Frans		Onima	
	Dry	Wet	Dry	Wet	Dry	Wet
<i>Ernodia litoralis</i>						
flowers	0.78	0.75				
ripe fruit	0.73	-0.18				
leaves	-1.00	-1.00				
<i>Aloe vera</i>						
flowers			-0.02			

* Pairs of values judged significantly different using criterion given in *Results: Diet selection by C. murinus*.

Annual nutrient intake

We compared intake by the lizards of protein (organic nitrogen), energy, and minerals at the three sites by calculating for each nutrient:

$$\left[\begin{array}{c} \text{nutrient per unit dry mass} \\ \text{of plant type} \end{array} \right] \cdot [1 - \%H_2O] \cdot \left[\begin{array}{c} \% \text{ plant type in diet} \\ \text{(annual average)} \end{array} \right]$$

This allowed comparisons among sites of amount of a nutrient in each gram of plant materials eaten, averaged over the entire year of the study (Table 6). Overall, intake of positive nutrients was highest at Playa Frans. The nutritional wisdom model predicts nutrient intake over a long period of time should be similar among sites. Comparing the values for each site shown in Table 6 reveals the highest and lowest values for each nutrient usually differ by a factor of about two. Are the observed differences among sites high or low, consid-

ering the different kinds of foods available to the lizards at those sites? Insight into this question can be obtained by comparing the high and low values for each nutrient for the plants actually eaten by the lizards at each site. This analysis compares, for example, the organic nitrogen that would be consumed if the lizards ate only the type of food with the lowest vs. the highest amount of protein at a site. The ranges of nutrients at each site were very broad (typically 10–100 fold for lowest vs. highest). These results argue that the differences among sites in actual nutritional intake were small against the background of what would be possible at each site, and that the lizards were selecting foods at each site that contained approximately the same nutritional balance.

DISCUSSION

Cnemidophorus murinus is clearly a generalist feeder, taking a wide variety of flowers, fruit, leaves, and occasionally nectar, as well as insects, snails, small vertebrates, and even their own and other animals' feces.

TABLE 3. Means of plant quality variables for Preferred (P) and Avoided (A) food items by site. *N* = number of plant food types analyzed at each site.

Variable	Site					
	Karpata (<i>N</i> = 26)		Playa Frans (<i>N</i> = 20)		Onima (<i>N</i> = 14)	
	P	A	P	A	P	A
Energy (kJ)	17.2	19.0	21.0	18.7	18.3	18.2
Water (% wet mass)	69.6	54.6*	59.4	52.9	80.9	68.0
Nitrogen (% dry mass)	0.6	2.1*	2.1	2.4	2.8	2.7
PAD† (% dry mass)	65.0	54.9	58.9	54.1	57.3	56.0
Cyanide (µg/g wet mass)	0	2.2	0	2.2	797.5	0*
Phenols‡	1.7	1.3	0.8	1.4	1.1	1.7
Alkaloids‡	0.4	1.0	0.8	1.5	2.3	1.6
Saponin (mm foam)§	0	2.0	1.8	2.2	0	2.0
Potassium (% dry mass)	1.5	2.0	1.5	2.4	3.5	2.7
Calcium (% dry mass)	0.55	0.80	0.78	0.64	1.1	0.87
Magnesium (% dry mass)	0.15	0.33	0.33	0.33	0.41	0.54
Phosphorus (% dry mass)	0.10	0.20	0.24	0.24	0.32	0.35
Sulfur (% dry mass)	0.13	0.56*	0.25	0.62	0.50	0.31

* Significant differences between Preferred and Avoided items at each site (Wilcoxon rank test $P < .05$).

† PAD = protein acid digestibility (pepsin digestion in 0.1 mol/L HCl).

‡ Color change ranked from 0 = none detected to maxima of 3 (phenols) or 4 (alkaloids).

§ Foam depth produced when 1 g is shaken with 10 mL of distilled water.

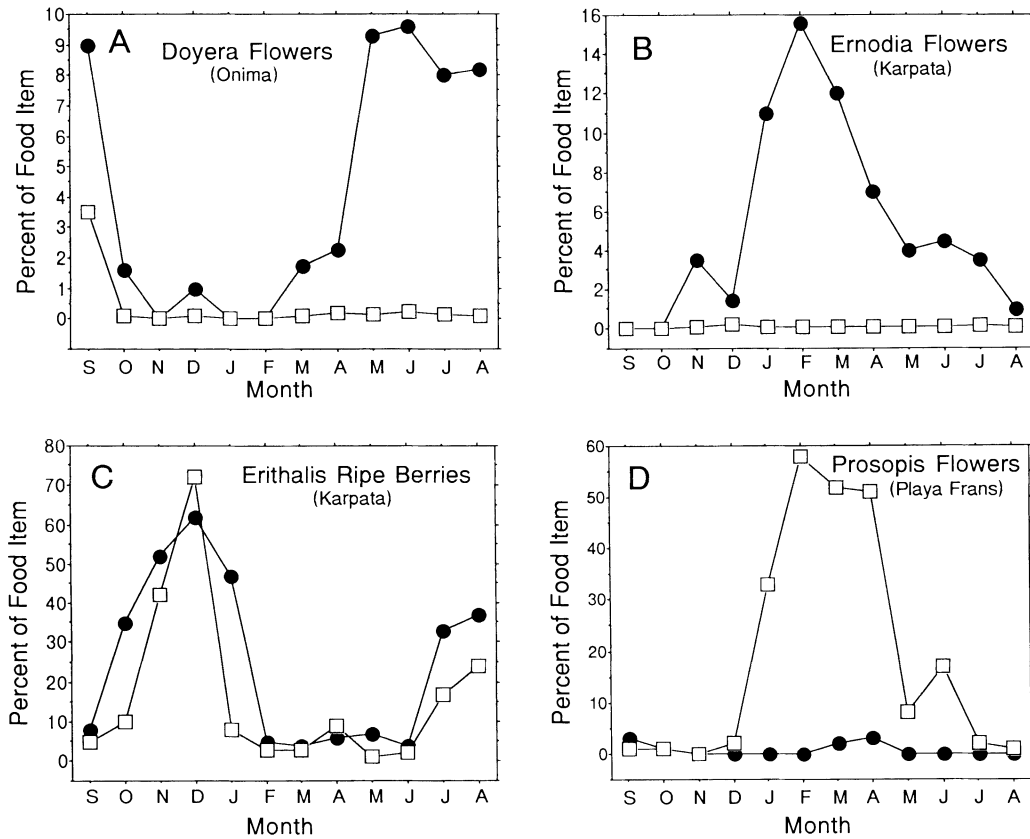


FIG. 3. (A) Percentages of *Doyera emetocathartica* flowers in the environment (□) and in the diet (●) of the Bonaire Island whiptail lizard (*Cnemidophorus murinus*) at Onima site. Open squares may hide solid points. Each solid point based on contents of 30 stomachs. Graph shows that during some months, the always rare *D. emetocathartica* flowers were frequently eaten. (B) Same as above, but for *Ernodia litoralis* flowers at Karpata site. These flowers were always rare, but during some months were often eaten by the lizards. (C) *Erithalis fructosa* ripe berries vary in their abundance, and their percentage in the lizard's diet closely tracks the fruit's abundance. (D) *Prosopis juliflora* flowers are shown to be abundant during some months, yet almost never eaten by the lizards.

We regard the Bonaire whiptail lizard more as a generalist herbivore, rather than an omnivore, because of the high proportion of plant material consistently present in its diet, and because most of the stomachs we examined contained only vegetative matter. The lizards, though, appear to be highly selective generalists;

foods are not consumed in their relative abundances in the environment. Some plant food types occurring in the whiptail's diet are abundant or highly conspicuous, so these widely foraging lizards could quickly fill their stomachs with a single kind of food. The lizards, however, usually take a variety of food types during

TABLE 4. Results of multivariate analysis on plant quality variables and food preference values showing the variables that give the best differentiation in a discriminant analysis. The partial R^2 indicates the portion of variability accounted for by the variable. Loading values (LV, i.e., the standardized canonical discriminant function coefficients) are listed for variables used in the discriminant analysis.

Site								
Karpata			Playa Frans			Onima		
Variable	Partial R^2	LV	Variable	Partial R^2	LV	Variable	Partial R^2	LV
Nitrogen	0.30	1.23	Nitrogen	0.55	-0.54	Water	0.30	6.3
Phenols	0.13	-0.72	Water	0.62	0.70	Calcium	0.60	-6.8
			Calcium	0.65	1.16	Cyanide	0.75	2.4
			Cyanide	0.79	0.81	Alkaloid	0.53	-1.2
			Alkaloid	0.84	1.28			
			Phenols	0.84	-0.68			

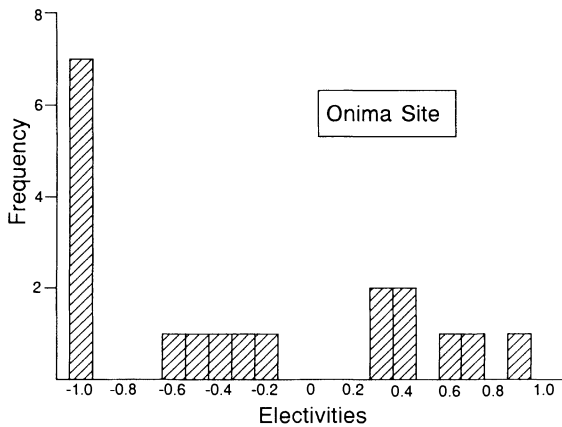


FIG. 4. Histogram of food preference scores (=“electivities” of Ivlev 1961) of different potential food types of the Bonaire whiptail lizard (*Cnemidophorus murinus*). Electivities range from -1 (avoided) to +1 (preferred); frequency shows number of potential food types with each preference value at the Onima site. Distribution of preferences among plant species was similar for other sites.

any one day. Figs. 3 and 4 and Table 2 illustrate the selective nature of the Bonaire whiptail’s feeding, but several examples emphasize this behavior of the lizards.

At Onima, leaves and, at times, the flowers of *Prosopis juliflora* were extremely abundant and made up the majority of leaves and flowers/fruits, respectively, at the site. Lizards would frequently climb into the trees, but almost never ate any part of *P. juliflora*, instead apparently searching out the tiny flowers and small fruits of a vine, *Doyera emetocathartica*. Perhaps not coincidentally, *Prosopis juliflora* contains a considerable amount of saponins, otherwise rare in Bonaire plants. *Jatropha gossypifolia*, a small shrub, produced small but very visible red flowers on branches close to the ground. The flowers were only very rarely found in stomach contents, and when they were, only

TABLE 5. Classification success matrices based on the discriminant function analyses. Given is the number of food types falling into each outcome. The probability of correctly predicting the status of a food item using the discriminant function is given in parentheses.

Actual status of food item	Predicted status of food item	
	Preferred	Avoided
Karpata site		
Preferred	3 (100%)	0
Avoided	4	13 (76%)
Playa Frans site		
Preferred	4 (100%)	0
Avoided	1	10 (91%)
Onima site		
Preferred	3 (100%)	0
Avoided	0	9 (100%)

TABLE 6. Nutrient consumption by the Bonaire whiptail lizard (*Cnemidophorus murinus*) at three study sites. Method used to estimate annual nutrient intake given in *Results: Annual nutrient intake*. Values represent quantity of nutrients consumed per gram of wet food eaten at each site.

Nutrient	Site		
	Karpata	Playa Frans	Onima
Energy (kJ/g wet mass)	3.77	5.03	2.15
Nitrogen (g/g wet mass)	0.233	0.636	0.354
K ⁺ (g/g wet mass)	0.0037	0.0043	0.0039
Ca ⁺⁺ (g/g wet mass)	0.0035	0.0026	0.0089
Mg ⁺⁺ (g/g wet mass)	0.0003	0.0006	0.0007
P (g/g wet mass)	0.0002	0.0006	0.0003
S (g/g wet mass)	0.0007	0.0028	0.0004

one flower was present in any stomach. The lizards were frequently seen traveling directly past a *J. gossypifolia* shrub as they climbed into vines of *Passiflora suberosa* to feed on the small flowers and ripe fruits.

At Playa Frans the lizards seem to seek out the bright red fruits of *Capparis cyanophallophora* that were found on branches as high as 5 m from the ground. At this site the lizards fed readily on the tender leaves of *Metastelma boldinghii* vines, which were often tangled around cactus or *Caesalpinia coriaria* trees. The whiptail lizards, however, did not feed on the abundant flowers and leaves of the *Caesalpinia* tree itself. This tree, the divi-divi, is well known for the high concentrations of tannins in all its tissues.

Cnemidophorus murinus is a widely foraging animal that appears to spend a large portion of its activity period moving through the habitat, climbing into shrubs and trees, and scratching and nosing into the leaf litter (Bennett and Gorman 1979; M. D. Dearing and J. J. Schall, *personal observations*). Almost certainly, the lizards are searching in the litter for insects, which make up ≈ 10–15% of their overall diet. Our subjective impression is that insects are rare in the environment on Bonaire and must require considerable effort by the lizards to locate. This effort may be necessary if insects supply a substantial portion of the protein needed by the whiptails.

If *C. murinus* is a highly selective feeder on plant material, what factors determine if a plant item is preferred or avoided? To answer this question, we now turn to a comparison among the models presented earlier, using our data to test predictions emerging from each of the models.

Comparison among models

The single-nutrient maximization model has been supported with studies on a variety of zoophagous animals (Werner and Hall 1974, Charnov 1976, Goss-Custard 1977). When extended to the diets of herbivores, modifications were necessary to improve the

model's predictability. Belovsky (1978, 1984, 1986) used linear programming techniques, assigning energy as the currency being maximized, but acknowledged only a few digestive constraints and nutrient requirements. These studies successfully predicted the diets of a variety of herbivores, but the predictive resolution was broad because in each case food plants were grouped into only two or three classes. For example, in a study of 14 species of herbivores on a Montana grassland, the model predicted only the percentages of monocots and dicots consumed by the herbivores (Belovsky 1986).

Single-nutrient maximization was not supported by our results. This model assumes that nutrients are positively correlated, such that a plant type high in one nutritional quality will be high in most others. Our data argue otherwise; ratios of nutrients varied greatly among plant types and no one or few plants ranked high on all nutritional properties. In contrast to the model, no single nutrient, including energy or protein, was correlated with a potential food item's preference. With the exception of some very tough plant types (succulents and tough seed pods), there were no morphological characteristics that distinguished foods that were preferred or avoided. Lizards did not specialize on any plant tissue type (leaves vs. fruit, for example). The model also predicts that less profitable foods might be consumed in a constant proportion if they contain an essential nutrient (that is, to meet a simple dietary requirement). However, no food item remained in a constant proportion in the diet throughout the year. Dietary diversity was broader than expected if only sampling was responsible for the complexity of the diet. Last, over both rainy and dry seasons, when food abundance varied, the diversity of food types taken did not vary, contrary to a prediction of the model.

The toxin-avoiding model has been supported in studies of many herbivores (Oates et al. 1977, Bryant and Kuropat 1980, Wiemer and Alces 1981, Buchsbaum et al. 1984, Smallwood and Peters 1986, Rockwood and Hubbell 1987). An unusual test of the importance of toxin mixing was done by Freeland et al. (1985). They demonstrated that mice fed experimentally fixed ratios of food items containing saponins and tannins exhibited ill effects, but when mice were allowed to select their own proportions of saponins and tannin-containing foods, the mice selected the amount of toxins that, through interaction effects of the compounds, negated their toxicity. The Bonaire whiptail samples a wide variety of potential foods in its environment, as predicted by the toxin model. However, no group of plant secondary compounds was consistently correlated with food preferences. The lizards readily ate some potentially toxic foods, including the leaves, flowers, and fruit of *Passiflora suberosa*, which contain cyanogenic compounds. *Nemidophorus* lizards appear to have a broad tolerance to cyanide in their diet (Schall and Ressel 1991). Strongly preferred foods at Onima were the flowers and fruits of *Doyera*

emetocathartica (Cucurbitaceae). These flowers and fruits contain both alkaloids and phenolics and, to the human mouth, are very bitter, perhaps from the presence of cucurbitacins (Tallamy and Krischik 1989).

It is interesting, though, that three of the five plants that were misclassified in the discriminant analysis into the "Preferred" category when they were actually "Avoided" contained secondary products. These were *Caesalpinia coriaria* leaves (tannins), *Croton flavens* leaves (Euphorbiaceae) (strong odor and is toxic to humans; Cozijnsen 1956), and *Metopium brownei* fruit (Anacardiaceae) (produces severe dermatitis in humans; Smith 1977; M. D. Dearing and J. J. Schall, *personal observations*). We suspect that our analysis for potential toxins was too limited. This was necessary as the physiological effects of plant secondary compounds on herbivorous reptiles have received scant attention (but see Schall and Ressel 1991 and Schall 1990). Thus, the toxin-avoiding model was, at best, only weakly supported by our results.

The nutritional wisdom model has been supported in studies on the protozoan *Stentor* (Rapport 1980), a tropical rodent, *Kerodon* (Willig and Lacher 1991), the howler monkey (Milton 1979), Canada Geese (Sedinger and Raveling 1984), kudu and impalas (Cooper et al. 1988), and chameleons (Eason 1990). An early (1940s–1950s) criticism of the nutritional wisdom hypothesis led from skepticism that grazing animals could develop specific hungers for each nutrient as that nutrient was physiologically required (older literature reviewed by Zahorik and Houpt 1977). However, hungers for specific nutrients would not be necessary if generalist herbivores instead seek out specific food types that ultimately satisfy physiological needs. This kind of nutritional wisdom would require "long-delayed" learning in which the delayed consequences of consuming a food type would aid in learning its relative value. Thus, the nutritional costs and benefits of any novel food item could be assessed by a herbivore hours or even days after the item is eaten. Long-delayed learning, first revealed in experiments by Garcia et al. (1955), has now been described for over 30 species of animals, including reptiles (Gustavson 1977).

We believe our study best supports the nutritional wisdom model. Ratios of nutrients vary among plant food types available to the lizards. No single plant is high in all necessary nutrients. The individual Bonaire whiptail typically consumes a variety of plant material each day even though they could easily gorge on a single preferred food type. This variety of food types found in individual stomachs cannot be accounted for only by sampling because often there is no single predominant food in the stomach (Fig. 2 bottom). There are strong food preferences, but these are not correlated with any single nutrient. Multivariate analysis demonstrated that at each site, a group of nutritional properties of available foods could be used to accurately

predict the degree of preference of that item. However, different sets of nutritional variables were important at each site. This would be expected if different potential foods were available at each site, and if the lizards then discriminate among plant types with respect to the variables that are the most limiting at that particular site. That is, a nutrient in short supply in one habitat (or season) may be abundant in another. The lizards would thus be expected to demonstrate localized preferences for nutritional resources in their immediate environment. In fact, the potential foods available did vary among sites (Table 1) and seasonally (Fig. 3). Experiments show the Bonaire whiptail varies greatly in its acceptance of foods laden with quinine, a model alkaloid, among seasons and sites (Schall 1990). Last, the overall nutritional intake of the lizards was similar among the three sites, despite differing plant communities, arguing again that the whiptails seek out a particular balance of nutrients. This kind of consistent nutrient intake despite varied backgrounds of food types may be the best indication of nutritional wisdom in a generalist herbivore (Willig and Lacher [1991] provide an experimental demonstration of this effect).

We are acutely aware of several important shortcomings in this study. The first has already been mentioned: the lack of knowledge of the effects of plant secondary compounds on lizards. A second problem derives from our sampling most plants for nutritional properties only once and from one or a few samples; plants may well vary among individuals and over time in their nutritional quality. Some plants, though, were sampled several times for some nutrients and toxins (for example, young and old *Passiflora* leaves for cyanide, *Doyera* fruits over their season for alkaloids and phenols), and no significant variation was observed.

A final problem also concerns our ignorance of an important aspect of the physiology of *Cnemidophorus murinus*. The fraction of measured potential energy bound in plant materials that is available to the lizards is unknown. A significant portion of energy in leaves, for example, is contained in cellulose, hemicellulose, and lignin (Milton 1979), which may not be available to the lizards. If the lizards are unable to digest cellulose, our measure of energy content of potential foods may say little about the energy available to the lizards, and the lizards may actually be selecting their diet primarily to maximize the intake of available energy. We doubt that this is true for two reasons. First, even for low-fiber foods (fruits) there is no correlation between foods chosen and energy content. Second, in dissecting over 1000 *C. murinus*, we were surprised to find a large intestine much larger than we have seen for insectivorous whiptail species. The large intestine was almost always packed with material, and the pungent odor of the contents suggested that fermentation was taking place there. Thus, it is possible that this lizard, so closely related to insectivorous species, is able to extract energy from cellulose.

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LITERATURE CITED

- Arnold, G. W. 1981. Grazing behavior. Pages 79–104 in F. Morley, editor. *Grazing animals*. Elsevier, Amsterdam, The Netherlands.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* **14**:105–134.
- . 1984. Herbivore optimal foraging: a comparative test of three models. *American Naturalist* **124**:97–115.
- . 1986. Optimal foraging and community structure: implications for a guild of generalist herbivores. *Oecologia (Berlin)* **70**:35–52.
- Bennett A., and G. Gorman. 1979. Population density and energetics of lizards on a tropical island. *Oecologia (Berlin)* **42**:339–358.
- Boyer, P. 1984. *Birds of Bonaire*. Stichting Nationale Parken Foundation, Bonaire, Netherlands Antilles.
- Broeders, A. N. 1964. *Zakflora. Wat in Het Wild Groet en Bloeit of Curacao, Aruba, en Bonaire*. Natuurwetenschappelijke Werkgroep Nederlandse Antillan, Curacao, Netherlands Antilles.
- Bryant, J. P., and P. J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* **11**: 261–285.
- Buchsbaum, R., I. Valiela, and T. Swain. 1984. The role of phenolic compounds and other plant constituents in feeding by Canada geese in a coastal marsh. *Oecologia (Berlin)* **63**: 343–349.
- Chapman, H. D., and P. F. Pratt. 1961. *Methods for soils, plants, and waters*. University of California, Division of Agricultural Science, Berkeley, California, USA.
- Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. *American Naturalist* **110**:141–151.
- Cooper, S. M., N. Owen-Smith, and J. P. Bryant. 1988. Foliage acceptability to browsing ruminants in relation to food selection in hand reared kudu and impalas. *Oecologia (Berlin)* **75**:336–342.
- Cozijnsen, M. 1956. *Pharmacologisch Onderzoek van Croton ovalifolius en Croton flavens*. Smits, Utrecht, The Netherlands.
- Eason, P. K. 1990. The effect of recent diet on prey choice in Senegalese Chameleons (*Chamaeleo senegalensis*). *Journal of Herpetology* **24**:383–387.
- Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of secondary plant compounds. *American Naturalist* **108**:269–289.
- Freeland, W. J., P. H. Calcott, and L. R. Anderson. 1985. Tannins and saponins: interaction in herbivore diets. *Biochemical Systematics and Ecology* **13**:189–193.
- Garcia, J., D. J. Kimeldorf, and R. A. Koelling. 1955. A

- conditional aversion toward saccharin resulting from exposure to gamma radiation. *Science* **122**:157–159.
- Goss-Custard, J. D. 1977. Optimal foraging and size selection of worms by the redshank, *Tringa totanus* in the field. *Animal Behavior* **25**:10–29.
- Gustavson, C. R. 1977. Comparative and field aspects of learned food aversions. Pages 23–43 in L. M. Barker, M. R. Best, and M. Domjan, editors. *Learning mechanisms in food selection*. Baylor University Press, Waco, Texas, USA.
- Ivlev, V. S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Connecticut, USA.
- Johnson, C. M., and A. Ulrich. 1959. Analytical methods in use for plant analysis. Part 2. California Agricultural Experiment Station Bulletin **766**.
- Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia (Berlin)* **52**:22–30.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100**:603–609.
- Maynard, L. A., and J. K. Loosli. 1969. *Animal nutrition*. McGraw-Hill, New York, New York, USA.
- Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist* **114**:362–378.
- Needham, A. E. 1964. *The growth process in animals*. Van Nostrand, Princeton, New Jersey, USA.
- Oates, J. F., T. Swain, and J. Zantovska. 1977. Secondary compounds and food selection by colobus monkeys. *Biochemical Systematics and Ecology* **5**:317–321.
- Rappart, D. J. 1980. Optimal foraging for complementary resources. *American Naturalist* **116**:324–346.
- Rockwood, L. L., and S. P. Hubbell. 1987. Host plant selection, diet diversity, and optimal foraging in a tropical leafcutting ant. *Oecologia (Berlin)* **74**:55–61.
- Schall, J. J. 1990. Aversion of whiptail lizards (*Cnemidophorus*) to a model alkaloid. *Herpetologica* **46**:34–39.
- Schall, J. J., and S. Ressel. 1991. Toxic plant compounds and the diet of the predominantly herbivorous whiptail lizard, *Cnemidophorus arubensis*. *Copeia* **1991**:111–119.
- Schoener, T. W. 1986. A brief history of optimal foraging theory. Pages 5–67 in A. C. Kamil, J. R. Krebs, and H. R. Pulliam, editors. *Foraging behavior*. Plenum, New York, New York, USA.
- Sedinger, J. S., and D. G. Raveling. 1984. Dietary selectivity and quality of food for goslings of Cackling Geese. *Auk* **101**:295–306.
- Smallwood, P. D., and W. D. Peters. 1986. Grey squirrel food preferences: the effect of tannin and fat concentration. *Ecology* **67**:168–174.
- Smith, J. P. 1977. *Vascular plant families*. Mad River Press, Eureka, California, USA.
- Stephens, W. S., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- STINAPA. 1977. *Guide to Geological Excursions on Curacao, Bonaire, and Aruba*. Stichting Nationale Parken Foundation, Curacao, Netherlands Antilles.
- Stoffers, A. L. 1966. The vegetation of the Netherlands Antilles. *Studies on the Flora of Curacao, Aruba, Bonaire, and other Caribbean Islands* **1**:1–142.
- Tabatabai, M. A., and J. M. Bremner. 1970. A simple turbidimetric method of determining total sulfur in plant material. *Agronomy Journal* **68**:805–806.
- Tallamy, D. W., and V. A. Krischik. 1989. Variation and function of cucurbitacins in *Cucurbita*: an examination of current hypotheses. *American Naturalist* **133**:766–786.
- Terry, R. A., and J. M. M. Tilley. 1964. The digestibility of leaves and stems of perennial ryegrass, cocksfoot, timothy, tall fescue, lucerne, and sainfoin, as measured by an in vitro procedure. *British Grasslands Society* **19**:363–372.
- Varian Techtron. 1972. *Analytical methods for flame spectroscopy*. Varian Techtron Property, Melbourne, Australia.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the selection size of prey taken by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**:1042–1052.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. *American Naturalist* **108**:290–304.
- . 1978. What are the biological bases of a varied diet? *American Naturalist* **112**:627–631.
- Wiemer, D. F., and D. C. Alces. 1981. Lasidol angelate: ant repellent sesquiterpenoid from *Lasianthea fruticosa*. *Journal of Organic Chemistry* **46**:5449–5450.
- Williams, H. J. 1979. Estimation of hydrogen cyanide released from cassava by organic solvents. *Experimental Agriculture* **15**:393–399.
- Willig, M. R., and T. E. Lacher, Jr. 1991. Food selection of a tropical mammalian folivore in relation to leaf-nutrient content. *Journal of Mammalogy* **72**:314–321.
- Zahorik, D. M., and K. A. Houpt. 1977. The concept of nutritional wisdom: applicability of laboratory learning models to large herbivores. Pages 45–67 in L. M. Barker, M. R. Best, and M. Domjan, editors. *Learning mechanisms in food selection*. Baylor University Press, Waco, Texas, USA.