Learning in Free-Ranging Populations of the Whiptail Lizard Cnemidophorus murinus

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LEARNING IN FREE-RANGING POPULATIONS OF THE WHIPTAIL LIZARD *CNEMIDOPHORUS MURINUS*

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ABSTRACT: The Bonaire island whiptail lizard, *Cnemidophorus murinus*, feeds primarily on plant materials but avoids those containing toxic compounds. I conducted experiments to determine if the lizards would learn to discriminate palatable (containing tomato juice) and distasteful (quinine hydrochloride added) artificial fruits (= "fruits") based on their color or location. In experiment 1, lizards were trained for 19 days with red (palatable) and green (toxic) fruits placed in vegetation. During days 20–21, only palatable fruits were presented; the lizards fed substantially more on red fruits. In experiment 2, all fruits were the same color at a site (green in vegetation at one site, red along a stick fence at another). Fruits placed at half the locations were consistently palatable and half toxic. After 11 days of training, only palatable fruits were presented at all locations at each site. Lizards fed more on the formerly always palatable fruits at one site (fruits in vegetation) but not at another (fruits placed on the uniform fence). Experiment 3 trained lizards with fruits (red toxic, green palatable) attached to the ground (low cost to approach and to test fruits). After 15 days of training, the lizards approached red and green fruits equally often. However, when the fruits were later placed into vegetation at the site (higher cost to approach the fruits), the lizards fed more on the green fruits. These experiments demonstrate that populations of *C. murinus* show rapid changes in behavior when presented with novel foods and suggest that individual lizards learn color and location as cues to avoid or to approach food items.

Key words: Learning; Diet selection; Plant toxins; *Cnemidophorus murinus*; Bonaire; Caribbean

INDIVIDUALS of the teiid whiptail lizard, *Cnemidophorus murinus*, of Bonaire island (Netherlands Antilles) are predominantly herbivores, consuming flowers, fruit, leaves, and even nectar of at least 25 species of plants (Dearing and Schall, 1992). Diet assembly is not random; that is, most foods are not taken in proportion to their abundance in the habitat. Dearing and Schall (1992) correlated electivity (proportion of food type in the diet adjusted for the plant type's abundance) with 13 nutritional measures and concluded that the Bonaire whiptails avoid several kinds of plant toxins while obtaining a balance of nutrients.

There are several mechanisms that could be used by the Bonaire whiptail lizards to avoid foods containing potentially toxic compounds. (1) The lizards could have genetically programmed diet preferences. The lizards disperse as juveniles, and the floral composition varies substantially among sites and over seasons at any one site. Therefore, a rigid diet selection program would require information about a large number of potential plant foods (Dearing and Schall, 1992). (2) Individuals of *C. murinus* could move randomly through the environment, sampling each potential food item via chemical cues. Using its chemosensitive tongue, Bonaire whiptails can detect an alkaloid in very low concentrations in experimental baits, even sensing the compound several centimeters from the bait (Schall, 1990). Continuous sampling of this kind would allow the lizards to avoid plant toxins but would clearly be an inefficient foraging tactic. (3) The lizards could continuously sample novel foods as they are encountered but learn which foods were free of toxins. Learning could be facilitated by observing the feeding behavior of conspecifics. The combination of learning from direct experience and socially facilitated learning would be an efficient way to limit visits only to novel potential foods and previously encountered foods that were palatable.

Could a generalist feeder such as individuals of *C. murinus* learn to distinguish a large number of potential food items? Studies on learning by lizards have been conducted primarily in a laboratory setting using negative stimuli such as electric shock and positive ones such as a heat

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source. Such studies, although often of dubious relevance to problems faced by lizards in nature, have demonstrated that lizards can learn simple tasks (Burghardt, 1977). Laboratory studies are hampered by the difficulty of maintaining lizards in naturalistic conditions in the laboratory. Although lizards may display a large repertoire of behaviors in the field (Brattstrom, 1971), they lose most of these behaviors in laboratory cages; this is especially true for widely foraging lizards such as *Cnemidophorus* (personal observations).

I report here on field experiments that tested the learning ability of Bonaire whiptail lizards. Individual lizards were not followed in these experiments, but instead changes in feeding behavior of populations of the lizards were observed. I chose this research tactic in part for logistical reasons; a very large number of lizards were active at each site (below), so marking them all would have been difficult. Also, a field study may be the only way to test ecologically relevant learning in *C. murinus*, and from the perspective of the plants, most important is the speed at which a population of potential herbivores begins to avoid toxins invested in plant tissue. The experiments examined three issues. First, the ability of the lizards to use color as a cue for the presence of an experimental toxin, the alkaloid quinine hydrochloride; second, the ability of the lizards to learn location as a cue for the presence of the toxin (which individual plants presented toxic fruits); and third, the ability of the lizards to retain in memory information about the presence of toxins to be used only later under different environmental conditions. These are the first experiments on learning ability of any lizard dealing with diet under field conditions.

METHODS

Populations of *Cnemidophorus murinus* were studied at four sites on Bonaire island. The sites were clustered within a 3-km diameter area. Each site was chosen because it was a discrete patch of more vegetated habitat (trees and columnar cactus) surrounded by habitat less suitable for the lizards (goat enclosure, open desert, and at one site by cliffs on one side). The lizards occur in dense populations, 556/ha (Bennett and Gorman, 1979), but adults remain within a small home range (Dearing and Schall, 1994). Individually recognizable marked animals (colored beads sewn to the base of the tail of a sample of the lizards at one site) were observed each day within a few meters of the location of their original capture, and many were recaptured at that same location 4 yr later (Dearing and Schall, 1994). No marked animals were ever observed at another of the experimental sites. Thus, the overlap of individual lizards among study sites was probably nil, and each of the experiments used different groups of lizards. I estimate from direct counts and mark-resighting studies, that there were 100–300 animals at each of the study sites used in this study. The Bonaire whiptail is an active animal, moving through the habitat, on the ground, over rocks, and climbing into vegetation while searching out food items. They are tolerant of human intrusion and can be observed either by naked eye or by using binoculars.

I constructed artificial fruits from 2-cm cubes of synthetic household sponge glued with silicone cement onto a 50 mm plastic Petri dish. The underside of the dish was colored with either red or green paint. A hole in the Petri dish allowed a 10-cm steel nail to fix the dish to the soil substrate or for the dish to be wired onto a plant. Once the paint and cement dried, with no residual odor detectable to human senses, the sponge was soaked with tomato juice. The nutritional content of the juice (91% water, 42kJ/g, 0.005 g protein/g, 0.044 g carbohydrates/g, and no lipids), was 20–25 times the energy content (dry mass) of plant materials commonly eaten by the lizards on Bonaire (Dearing and Schall, 1992). The artificial fruits were large compared to some natural fruits eaten by the lizards (*Passiflora suberosa* or *Erithalis fruticosa*) but similar or even smaller than some others that were taken as pieces (*Cereus repandus* or *Casearia tremula*).

Once placed in the environment, the ar-

tificial fruits (subsequently termed here as "fruits") quickly attracted crowds of lizards which avidly licked, bit, and chewed the sponge. Over time the sponge was chewed off the dish. Individually marked lizards at one of the sites were seen feeding on the fruits throughout the experiments arguing that the plastic sponge was inert and did not kill the lizards or reduce their interest in the fruits. No other animal besides the whiptails was ever seen feeding on the fruits. A fruit containing only tomato juice is referred to here as "sweet fruit". For the toxic fruits, quinine hydrochloride was added to the tomato juice at 1 part:500 parts juice, a concentration that deterred feeding by most lizards (Schall, 1990). To human taste, this mixture was extremely bitter. These are referred to as "toxic fruits".

Initial preference for color of the fruits was first tested with sweet fruits of each color to eliminate the possibility of bias by color in the animals' choice of fruit by color. Red and green fruits were placed on the ground and observed over a two-day period; 163 visits were observed to red fruits and 179 to green fruits (χ^2 test, $P > 0.05$). Thus, there was no preference by color.

The basic design of the three experiments was similar. To assure that all the fruits used in each experiment were visible to the lizards, on day 0 only sweet fruits were presented. Beginning on day 1, the lizards were trained on fruits that were either sweet or toxic. After the training period, the lizards were tested with all fruits containing only tomato juice.

Use of the fruits was assayed by either counting number of lizards seen feeding, number of damaged fruits, or by the amount of the sponge missing. The percentage of missing sponge was estimated by eye to the nearest 10% by comparing the experimental fruit with a fresh specimen. Observations of lizards feeding on the fruits revealed that a large whiptail lizard could eat off most of the sponge, but in most cases, several to many visits were required for the entire sponge to be removed. Thus, the proportion missing from the sponge was weakly correlated with number of lizards feeding at that fruit. Different response measures (number of fruits damaged by feeding, percent of sponge missing, or number of lizards seen visiting) and unequal duration of observations were used for each experiment because of difficulties at some sites in observing all of the fruits or time limitations when two experiments were being conducted simultaneously.

In experiment 1, the lizards were tested for their ability to learn the color of fruit associated with presence of a bitter alkaloid. Wire hooks were placed at 42 locations in the vegetation (limbs and branches of *Acacia tortuosa* and *Prosopis juliflora* and on the columns of the cactus *Cereus repandus* and *Lemaireocereus griseus*) from 1.2–1.7 m above ground. Lizards were frequently seen in vegetation at this range of heights in trees and shrubs prior to the beginning of the experiments, but only rarely on cactus. The fruits were placed within an area of 255 m². Every morning during the training period, prior to the activity period of the lizards (0830–0930 h), each wire was randomly assigned a red or green fruit. Thus, the color of the fruit varied at any one plant location over the course of the experiment. Red fruits were sweet and green fruits toxic. The fruits were left at their location until the next morning when they were replaced at each hook. The fruits were soaked with the appropriate juice several times during the day and, if the entire sponge was removed by the lizards, the fruit was replaced. On days 20 and 21 of the experiment, the fruits were replaced, but no quinine hydrochloride was placed in the juice of the green fruits. The volume of the sponge remaining on the fruits was estimated after 1.5 h and the number of damaged fruits was recorded.

In experiment 2, the lizards were tested for their ability to learn the location of sweet versus toxic fruits. Two sites were chosen. At one, a site of 112 m², all fruits ($n = 20$) were green, but half were toxic and half sweet based on location. That is, each location for the fruit was consistently assigned as either sweet or toxic. The fruits at this location were again placed in trees

and cactus as in experiment 1. At the second site, all fruits were red ($n = 18$), but they were placed along a fence that had been constructed of sticks and brush (28 m long). For 11 days, half the fruits were toxic and half were sweet, randomly assigned on the first day. On day 12, sweet fruits were placed at all locations for both sites. After 5 h, fruits were scored as chewed or not chewed based on the condition of the sponge. On day 13, all fruits were again sweet, and the percent of sponge missing was estimated after 4 h.

Experiment 3 tested for the ability of the lizards to retain a memory of color associated with toxic fruits without any change in their behavior until the environment of the fruits was altered. Red and green fruits were attached to the ground (15 fruits each within a 16-m² area). Red fruits were toxic in this experiment. On day 16, the lizards were presented with only sweet fruits of each color. The number of visits by lizards to each fruit color was recorded for 1 h. Every few minutes, the lizards were chased from the fruits (when more than one lizard was seen at any fruit). Each visit by a lizard was scored as an independent event, because even if individual lizards returned several times to the fruits, they would be choosing among 30 fruits within a fairly small area crowded with other lizards. On day 17, the fruits were removed from the ground and were placed on columns of cactus 2–2.5 m above ground in plants surrounding the clearing. All fruits on this day were soaked with the sweet tomato juice. Visits to these fruits were counted for 45 min after the lizards became active. On day 18, sweet fruits were again placed in the vegetation and the number of visits recorded for 45 min, and damage to the fruits was estimated after 2.5 h. Thus, the initial training period allowed the lizards to visit the fruits with very low cost, but on the two test days of the experiment, fruits were placed in a new environment where some effort by the lizards was required to climb into the vegetation to feed on them.

RESULTS

At the color site and both place sites, every fruit was visited by lizards on day 0

TABLE 1.—Experiment 1 tested the ability of a population of Bonaire whiptail lizards (*Cnemidophorus murinus*) to learn the color of toxic versus palatable artificial fruits. Red fruits were sweet and green fruits toxic for 19 days, followed by two days in which all fruits were sweet. Volume of sponge missing after 1.5 h was estimated and number of damaged and untouched fruits counted for two test days.

	First test day		
	Median % fruit missing	Range	
Red	15%	0–100%	U-test, $P = 0.0008$
Green	0%	0–60%	
	Red	Green	
Damaged	19	7	
Not damaged	3	14	G-test, $P < 0.05$
	Second test day		
	Median % fruit missing	Range	
Red	20%	1–100%	U-test, $P < 0.0001$
Green	0%	0–40%	
	Red	Green	
Damaged	20	9	
Not damaged	2	12	G-test, $P < 0.05$

of the experiments when the fruits contained only tomato juice. That is, either lizards were seen feeding on the fruits or the sponges on each fruit had been chewed by the end of the observation period. On many occasions, two or more lizards were seen feeding at a single fruit. The lizards appeared to be observing the behavior of others; once the first lizard discovered a fruit, other lizards nearby appeared to watch its feeding, then climb into the tree or cactus to approach the fruit and feed. Unlike primarily arboreal lizards such as *Anolis,* individuals of *C. murinus* climbed only slowly through the trees and on cactus.

In experiment 1, during the test days when only sweet fruits were presented to the lizards, the formerly toxic fruits (green) sustained significantly less feeding damage than the formerly always sweet fruits (red) (Table 1). Overall, only 13% of the red fruits had not been chewed, but 62% of green fruits were intact during the two test days. Note that the apparent preference for the red fruits continued during the two test days although all the fruits were now palatable. I conclude that the

TABLE 2.—Experiment 2 tested the ability of a population of Bonaire whiptail lizards (*Cnemidophorus murinus*) to learn the location of toxic versus palatable fruits. At site A, all fruits were green and placed in trees and cactus; at site B, all fruits were red and placed along a stick and brush fence. At each site, half the fruits were toxic and half sweet for 11 days; all fruits were sweet during the following two test days. The volume of sponge missing after 1.5 h was estimated, and number of damaged and untouched fruits counted for 5 and 4 h on the test days.

Site A—In vegetation

First test day	Always sweet	Formerly toxic	
Damaged	10	3	Fisher exact test
Not damaged	0	7	$P < 0.01$

Second test day	Median % fruit missing	Range	
Always sweet	70%	10–100%	U-test
Formerly toxic	5%	0–95%	$P = 0.0156$

Site B—Along stick/brush fence

First test day	Always sweet	Formerly toxic	
Damaged	9	3	Fisher exact test
Not damaged	0	6	$P > 0.05$

Second test day	Median % fruit missing	Range	
Always sweet	50%	10–100%	U-test
Formerly toxic	40%	0–90%	$P > 0.05$

lizards learned to associate a color (green) with presence of a toxin in the fruits.

Contrasting results emerged for the two sites used in experiment 2. At the site where fruits were placed into trees, shrubs, and cactus, the lizards fed significantly more on the formerly always sweet fruits (Table 2). For example, during the test days, 100% of the formerly always sweet fruits were damaged by feeding lizards, but only 30% of the formerly toxic fruits were damaged. At the site where the fruits were placed along a uniform stick fence, no difference in feeding was observed for the formerly always sweet and formerly toxic fruits. I conclude that the lizards are able to learn to associate a particular plant with palatable versus toxic fruits, provided sufficient cues are available to assist learning the location of safe fruits.

On the first test day in experiment 3,

TABLE 3.—Experiment 3 tested the ability of a population of Bonaire whiptail lizards (*Cnemidophorus murinus*) to retain in memory the color associated with toxic (red) versus sweet (green) artificial fruits. After 15 days when all fruits were on the ground and easily approached, lizards were presented on the first test day with only sweet fruits. The number of visits to the fruits were recorded for 1 h. On the second test day, the fruits were again all sweet, but placed into vegetation. Number of visits were counted for 45 min and damage to fruits assessment after 2.5 h.

First test day	Number of visits	
Green	43	
Red	41	χ^2 test, $P > 0.05$

Second test day	Number of visits	
Green	48	
Red	18	χ^2 test, $P < 0.05$

	Median % fruit missing	Range	
Green	10%	10–100%	U-test,
Red	0%	0–95%	$P = 0.067$

lizards were presented with only sweet fruits fixed to the ground where the cost of approach and tasting the fruits was low. No significant difference was observed for number of visits to red (formerly toxic) and green (formerly always sweet) fruits (Table 3; approximately half of the visits were to each color fruit). However, on the second test day, when the fruits were placed into vegetation where approach was far more difficult, there was a significantly lower number of visits to the red, formerly toxic fruits (only 27% of the visits were to the red fruits; Table 3). Damage to the red versus green fruits differed by only marginal significance. I conclude that the lizards had learned to associate color with presence of the toxin, but they did not reveal this retained information until the placement of the fruits made approach more costly.

DISCUSSION

For many years, behaviorists concluded that reptiles possessed minimal learning ability. For example, Jerison (1973) opined that reptiles are "essentially reflex machines with few requirements for plasticity or flexibility." Such views are surprising because numerous laboratory studies have

revealed that reptiles, including lizards, can learn to avoid noxious stimuli. In a model study, Benes (1969) showed that individuals of *Cnemidophorus tigris* were able to discriminate between disks of very similar color and to learn which color was associated with small electrical shocks. A general conclusion of many studies, though, is that under laboratory conditions, lizards and other reptiles require a large number of training episodes (sometimes hundreds) to learn simple information (Burghardt, 1977). Performance in laboratory experiments improve when lizards are maintained at their normal body temperatures achieved in nature and when the tasks assigned mimic those faced in the wild (Brattstrom, 1978). Experiments with free-ranging lizards in their natural habitat reveal rapid learning (Marcellini and Jenssen, 1991).

The present study mimicked naturalistic events: novel fruits appeared in the environment, some providing nutrients favored by the lizards (energy and protein), but some containing an alkaloid, a potentially toxic class of compounds found in many of their environment's plants (Dearing and Schall, 1992). After a training period, the lizards were presented with uniformly palatable fruits to determine if the formerly toxic fruits (by color or location) were avoided. The study demonstrated that the Bonaire whiptail lizard learned to discriminate toxic versus palatable novel food items based on color and location, two cues normally associated with naturally occurring potential plant foods. This was observed as a change in the overall behavior of a large population of lizards rather than for individual animals. Therefore, a large number of lizards apparently learned the cues and altered their behavior after a training period lasting only 12–20 days.

In experiments 1 and 3, lizards learned to associate color with the toxic food. This is not surprising because lizards of the genus *Cnemidophorus* have excellent color vision (Benes, 1969), and the naturally occurring flowers and fruit on Bonaire vary greatly in color (personal observations). In experiment 2, the lizards appear to have learned the location of the toxic versus palatable fruits. Spatial memory, however, is difficult to demonstrate unequivocally (Janson, 1998). In the case of experiment 2, the lizards may not have formed a mental map of the area, but instead learned the appearance of each plant hosting a fruit. Learning was clear at the site where the fruits were placed in trees and cactus, but at the fence site the effect was weak or perhaps absent. The fence appeared uniform to the human observer (the investigator needed to read numbers drawn on sticks nearby to recognize the individual fruits) and perhaps presented few cues to allow the lizards to learn location of palatable fruits.

In experiment 3, behavior of the lizards throughout the training period was similar to that reported by Schall (1990). Many lizards approached the toxic fruits that were attached to the ground, but they left within a few seconds after a few tongue flicks. Once lizards approached the palatable fruits, they would begin to feed on the tomato juice. No learning of color was apparent when the sweet and toxic fruits were attached to the ground. When the fruits were placed in difficult to reach locations (in trees and cactus), a change in behavior was clear; the whiptail lizards visited the green fruits more often than the formerly toxic red fruits. Thus, information on the relationship between color and palatability was retained by the lizards without a change in their behavior when the cost of sampling the fruits was slight (when fruits were on the ground). Travel along the ground's surface was easy and rapid for the lizards, and the potential foods were within a small area. Once the foraging cost was high (the necessity of climbing into plants), the previously acquired information was used to alter foraging behavior. I believe this is the first demonstration that a reptile can retain a memory that does not alter its behavior in the situation where the information was acquired, but only under different environmental conditions.

In these experiments, there was the danger of spurious results emerging if the lizards had an initial preference for the artificial fruits based on color. For example, naturally occurring red fruits might be

more often palatable and green fruits toxic, thus leading to a preference for anything red. The test for this situation showed no such bias, but the fruits were attached to the ground where weak preferences may not be revealed because of the ease of approach to these fruits. However, in the experiments, the colors were switched, green for toxic in experiment 1, green at one site and red at the other in experiment 2, and red toxic in experiment 3. All results were consistent; the lizards were learning to associate color with flavor of the fruits, and if any initial preference existed, it did not affect the outcome of the training experiments.

Socially facilitated learning (= observational learning) appears to play an important role in flocking behavior by birds (Sasvari and Hegyi, 1998) and finding and choosing foods in rats (Galef and Whiskin, 1998; Galef and White, 1997). Social learning has not been demonstrated in reptiles. Although such learning was not formally studied in my experiments, observations during each experiment suggested that the lizards in these dense populations closely watched the behavior of conspecifics. Once a fruit was visited and fed upon by a lizard, others would begin climbing the tree or cactus and group feeding would ensue. Other lizards appeared to be watching the feeding of solitary animals or groups at the fruits. In rats, social learning appears useful when the quality or location of foods quickly changes, but social learning creates a durable change in behavior only when the rat receives supporting information from its own experience (Galef, 1995). The preliminary observations reported here suggest that free-ranging lizards could provide a model system for comparisons of social learning by reptiles to compare with the complex nature of learning by mammals.

Socially facilitated learning by the Bonaire lizards would benefit the plants as well as lizards, because a newly arriving plant species that invests in toxins to protect its fruit or other tissues would be quickly avoided by an entire population of herbivores. However, individual plants or fruits that "cheated" by presenting a false signal would also be quickly discovered. In the experiments, although most formerly toxic fruits were untouched, those that were visited were often heavily fed upon (up to 95% of the sponge removed). Thus, once discovered, a "cheating" fruit was sometimes visited by groups of lizards that may have been drawn there by sight of a feeding conspecific.

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ECOLOGICAL PATTERNS OF BODY-SIZE AND CLUTCH-SIZE VARIATION IN THE PARTHENOGENETIC TEIID LIZARD *CNEMIDOPHORUS TESSELATUS*

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ABSTRACT: Pattern class C of parthenogenetic *Cnemidophorus tesselatus* reaches its southern range limit at Sumner Lake State Park, De Baca County, New Mexico, where it is syntopic at several sites with a northern population of pattern class E of the same species. Samples collected at Sumner Lake in 1997 confirmed significant differences between the two pattern classes in body length and clutch size initially observed in samples collected in 1995 and 1996. In contrast, these characteristics were non-significantly different in pattern classes C and Colorado D, sympatric (and marginally syntopic) at sites near the historic town-site of Higbee, Otero County, Colorado. The difference between each pair of sympatric pattern classes is based on different mean body sizes and a positive relationship between clutch size and body size in *C. tesselatus.* A comparison of 10 samples of three color pattern classes of *C. tesselatus,* spanning approximately 1100 km of latitudinal range, revealed that the small clutch size characterizing pattern class E at Sumner Lake was found in other populations of pattern class E and in one population of pattern class C as well. Similarly, the larger clutch size of pattern class C at Sumner Lake was found in the Higbee population of pattern class C and in some populations of pattern class E. Therefore, despite constraints on variability predicted from a parthenogenetic reproductive mode, reproductive characteristics are remarkably variable both within and between pattern classes. In the absence of conclusive evidence of more than one hybridization event in the origin of *C. tesselatus* and the geographic proximity of only pattern class E to the progenitor species, we hypothesize, from color pattern and meristic evidence, that pattern class C was most likely derived from one or more E-like individuals, and that pattern classes New Mexico D and Colorado D were derived from individuals of pattern class C. Mutations could also have modified reproductive characteristics permitting *C. tesselatus* to expand its distribution beyond that available to a general-purpose genotype derived from the progenitor species *C. tigris marmoratus* and *C. gularis septemvittatus* and expressed in pattern class E. In addition to its extensive geographic range, the ecological success of *C. tesselatus* can be gauged by the fact that nine of our 10 samples of *C. tesselatus* were from populations sympatric with 1–3 sexual species and 1–2 parthenogenetic species of *Cnemidophorus.*

Key words: Reptilia; Squamata; *Cnemidophorus tesselatus*; Color pattern classes; Evolution; Geographic variation; Parthenogenesis; Reproductive strategy; Clutch size; General-purpose genotype hypothesis; Ecology

UNTIL recently, parthenogenetic *Cnemidophorus tesselatus* was included as an undiagnosed species within the diploid-triploid *C. tesselatus* complex. This dilemma was resolved (Walker et al., 1997) by partitioning the *C. tesselatus* complex into two species to reflect their separate origins. The name *C. tesselatus* was retained