



Aversion of Whiptail Lizards (*Cnemidophorus*) to a Model Alkaloid

Author(s): Jos. J. Schall

Source: *Herpetologica*, Vol. 46, No. 1 (Mar., 1990), pp. 34-39

Published by: Herpetologists' League

Stable URL: <https://www.jstor.org/stable/3892600>

Accessed: 17-07-2021 13:49 UTC

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/3892600?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Herpetologists' League is collaborating with JSTOR to digitize, preserve and extend access to *Herpetologica*

AVERSION OF WHIPTAIL LIZARDS (*CNEMIDOPHORUS*) TO A MODEL ALKALOID

JOS. J. SCHALL

*Department of Zoology, University of Vermont,
Burlington, VT 05405, USA*

ABSTRACT: Baits of small sponges soaked with tomato juice were offered to free-ranging whiptail lizards, *Cnemidophorus arubensis*, on Aruba and *C. murinus* on Bonaire, both in the Netherlands Antilles. Some baits contained quinine, an alkaloid, in concentrations varying from 1:250–1:267,000 by mass. Lizards readily approached baits, almost always feeding on those free of quinine but rejecting those with quinine even when concentration of the alkaloid was extremely low. Lizards approaching a bait sampled the quinine-treated and control baits differently, suggesting that they could detect quinine remotely. Tolerance for quinine differed between the two species and varied among sites and times of year on Bonaire. Reptiles are reputed to have poor ability to detect alkaloids in their foods, but these results contradict that suggestion.

Key words: Plant toxins; Lizards; Alkaloids; *Cnemidophorus*; Food aversions

SWAIN (1976) proposed an ecological explanation for the late Cretaceous extinction of terrestrial archosaurian reptiles. He argued that the advent of complex plant toxins during the evolution of the angiosperms presented a barrier to the success of herbivorous reptiles because they were unable either to detect or process such toxins. Fossil remains of stable hydrocarbons, and the distribution of secondary compounds in modern plants, argue that the complexity and diversity of potentially toxic plant compounds increased during the radiation of the angiosperms in the Cretaceous at the very time the archosaurs experienced their decline (Niklas and Gensel, 1977; Swain, 1976, 1978). Although theories of the catastrophic extinction of large Mesozoic reptiles have become popular in more recent years (Alvarez et al., 1980), Swain's hypothesis remains an intriguing, but poorly explored, idea.

In support of his hypothesis, Swain (1976) presented preliminary data on the ability of a tortoise (*Testudo graeca*) and a lizard (*Lacerta viridis*) to detect and avoid a common plant secondary compound, an alkaloid. Quinine was used as the model alkaloid; this was reasonable as most alkaloids are similar in taste: i.e., bitter (Rhoades, 1979). Swain found that the two reptiles apparently did not detect the quinine until the concentration was approximately 30 times the dose detectable by

humans. Even more striking, the *L. viridis* readily ate quinine in lethal concentrations. Swain concluded that reptiles may not be able to detect the bitter taste of alkaloids, making a herbivorous feeding mode problematic for these animals. The very distant relationship of mesozoic archosaurs to lizards and turtles makes the relevance of these observations to Swain's hypothesis questionable. However, his behavioral data are still relevant to the feeding ecology of modern herbivorous reptiles that must frequently confront the presence of potentially toxic alkaloids in their food plants (Dearing, 1988; Schall and Ressel, 1990).

Swain's paper has been discussed in both the popular (Greenberg, 1983) and technical (Benton, 1979; Bjorndal, 1985; Oates et al., 1977; Schall and Ressel, 1990; Siegel, 1979, 1989; Swain, 1978) literature, but his results on detection of alkaloids by reptiles have not been pursued. Here I report the outcome of experiments on the ability of two herbivorous lizards, *Cnemidophorus arubensis* from Aruba Island and *C. murinus* from Bonaire Island, both in the Netherlands Antilles, to detect quinine. Free-ranging, undisturbed animals were used in these experiments. The results are of interest because they call into question Swain's conclusion and may be relevant to the concept of dietary wisdom in generalized herbivores (Westoby, 1974).

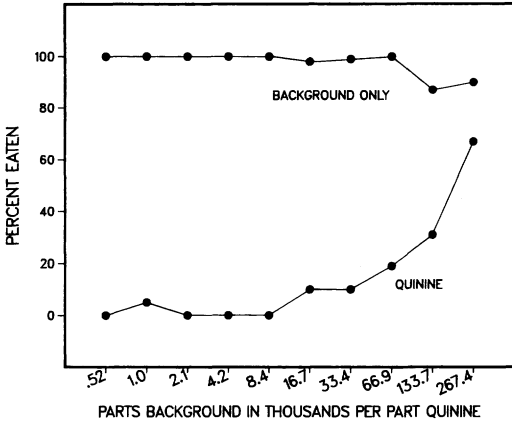


FIG. 1.—Comparison of response of *Cnemidophorus arubensis* to baits containing a model alkaloid, quinine, with those containing no quinine (background of tomato juice only). The proportion of lizards visiting baits that fed is given (“Percent Eaten”). Each point for quinine-treated baits represents 15–51 observations, and for the control baits 31–125 observations. The total number of observations was 1290.

METHODS

The study was conducted at a sandy high beach site on Aruba Island near Malmok (the “Strand” site of Schall and Ressel, 1990), and at three sites on Bonaire that differed in their floral composition and vegetative structure (Onima, Playa Benge, and Playa Funchi). Experiments were conducted during a single week in the rainy season (November) on Aruba, and during four 2 wk periods in both rainy (September and November) and dry (March and April) seasons on Bonaire.

For each experiment, 1 cm cubes of plastic sponge were glued with silicon rubber aquarium cement onto 50 mm petri dishes. The underside of each dish was painted bright red after preliminary trials demonstrated that lizards came more often to a dish painted red than one without color. The bright color also allowed the observer to locate the dishes through binoculars from long distances. After preparing the dishes, they were allowed to air dry until no odor of paint or glue solvent (acetic acid) was apparent (at least 1 wk for the paint, and overnight for the glue). A small hole was made in each dish to allow a 10 cm steel nail to fix the dish firmly onto the ground.

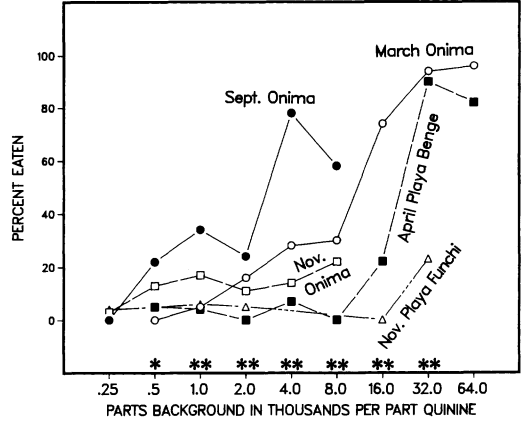


FIG. 2.—Response of *Cnemidophorus murinus* to a model alkaloid, quinine, in baits. “Percent Eaten” is the proportion of lizards visiting the baits that fed. Each point represents 11–160 observations. Total observations for all experiments was 3621, including lizards coming to control baits free of quinine. Significance of two-way G-tests for comparison of sites and times for each concentration is given as * ($P < 0.05$) and ** ($P < 0.01$).

The sponges on the dishes were soaked in commercial tomato juice prior to the start of each experiment. Various concentrations of quinine hydrochloride were added to the tomato juice used to soak the sponges of half the dishes in each experiment (these concentrations are given in Figs. 1 and 2). On Aruba, the concentrations were determined by volume and later recalculated by mass for analysis. Hence, concentrations reported here are not round values. A balance was available on Bonaire, so concentrations there were determined by mass. The highest concentration chosen was 1 quinine : 500 tomato juice, because this was the concentration that was usually avoided by the lizards during preliminary trials. A series of decreasing concentrations was then produced, each reduced by a factor of two. On Aruba, the series ended when a concentration was reached that was eaten by a substantial proportion of the lizards. On Bonaire, time constraints limited most series to 6–8 concentrations. The order in which various quinine concentrations were used in the experiments was randomized.

I used 2–4 baits for each experiment, depending on the number that could be

TABLE 1.—Behavior of whiptail lizards during initial sampling of baits of tomato juice on a small sponge. Some baits contained quinine in the given concentrations, or were controls (no quinine). Sample size of number of lizard approaches is given as well as percent of each of four kinds of sampling behavior.

n =	Aruba		Bonaire	
	Control 63	1:1000 48	1:64,000 47	1:1000 47
Tongue flick	11%	63%	28%	64%
Lick	66%	33%	57%	23%
Nose tap	13%	4%	0%	13%
Bite	10%	0%	15%	0%

readily observed with binoculars from a single vantage point (determined by the vegetative structure of the habitat). Dishes were placed in pairs (one with only tomato juice, the other with quinine) 0.5–1.0 m apart. Pairs of dishes were 3–10 m apart. I observed the dishes through binoculars from 12–15 m away and made no effort to conceal myself from the animals' line of sight.

Lizards in large numbers readily came to these baits and chewed on the sponges to drink the juice. Lizards approaching the baits were free ranging, so some individual lizards were certainly scored several times as they sampled a bait, left the area briefly, then resampled baits later. This possible source of bias was minimized because of the very large number of lizards present and observed inspecting the baits. At each site, 100–200 lizards were marked with individually recognizable sequences of colored beads sewn onto the base of the tail. Although marked animals were frequently seen, they were always outnumbered by at least 10:1 by unmarked animals. Individual marked animals were not seen to visit a single bait repeatedly. To reduce possible social interaction at the baits, I walked through the site chasing away all lizards when more than two animals were near a bait.

Each lizard that inspected a bait was observed for its response. If the animal began to feed on the tomato juice, it was scored as "bait eaten"; if the lizard left the bait after inspecting it, it was scored as "bait rejected".

To determine the type of initial sampling behavior used by lizards as they approached a bait, super-8 motion pictures (Aruba) or video recordings (Bonaire) were made of some baits by remotely controlled cameras. On Aruba, comparisons were made of baits without quinine versus those with quinine added in a concentration of 1:1000. On Bonaire, the lizards were offered baits with quinine at concentrations of either 1:64,000 or 1:1000. The films or tapes were later examined frame-by-frame to quantify sampling behaviors.

RESULTS

Film and video recordings showed the lizards approached baits and responded most commonly in one of four ways: (1) tongue flick—the tip of the bifurcated tongue was extruded very briefly (approximately 0.10 s; time estimated by number of super-8 frames at 18 or 52 ps, or video images at 30 ps in which the tongue was visible) to touch the bait; (2) lick—the entire tongue was used to lick the bait, lasting approximately 0.25 s; (3) nose tap—the tip of the apparently closed mouth touched the bait and the tongue was not visible; or (4) bite—the bait was bitten.

Bait-sampling behavior by lizards differed depending on the concentration of quinine present (Table 1). Because of small sample sizes, cells were collapsed into tongue flick versus all other behaviors (those that involved actually touching the bait); log likelihood ratio tests (*G*-tests) were significant ($P < 0.01$) for these 2×2 tables. When quinine was present at 1:1000 concentration, lizards on both Aruba and Bonaire were more likely to sample the bait with tongue flicks. When quinine was absent (Aruba) or in very low concentration (Bonaire), lizards would more often lick or bite the bait when they first approached. Thus, the lizards appeared to detect quinine even before closely approaching the bait.

After one to several quick samplings, lizards either began to ingest the juice by vigorous licking and biting, or drinking, or rejected the bait. The distinction between sampling behavior (quick, tentative behaviors) and feeding (longer term and

vigorous) was usually obvious, but any lizard that remained at a bait for longer than approximately 5 s and continued to consume the tomato juice was scored as "feeding". After sampling a bait containing quinine, lizards would often "gag" (open the mouth widely) or wipe their mouths against the ground. At lower concentrations of quinine, lizards that accepted the bait and fed would still perform such behavior periodically while feeding, suggesting that they were still able to taste the quinine.

Results (Fig. 1) illustrate that *Cnemidophorus arubensis* almost always fed on tomato juice baits lacking quinine but rejected the baits when the model alkaloid was present, even when it was in extremely low concentrations (*G*-tests, regarding each concentration trial as a separate experiment: $P < 0.01$ for all concentrations except for 1:267,000 when $P < 0.05$). At one part quinine in 267,000 parts of tomato juice, 35% of lizards still rejected the bait, and those feeding often would still periodically "gag" and wipe their mouth on the ground.

Statistical comparisons between data from Aruba and Bonaire lizards are not possible because different concentrations of quinine were used in experiments. However, examination of Figs. 1 and 2 suggests that *C. murinus* was more tolerant of quinine. In some experiments on Bonaire, a sizable fraction of the lizards accepted baits when the quinine was in concentrations as high as 1:1000.

On Bonaire, the lizards also responded differently to the control (no quinine) and quinine-treated baits. For each experimental trial (different concentrations at each site), fully 97–100% of lizards approaching a control bait fed on the juice, whereas the percent accepting the various concentrations of quinine was significantly lower in 31/33 trials (*G*-tests, $P < 0.05$). Moreover, Fig. 2 shows response of the lizards on Bonaire to quinine varied among sites as well as time of year at the Onima site (*G*-tests, $P < 0.01$ or $P < 0.05$ regarding each concentration as an independent experiment). Trials were run three times at Onima, twice in the rainy season and once in the dry season. Lizards appeared

much more tolerant of quinine in September than in November and March. At two other sites, Playa Funchi and Playa Benge, tolerance for the alkaloid was lower than at Onima during the same time period.

DISCUSSION

The Aruban and Bonaire whiptail lizards were clearly able to detect, and would often avoid, quinine in low concentrations. In some experiments, the lizards avoided quinine in far lower concentrations than the detection threshold of most humans (1:30,000 in distilled water: Windholz, 1983). The effect was all the more striking because the alkaloid was presented in tomato juice which masks its odor and flavor (at least for humans). In preliminary experiments, baits were made from a mixture of agar, fructose, and cellulose powder to simulate the taste and texture of fruit. However, when quinine was added to these artificial fruits in concentrations of 1:1000 by mass, the Aruban whiptail apparently could detect the toxin from as far as 15 cm away. Lizards would approach the baits, and sharply turn away from the quinine-treated artificial fruit, to walk directly to the nontoxic bait. In those experiments, no lizards were seen to approach the quinine-treated baits. The sponge bait with tomato juice was then used to assure that lizards would closely approach and sample each bait. The whiptails apparently could detect the quinine from some distance on these baits as well, because their sampling behavior differed depending on the presence or absence of the alkaloid. It is possible that social interactions resulted in different sampling behavior of quinine and control baits; that is, lizards might have been more tentative when approaching a bait where they observed another lizard wiping its mouth. I do not discount such social facilitation of feeding, but I saw many cases of the first lizard to approach a quinine-treated bait apparently behaving cautiously. I conclude that whiptail lizards are able to detect one important class of toxic plant compounds, the alkaloids, in very low concentrations.

Two questions emerge from these experiments. First, why did the results of

experiments on Bonaire and Aruba differ from those of Swain (1976) in the laboratory? The experimental design of the two studies were quite different, not allowing precise comparisons in tolerance of the reptiles observed, but the results show that the whiptail lizards were at least two orders of magnitude more sensitive to the flavor of quinine. Second, why did the whiptail lizards studied here apparently vary in their tolerance for quinine, both between species, and among sites and over time on Bonaire? The first question might be answered simply if reptiles vary enormously among species in their ability to detect alkaloids. Variation in chemosensory ability among reptile taxa is highly likely, but, as the two reptile species studied by Swain consume plant materials naturally, they also must meet alkaloid-laden plants in their natural environments. Natural selection would be expected in such species to favor the ability to detect alkaloids in potential plant foods.

The kind of variation in tolerance for a plant toxin described here is predicted by the dietary wisdom hypothesis (Westoby, 1974; Zahorik and Houpt, 1977) which holds that generalist herbivores seek out an optimal mix of nutrients, selecting food items based on how they integrate into the optimal diet. The level of tolerance for toxins in food items would vary depending on the recent feeding history of the animal. Westoby (1974) reviewed experiments with sheep that show individual animals may avoid quinine, only later to favor the compound.

The floral composition at the study sites on Aruba and Bonaire varies both among sites and over time; likewise, there are both spatial and temporal differences in the lizards' diet (Dearing, 1988; Schall and Ressel, 1990). Some of the plants eaten by *C. arubensis* and *C. murinus* contain alkaloids or other bitter compounds, and these species vary in abundance both in the environment and diet over the year (Dearing, 1988; Schall and Ressel, 1990). As these food items wax and wain in abundance in the diet of the whiptails, the overall nutritional history of the lizards would be changing constantly. The tolerance for al-

kaloids might then change over time, just as it does in other species described by Westoby (1974). Experiments in the laboratory, with stressed animals of unknown dietary histories, could yield results not typical for the species studied.

Acknowledgments.—The research was supported by grants from the Whitehall Foundation. I thank E. Newton of the Karpata Ecological Center for hosting me on Bonaire. D. Dearing assisted with some of the field study and suggested the importance of the dietary wisdom hypothesis. The ecology lunch group at the University of Vermont offered useful comments.

LITERATURE CITED

- ALVAREZ, C. W., W. ALVAREZ, F. ASARO, AND H. V. MICHEL. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* 208:1095–1108.
- BENTON, M. J. 1979. Ecological succession among late paleozoic and mesozoic tetrapods. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 26:127–150.
- BJORNDAL, K. A. 1985. Nutritional ecology of sea turtles. *Copeia* 1985:736–751.
- DEARING, M. D. 1988. Are herbivorous lizards nutrient mixers, toxin avoiders, or amount maximizers? A test of three models on diet selection by *Cnemidophorus murinus*. M. S. Thesis, University of Vermont, Burlington.
- GREENBERG, J. 1983. Natural highs in natural habitats. *Sci. News* 124:300–301.
- NIKLAS, K. J., AND P. G. GENSEL. 1977. Chemotaxonomy of some paleozoic vascular plants: Part II. Chemical characteristics of major plant groups. *Brittonia* 29:100–111.
- OATES, J. F., T. SWAIN, AND J. ZANTOVSKA. 1977. Secondary compounds and food selection by colobus monkeys. *Biochem. System. Ecol.* 5:317–321.
- RHOADES, D. F. 1979. Evolution of plant chemical defense against herbivores. Pp. 4–54. *In* G. A. Rosenthal and D. H. Janzen (Eds.), *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York.
- SCHALL, J. J., AND S. RESSEL. 1990. Toxic plant compounds and the diet of the herbivorous whiptail lizard, *Cnemidophorus arubensis*. *Copeia* 1990:In press.
- SIEGEL, R. K. 1979. Natural animal addictions: An ethological perspective. Pp. 29–60. *In* J. D. Keehn (Ed.), *Psychopathology in Animals*. Academic Press, New York.
- . 1989. *Intoxication*. E. P. Dutton, New York.
- SWAIN, T. 1976. Angiosperm-reptile co-evolution. Pp. 107–122. *In* A. D'A. Bellairs and C. B. Cox (Eds.), *Morphology and Biology of Reptiles*. Academic Press, New York.
- . 1978. Plant-animal coevolution—Syntopic view of the paleozoic and mesozoic. Pp. 3–19. *In* J. B. Harborne (Ed.), *Biochemical Aspects of Plant and Animal Coevolution*. Academic Press, New York.

- WESTOBY, M. 1974. An analysis of diet selection by large generalist herbivores. *Am. Nat.* 108:290-304.
- WINDHOLZ, M. (Ed.). 1983. *The Merck Index*, 10th ed. Merck and Co., Rahway, New Jersey.
- ZAHORIK, D. M., AND K. A. HOUP. 1977. The concept of nutritional wisdom: Applicability of laboratory learning models to large herbivores. Pp. 45-67. *In* L. M. Barker, M. R. Best, and M. Domjan (Eds.), *Learning Mechanisms in Food Selection*. Baylor University Press, Waco, Texas.

Accepted: 3 April 1989

Associate Editor: Robert Kaplan

Herpetologica, 46(1), 1990, 39-42
© 1990 by The Herpetologists' League, Inc.

THE EFFECT OF INGESTED TRANSMITTERS UPON THE TEMPERATURE PREFERENCE OF THE NORTHERN WATER SNAKE, *NERODIA S. SIPEDON*

WILLIAM I. LUTTERSCHMIDT¹ AND HOWARD K. REINERT

*Department of Biology, Allentown College of St. Francis de Sales,
Center Valley, PA 18034, USA*

ABSTRACT: The mean temperature selected by post-absorptive *Nerodia s. sipedon* in a laboratory thermal gradient was 27.7 C (SE = 1.42, $n = 5$). The mean temperatures selected by the same snakes following the ingestion of natural food items and model transmitters were 36.0 C (SE = 2.33, $n = 5$) and 36.4 C (SE = 2.31, $n = 5$), respectively. A repeated measures ANOVA indicated that the substrate temperatures selected after ingestion of either food or transmitters were significantly higher than those selected when post-absorptive. These results suggest that studies using ingested transmitters may bias their observations in favor of post-ingestion behavior.

Key words: *Nerodia s. sipedon*; Radiotelemetry; Serpentes; Temperature preference; Transmitters

MANY radiotelemetric studies of snake behavior have used transmitters that either were palpated into the stomach or ingested while disguised in food items (e.g., Brown and Parker, 1976; Fitch and Shirer, 1971; Hammerson, 1979; Landreth, 1973; Moore, 1978; Osgood, 1970; Parker and Brown, 1980; Reinert and Kodrich, 1982; Shine, 1987). Despite evidence that food ingestion results in thermophilic responses by several species of snakes (e.g., Lysenko and Gillis, 1980; Naulleau, 1983; Regal, 1966; St. Girons, 1975), the effect of ingested transmitters upon snake behavior has not been experimentally evaluated. However, snakes with ingested transmitters exhibited slower rates of travel than snakes studied in the same area using mark and re-

capture efforts (Fitch and Shirer, 1971), and the basking of *Crotalus viridis* on winter days might have been induced by the presence of transmitters in the stomachs of the snakes (Jacob and Painter, 1980). Such observations suggest that the use of ingested transmitters may influence activity patterns and result in an observational bias in favor of post-ingestion behavior. The current study compared the effects of ingested transmitters and natural food items upon substrate temperature selection, because this aspect of snake behavior can be quantified objectively, correlates strongly with body temperature (Lysenko and Gillis, 1980), and has broad physiological and ecological implications (Huey, 1982).

MATERIALS AND METHODS

Five water snakes, *Nerodia s. sipedon* (Colubridae), were obtained from natural

¹ PRESENT ADDRESS: Department of Biological Sciences, Southeastern Louisiana University, P.O. Box 814, Hammond, LA 70402, USA.