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Toxic Plant Compounds and the Diet of the Predominantly Herbivorous Whiptail Lizard, *Cnemidophorus arubensis*

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The diet of the predominantly herbivorous whiptail lizard, *Cnemidophorus arubensis,* was examined at four sites on the Caribbean island of Aruba. The lizard's diet was compared with the abundance of each type of plant material at the sites and the presence of four classes of potentially toxic compounds in the plants. Flowers, fruit, and leaves make up 80–90% of the Aruban whiptail's diet. Foods were not taken in their proportion in the environment; some common potential foods were never or rarely eaten, and some rare plants were commonly consumed. Behavioral observations suggest that the lizards actively search for preferred food types. There was a significant relationship between presence of potential toxins in plant materials and their exclusion from the lizard's diet. Plant materials with large quantities of phenolics, saponin, or alkaloids were usually rarely or never eaten. However, some potentially toxic plant materials, including one containing a cyanogenic compound, were eaten. In a laboratory experiment, a chronic cyanide dose far greater than normally consumed by the lizards under natural conditions did not appear to cause hematological, physiological, or behavioral changes. Thus, some, but not all, types of secondary plant compounds appear to play a role in shaping the diet of C. *arubensis.*

CNEMIDOPHORUS lizards sometimes are presented as the archetypical example of a widely-foraging predacious lizard (Pianka, 1970; Regal, 1978). Some populations of *Cnemidophorus,* though, conflict partially with this stereotype because their diet consists primarily of plant material. These include some Caribbean island endemics and certain populations on the mainland of South America (M. Robinson, D. Harris, pers. comm. and pers. observ.). The presence of both strictly insectivorous and predominantly herbivorous forms among the approx. 35 species of *Cnemidophorus* provides a useful, but unexploited, system to study the ecology, physiology, and evolution of herbivory in lizards.

An important challenge facing any herbivorous animal is the presence of potentially toxic compounds stored by many plants in their tissues, presumably as a deterrent against herbivores, parasitic bacteria, and fungi (Rhoades, 1979; McKey, 1979). The impact of such toxins on the evolution of insects is now well established (Carroll and Hoffman, 1980; Feeney, 1975; Rhoades, 1979), but their importance for generalized vertebrate herbivores remains controversial (Arnold and Hill, 1972; Bryant and Kuropat, 1980; Oates et al., 1980). Most studies on plant toxins and vertebrate diets have been conducted on mammals; knowledge of how herbivorous reptiles deal with secondary plant compounds is scant. Several authors have suggested that toxic plant products could be important in structuring the diets of lizard herbivores (Auffenberg, 1982; Iverson, 1982; Rand, 1978), but field and laboratory studies on the subject are lacking.

We examined the diet of the endemic whiptail lizard, *Cnemidophorus arubensis,* of Aruba Island in the Netherlands Antilles. The lizard is primarily a herbivore; about 80% of its diet consists of plant material (Wagenaar Hummelinck, 1940; below). Our goals here are: 1) to describe the diet of the Aruban whiptail, the first data on the exact diet of any herbivorous *Cnemidophorus*; 2) to compare the diet with the relative abundance of plant materials available to the lizards to detect any selectivity in diet by the lizards; 3) to correlate the diet of *C. arubensis* with the presence of toxic products in potential food items; and 4) to determine experimentally the effects of a chronic dose of an important plant toxin, cyanide, on these lizards. To our knowledge, this is the first examination of the role of plant toxins in structuring the diet of a herbivorous lizard and, except for Swain's (1976)

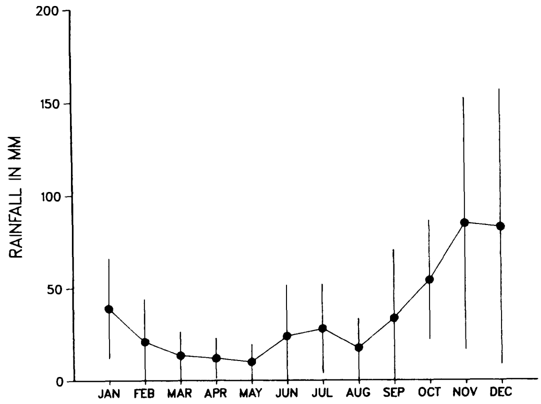

Fig. 1. Mean (points) and SD (vertical lines) for total monthly rainfall on island of Aruba. Results were calculated for 15 yr of data. Figure illustrates duration of rainy season from Sept.–Jan.

brief study, the only experimental assessment of the effects of a plant secondary product on a herbivorous reptile.

Methods and Study Sites

Aruba is a small (175 km²) xeric island lying off the coast of Paraguana, Venezuela. Mean temperature varies only slightly throughout the year ($\bar{x}$ monthly high temperature varied only 3 C, based on 14 yr data from the Netherlands Antilles Meteorological Service [NAMS]); rainfall is seasonal. Most precipitation falls between Sept.–Jan. (Fig. 1); in some years no rain falls at all during the dry season. There is great variation among years in rainfall (from 175–675 mm from 1965–79 [NAMS data]).

We chose four study areas on Aruba that varied in their physical structure and flora composition. The "Strand" site was a heavily vegetated sandy high beach, located approx. 0.5 km from the ocean on the southern coast of the island. The "Coco" site was an abandoned coconut plantation, approx. 0.5 km inland from the Strand site. Living and dead coconut trees were common, along with an understory of shrubs and small trees. The "Hill" site was located another 1 km inland on a gentle hillside of fossil coral and was covered with a mixture of cactus patches and woodland. Last, the "Coral" site was a fossil coral flat adjacent to a salt meadow. Vegetation structure here was simple, perhaps due to periodic flooding.

Each species of plant on the sites was identified, and samples of various tissues (leaves, fruit, flowers) preserved in ethanol. To assess relative abundance of each plant species, we established transects by blindly throwing a stick, randomly picking a compass point, then walking in a straight line from that point. We stopped at each plant encountered during these walks (minimum of 500 plants/site), and estimated its volume in m³ by measuring the plant with a meter rule. Also, the number of flowers and fruits on each of the plants was determined by either actually counting the number on the plant (if the flowers and/or fruit were few), or picking several branches to count, then multiplying this figure by the number of branches on the plant.

Relative abundance of leaves was estimated from data on the total volume of each species of plant divided by the total volume of all plants on the transects. Each species could then be ranked from least to most common. For flowers and fruit, rank order of abundance was estimated from data on numbers of each kind of flower and fruit on the transect divided by the total number of flowers and fruit of all species counted. Some kinds of flowers and fruit were much larger than others, so their estimated number was increased by multiplying by a constant determined by comparing their volumes with other types of flowers and fruit.

Whenever possible, leaves, unripe and ripe fruits, and flowers of each species of plant were tested for four classes of important secondary plant products. To measure saponin, 2 g of ground plant material were placed into 10 ml of distilled water in a vial, shaken for 2 min, allowed to stand for 2 min, and the column of foam measured. For alkaloids and phenolics, qualitative tests were used. This was appropriate because alkaloids and phenolics are very diverse in their effects on vertebrates; quantitative measures are appropriate only when specific compounds with known physiological impact are scrutinized. Some plant material was ground and pressed into a piece of filter paper and exposed to reactive reagents (Harborne, 1973). Alkaloids produced an orange to red color when exposed to Dragendorff reagent (Oates et al., 1977). Phenolics yielded a brown precipitate in the presence of p-Nitroaniline. We ranked color from 0 (no change) to 3 (great change). The effects of cyanide on some vertebrates is known, so cyanogenic compounds were measured quantitatively using a colorimetric method adapted from Williams (1979) and Williams and Edwards (1980). A known mass of plant material was exposed to a few drops of toluene and evolving cyanide gas passed over alkaline picrate solution on filter paper. The picrate, now altered in color, was eluted into distilled water and absorbance read at 510 nm. Standards were prepared from solutions of potassium cyanide.

Diet was determined by collecting lizards at each site (permission granted by the proper agencies of the Netherlands Antilles), then preserving the specimens for later examination of stomach contents. Stomach contents were identified by comparison with the preserved plant specimens. Results are expressed as percent of stomach content volume which was determined by water displacement. Feeding behavior was also observed at each site and notes kept of foods taken. Preliminary observations demonstrated that the fruits of a common shrub, *Crossopetalum rhacoma*, were an important component of the lizard's diet. Therefore, these fruits were gathered, separated into four degrees of ripeness by color, and placed into the environment in petri dishes to determine preference for these fruits.

The lizards commonly eat one food type that contains cyanogenic compounds (Results), so the effect of chronic cyanide consumption was experimentally assessed. Live lizards were collected and kept in 2 m × 1 m seminatural pens (Schall, 1986). A diet of vegetarian strained baby foods was fed to the lizards in measured quantities through a 2 mm Tygon tube slipped into the stomach via the mouth. Cyanide was added to the food of some lizards as aqueous solutions of KCN diluted in distilled water; standard tests (above) confirmed the cyanogenic activity of experimental foods.

Three groups of 10 adult males were used. The first was a control and received 1 g of food with each feeding. The second received 1 g of food containing 15 μg of cyanide, and a third received 75 μg of cyanide in each dose of 1 g of food. Each animal was fed every other day for 42 d (21 feedings). In preliminary trials, using different animals, the lizards were kept in cages lined with white paper to detect any vomiting of the food. No such loss was observed. All animals appeared healthy and were active in their pens throughout the study. On day 42 all lizards were tested for several hematological, physiological, and behavioral characteristics that should be affected by cyanide intoxication (Conn, 1979; Osuntokun, 1968). Measured were proportion of immature erythrocytes in the blood, hematocrit, hemoglobin concentration in the blood, and maximal oxygen consumption after 2 min of strenuous activity (see Schall [1986] for descriptions of methods used). As a measure of general health, absolute liver mass, relative liver mass (liver mass/total body mass), absolute fat body mass, relative fat body mass, and body mass were determined.

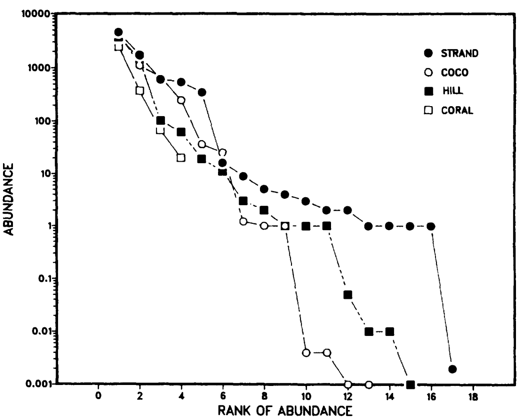

Fig. 2. Abundance of each plant species on four study sites discussed in text given in m^3. The species are ordered on the graph from most common (rank = 1), to least common. Plot is semilog and demonstrates that a few plants are common at each site and the others are rare. Thus, diversity of potential plant foods available for the Aruban whiptail lizard is low.

Results

Flora of the study sites and distribution of plant toxins.—Only 8–16 plant species occurred on any site (Table 1). All are common components of the flora of dry habitats throughout the Caribbean basin (Broeders, 1964; Stoffers, 1966). Figure 2 demonstrates that the structure of the plant communities approximated a geometric series typical of simple plant assemblages in dry environments (Whittaker, 1975). New growth and availability of fruits and flowers varies during the year and probably varies greatly among years as well in response to fluctuations in rainfall (Fig. 1). In the rainy season most plants appear lush with new growth of leaves, flowers, and fruit, but in the dry season only a few species are in flower or fruit. In summary, the lizards had a low diversity of plant types available as foods, most plant species were rare, and availability of foods must vary greatly over time.

Most plants surveyed contained some potentially toxic compounds in their tissues. Some

TABLE 1. PLANT SPECIES FOUND ON FOUR STUDY SITES ON THE ISLAND OF ARUBA, NETHERLANDS ANTILLES. Their distribution among the study sites is given and the rank order of abundance (1 = most abundant) is given for the most abundant species (>1% proportion in the habitat). Sites are described in text.

	Family	Site			
		Strand	Coco	Hill	Coral
Acacia tortuosa	Mimosaceae	4	4	1	
Agava vivipara	Agavaceae	X	X		
Aloe vera	Liliaceae	X			
Boerhavia erecta	Nyctagineaceae			X	
Caesalpinia coriaria	Fabaceae			2	
Cassia obovata	Fabaceae	X		X	X
Cenchrus echinatus	Gramineae	X	X		
Cereus sp.	Cactaceae			X	
Chloris inflata	Gramineae	X			
Coccoloba uvifera	Polygonaceae	1	1		
Conocarpus erecta	Combretaceae			X	1
Corchorus hirsutus	Tiliaceae	X		X	
Crossopetalum rhacoma	Celastraceae	2	3		
Croton sp.	Euphorbiaceae			X	
Cynodon dactylon	Gramineae				X
Erithalis fruticosa	Rubiaceae	5	X	X	X
Euphorbia thymifolia	Euphorbiaceae		X	X	X
Fimbristylis cymosa	Cyperaceae	X			
Jatropha gossypifolia	Euphorbiaceae	X	X	X	4
J. urens	Euphorbiaceae			X	
Lantana camara	Verbenaceae		5		
Matelea maritima	Asclepiadaceae		X	X	
Melocactus sp.	Cactaceae			X	
Opuntia sp.	Cactaceae	X		4	2
Prosopis juliflora	Mimosaceae	3	2	3	X
Sesuvium portulacastrum	Aizoaceae				3
Solanum agrarium	Solanaceae			5	
Suriana maritima	Simaroubaceae	X			

plants with soft, small leaves or flowers contained substantial amounts of noxious substances. Both the leaves and flowers of *Prosopis juliflora* harbored large amounts of saponin. The fruit of *Coccoloba uvifera* is large and very juicy, but the flesh contained phenolics and, to the human mouth, tasted astringent. Two common shrubs produce small brightly colored fruits, *Crossopetalum rhacoma* and *Erithalis fruticosa*. The unripe fruits of *C. rhacoma* contained copious amounts of phenolics; these were absent only in the very ripest fruit. The unripe *E. fruticosa* fruits contained a small amount of phenolics, but were also devoid of this class of potential toxin when ripe. *Acacia tortuosa* leaves, flowers, and pods all contained cyanogenic compounds.

Some plants contained noxious substances not formally identified here, such as *Jatropha* (=*Cnidoscolus*) *urens* (urticating compounds), *Sesuvium portulacastrum* leaves (very salty to the human taste), and *Corchorus hirsutus* (very pungent odor). Other species have a texture that makes them unlikely foods for *Cnemidophorus*, such as cactus (except for flowers), grasses, and *Conocarpus erecta* spiny fruit.

Diet of Cnemidophorus arubensis.—A large proportion of the whiptail's diet consisted of flowers and fruit (Table 2). Plant materials were not eaten in their proportion in the environment. Although leaf material was the most common plant type at each site, the only type of leaves taken in any significant quantity was from *Euphorbia thymifolia*, the rarest plant on the three sites where it occurred. Among flower and fruit types, there was also no relationship between availability in the environment and amount eaten by the lizards (Fig. 3; Spearman rank correlation for only those species of plants ever eaten = 0.007, $P > 0.05$).

Behavioral observations also support a conclusion of selective feeding by the lizards. Most stomachs contained *Crossopetalum rhacoma* fruits at the two sites where this plant was found, and some stomachs were packed with the fruits. The lizards appeared to seek these drupes actively, traveling from shrub to shrub, picking fallen fruit off the ground, and climbing into shrubs to feed. Only ripe fruits were found in stomachs or seen to be eaten. *Crossopetalum rhacoma* fruits placed into the habitat on petri dishes were readily visited by numerous whiptail lizards. The preference of the lizards for the ripest fruits (dark red in color) was apparent on each of 7 d the trials were run (χ^2 tests, 4 × 2 tables, $P < 0.05$). In summary, 73.4% of 290 dark red fruits were taken, 19.6% of 325 red fruits, 20.7% of 348 light red fruits, and only 7.7% of 540 green fruits.

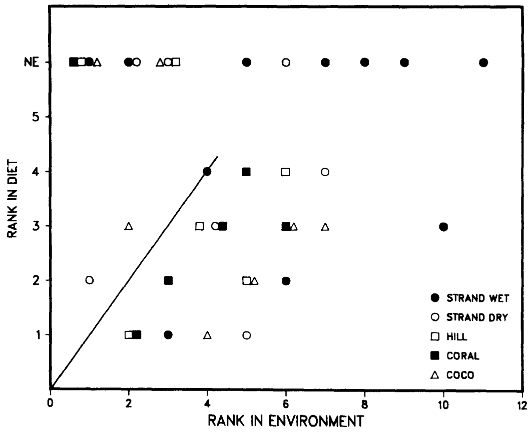

Fig. 3. Rank of abundance in environment and abundance in diet of the Aruban whiptail lizard of flowers and fruit at four study areas. Only fruits that were of size and texture possible for the lizard to eat are included here. NE = Not eaten. Straight line indicates equal rank in environment and diet.

Both ripe and unripe fruits of *Erithalis fruticosa* were found in stomachs. The rather low frequency of these fruits in the stomachs is surprising because we have often observed these lizards climbing into *E. fruticosa* shrubs to feed. The lizards we observed did not seem to differentiate between ripe and unripe fruits, nipping off and swallowing whole from six to a dozen fruits within 30 sec. Lizards ate unripe fruits when ripe ones were within a short distance on the shrub.

The Aruban whiptail ate inflorescences of

TABLE 2. STOMACH CONTENTS OF *Cnemidophorus arubensis* GIVEN AS PERCENT OF TOTAL VOLUME. Four sites are listed; see text for their description. Two samples are given for the Strand site, one in the dry and the other in the rainy season; other samples were taken in the wet season. Also given is the sample size.

n =	Strand (dry) 50	Strand (wet) 49	Coral 22	Hill 12	Coco 52
Crossopetalum ripe fruit	23.7	43.0	—	—	57.0
Erithalis fruit	2.9	11.2	2.0	0.6	1.0
Acacia flowers	19.9	1.0	—	28.0	2.4
Acacia leaves	2.9	0.2	—	1.1	0.3
Prosopis flowers	1.6	—	—	—	0.4
Prosopis leaves	0.8	1.8	0.1	—	—
Cassia flowers	—	2.2	2.7	1.6	—
Grass flowers	—	—	6.8	2.5	0.5
Grass leaves	0.2	3.4	2.2	1.2	0.4
Euphorbia flowers	—	—	6.8	3.8	0.3
Euphorbia leaves	—	—	6.9	6.1	0.7
Jatropha gossypifolia flowers	—	—	15.0	—	0.3
Sesuvium flowers	—	—	22.1	—	—
Unidentified plant material	34.9	22.5	14.4	35.6	17.3
Lizard feces	0.5	—	—	15.0	—
Other knowns	0.2	0.4	—	—	2.3
Insects	9.4	12.9	20.0	3.5	17.1
Sand	3.0	1.4	0.4	0.8	0.1
Flowers and fruit (of knowns)	74%	74%	65%	57%	76%

TABLE 3. FLOWER AND FRUIT TYPES EITHER EATEN (EVEN IF ONLY RARELY) OR NOT EATEN BY THE ARUBA WHIPTAIL LIZARD. Only flowers or fruits that were of a size and texture that might allow the lizards to eat them are included in the table. Plant materials that contained significant amounts of three potentially toxic compounds are distinguished from those kinds that did not contain any such compounds. These compounds were: P = phenolics, A = alkaloids, CN = cyanide. Saponins were not present in any of the fruits or flowers. Quantity for cyanide is $\mu g/g$, and for other compounds ranges from 0 for none present, to three for large amount (see Methods for details).

	Eaten	Not eaten
Not toxic	Grass flowers (2 species) *Crossopetalum* ripe fruit *Erithalis* ripe fruit *Erithalis* unripe fruit (P = 1) *Euphorbia* flowers *Sesuvium* flowers n = 7	n = 0
Toxic	*Acacia* flowers (CN = 40) *Cassia* flowers (A = 2; P = 2) *Jatropha gossypifolia* (A = 1; P = 2) *Prosopis* flowers (A = 4) n = 4	*Aloe* flowers (P = 3; A = 1) *Caesalpinia* flowers (P = 3; A = 3) *Coccoloba* ripe fruit (P = 3) *Crossopetalum* unripe fruit (P = 4) *Croton* flowers (P = 2; A = 2) *Lantana* flowers *Suriana* flowers (A = 2; P = 1) *Solanum* fruit (A = 2) n = 8

Acacia tortuosa, but in proportions far below the availability of this food source in the environment. A single *A. tortuosa* tree produces hundreds to thousands of inflorescences. The lizards climbed into *Acacia* trees, traveling among numerous sharp spines, to reach clumps of inflorescences, but ate only one or two before descending. During the dry season when the inflorescences were most abundant, hundreds fell under each tree. Lizards would enter such areas, eat a single inflorescence, then leave. This perplexing behavior is reflected in the small numbers of inflorescences found in any stomach. Although a *C. arubensis* stomach could easily hold 25 inflorescences, and a lizard could readily harvest a full stomach of flowers in a few minutes, most stomachs contained only one inflorescence. Of 29 stomachs containing *A. tortuosa* flowers, 18 (62%) contained one inflorescence, 7 (24%) held two, 2 (7%) had three, 1 (3%) contained five, and a single stomach contained nine.

Aruban whiptails eat some very tough plant materials. We have seen them biting off and swallowing pieces of the leaves of *Erithalis fruticosa* and the spiny fruiting body of *Cenchrus echinatus.* Lizard feces were also occasionally found in stomachs; one individual had its stomach full of lizard fecal pellets.

Secondary compounds and diet.—Table 3 examines the relationship between presence of potential toxins in flowers and fruit types and their presence in the diet of *C. arubensis.* Although the relationship is significant when numbers of species in each cell of the 2×2 table are considered (Fisher exact test, $P < 0.05$), there are several potentially toxic plants that were frequently eaten by the lizards. Also, of four leaf types eaten, two contained potential toxins (*Acacia* [cyanide] and *Prosopis* [saponin]) and two did not (grass and *Euphorbia* [although this species contained a sticky latex typical of plants in the Euphorbiaceae]).

Effect of cyanide on Cnemidophorus arubensis.—The concentration of cyanide in 10 inflorescences from five *Acacia tortuosa* trees was determined to compare with the concentration fed to experimental lizards (=3.75–12.5 *A. tortuosa* inflorescences per feeding for the low dose group, and 18.75–62.5 for the high dose liz-

TABLE 4. HEMATOLOGICAL, PHYSIOLOGICAL, AND ANATOMICAL MEASURES FOR THREE GROUPS OF ARUBAN WHIPTAIL LIZARDS. Each was fed an artificial diet in the laboratory. The "Low CN" group received a low dose of cyanide in their food, the "High CN" group received five times the low dose (15 μg CN/feeding vs 75 μg CN/feeding). Sample size was 10 for each group. Means and SD given along with the results of Kruskal-Wallis tests. $\dot{V}O_2$ = Maximum oxygen consumption in ml O_2/g·h; [Hb] = hemoglobin concentration in blood in g/100 ml; iRBC = percent of immature erythrocytes out of total erythrocytes in blood; hematocrit is given in percent and liver mass in g; relative liver mass and relative fat mass are calculated as organ mass/total body mass.

	Control	Low CN	High CN	*P*
$\dot{V}O_2$	.8883	1.1411	1.1523	>0.05
	(.3084)	(.3036)	(.3468)	
Hematocrit	32.0	36.0	32.7	>0.05
	(8.65)	(5.22)	(2.50)	
[Hb]	9.68	10.50	9.95	>0.05
	(1.56)	(2.26)	(2.32)	
iRBC	.0067	.0100	.0106	>0.05
	(.0117)	(.0279)	(.0122)	
Liver mass	.6279	.6817	.6439	>0.05
	(.1827)	(.0070)	(.1634)	
Relative liver mass	.0236	.0233	.0252	>0.05
	(.0034)	(.0020)	(.0040)	
Fat mass	.2361	.3178	.3499	>0.05
	(.3333)	(.2936)	(.4172)	
Relative fat mass	.0077	.0110	.0117	>0.05
	(.0098)	(.0109)	(.0126)	

ards, assuming that all of the cyanide liberated from plant materials in laboratory measurements is also either released in the lizard's alimentary tract or after cyanogenic compounds are absorbed). The low dose group received a level of cyanide in the upper end of the range taken by lizards during normal feeding in the wild, whereas the high dose group received cyanide considerably above what is naturally taken by the lizards in natural conditions (1–9 inflorescences).

Table 4 summarizes the various hematological, physiological, and anatomical measures for the controls and two experimental groups. There were no significant differences among the three groups, and all lizards seemed healthy at the end of the experiment.

DISCUSSION

Cnemidophorus arubensis is a generalist feeder, consuming a variety of leaves, flowers, fruit, and insects in both wet and dry seasons. Feeding was selective, as plant foods were not taken in their proportion in the environment and lizards actively sought preferred food types (Fig. 3). The Aruban whiptail is thus a "selective generalist" (Dearing, 1988). What factors determine which foods are preferentially eaten by the lizards?

There is an association between presence of plant secondary compounds and the kinds of plant materials that were consumed by *C. arubensis*; plants that contained potential toxins generally constituted a small portion of the animal's diet (Table 3). This association does not in itself demonstrate a causal relationship, but several lines of evidence do suggest that assembly of the diet of *C. arubensis* is influenced by potential toxins in available plant types. (1) All of the types of flowers and fruit not eaten contained toxins and some of these were common at the sites (*Caesalpinia* flowers, *Coccoloba* fruit, *Crossopetalum* unripe fruit). (2) In the experiment in which *Crossopetalum* fruits of various degrees of ripeness were offered to the lizards, only the ripest ones were frequently taken. The phenolics present in these fruits are withdrawn just as the fruit reaches its maximum degree of ripeness. Perhaps ripe fruits simply contain more fructose and are preferred because they contain more energy. The Aruban whiptail, though, readily harvests both ripe and unripe *Erithalis* fruits, neither of which contain significant secondary compounds. (3) We have often seen foraging lizards apparently examining a tender fruit or flower, but those containing secondary compounds were not eaten (*Coccoloba* fruit, *Prosopis* flowers, *Solanum* fruit, unripe *Crossopetalum* fruit). (4) Comparison between wet and dry season samples at the Strand site shows small amounts of potentially toxic *Acacia* leaves and *Prosopis* flowers appearing in the diet and an increase in number of *Acacia* flowers in the diet when nontoxic fruits of *Crossopetalum* and *Erithalis* are rare. (5) In field experiments, the Aruban whiptail avoided artificial fruits containing a model alkaloid, quinine, in very low concentrations suggesting it also fastidiously avoids some alkaloids in natural plants (Schall, 1990).

The influence of secondary plant compounds on the Aruban whiptail's diet is not absolute because some potentially toxic materials are eaten. For example, inflorescences of *Acacia tortuosa* are eaten despite the presence of cyanogenic compounds in these flowers. The Aruban whiptail may limit intake of the cyanogenic flowers to a threshold containing a total cyanide dose that is readily detoxified. Thus, the energetic benefit derived from a small amount of the plant material might exceed the cost of processing the level of cyanide consumed, whereas larger quantities would exceed this threshold. The experimental feeding of cyanide to the lizards, though, revealed that a chronic dose comparable to over 50 inflorescences every 2 d appeared to cause no harm to the lizards. Perhaps another compound is present in *A. tortuosa* inflorescences that accentuates the effects of the cyanide, so the doses of cyanide used in experimental foods may have been too low to mimic the real effects of eating *A. tortuosa* flowers (Muhtasib and Evans, 1987). Alternatively, the Aruban whiptail may be very tolerant of cyanide in its foods, and have efficient means to limit any damage done by the compound. Some other species of *Cnemidophorus* are known to eat substantial numbers of millipedes which generate cyanide as a defensive mechanism (L. Vitt, pers. comm.), so perhaps whiptail lizards are preadapted to eating cyanogenic plant materials.

These results argue that plant secondary compounds vary in their influence on the Aruban whiptail as it selects food items. Some, such as phenolics and saponin, appear to be effective deterrents to feeding, alkaloids seem to vary substantially in their influence on the diet, and cyanide has little effect. As the lizard assembles its diet to consume needed energy, water, protein, and minerals, it undoubtedly balances the availability of nutrients with the toxicity of various secondary compounds in each food item. We predict, therefore, that the plant materials eaten that contain secondary compounds, either contain specific compounds that are readily detoxified by the lizard, or contain rare nutrients required by the lizards.

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