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## Avoidance Learning by the Curly-tailed Lizard, *Leiocephalus schreibersi*: Implications for Anti-predator Behavior

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Recognition and avoidance of predators is an ecologically relevant task which has been found to have innate components (e.g., Morse, 1970; Curio 1976), especially in the co-evolved relationships where a prey species employs special avoidance behaviors to counter the hunting strategies of a specific predator (e.g., Edmunds, 1974). However, if a species is relatively long-lived and likely to encounter an unpredictable number of life-threatening stimuli, one would expect a selective advantage for individuals which also possess a facility to recognize novel predators through conditioned learning. There are some reliable data on the relative responsiveness of a prey species in learning to recognize a novel predator (e.g., Csanyi, 1985, 1986), but there are no such studies for lizards.

The demonstration of learning by reptiles to avoid predators rests primarily on anecdotal evidence (reviewed by Greene, 1988, but see possible exception of Rodda et al. 1988). Reptiles are known to exhibit conditioned learning through negative reinforcement (reviewed by Burghardt, 1977; Brattstrom, 1978; Rothblum et al., 1979), which is a prerequisite for avoidance learning. However, past studies required many trials (sometimes hundreds) to condition an avoidance response. Therefore, predator avoidance by means of conditioned learning would not seem a practical mechanism of survival since few predators would permit a reptilian prey the luxury of multiple learning trials. Our study, however, reverses this perspective; using Pavlovian conditioning within a natural setting, our data show that the lizard *Leiocephalus schreibersi* quickly learned to avoid a novel predator.

Our subject species is a thermophilic ground-dwelling iguanid which uses moderate-sized rocks for surveillance and basking sites, and nearby burrows and rock crevices for nocturnal retreats and diurnal refugia from predators (Marcellini and Jenssen, 1989). Its natural predators include ground-hunting snakes, such as *Alsophis* spp. and *Hypsirhynchus ferox*, and large birds, such as lizard cuckoos and sparrow hawks (Henderson et al., 1988; pers. obs.). Data were collected on a study site in the northwest corner of the Dominican Republic, 2 km E of Montecristi, during 17–20 May 1989. The site was an open field (approx. 200 m<sup>2</sup>) littered with rocks and bordered by rock walkways and walls; without moving, an observer could monitor almost all of the study area.

We measured avoidance learning in *L. schreibersi* with the following procedures. Four test periods, one per day, were established between 0900 and 1030 h. During this period the lizards were conspicuously

visible on surveillance perches, and at or near their average activity body temperature (Marcellini and Jenssen, 1989). To begin each test period, three people stood away from the study site and used binoculars to locate lizards on the study area. From this, we planned a route through the study area to be able to test sequentially each observed lizard with least disturbance to those which had yet to be approached. This route varied somewhat between test periods, as it depended on the spatial distribution of our subjects. Next, one person, designated the "stalker," entered the area. This person was always dressed in the same clothing and used the same approach speed and technique. The aspect of the stimulus complex nearest to the subject was a slip noose tied to the end of a 0.3 m length of monofilament thread which was attached to the tip of a thin, 3.1 m fiberglass pole. The stalker attempted to catch each subject. If it was a lizard's first capture, we measured its snout-vent length (SVL), toe-clipped it for permanent identification, painted it with an individual identification code, and released it at the capture site. If recaptured, the subject was simply released. A lizard was stalked only once per day. After initial capture, there were three subsequent opportunities for capturing a subject during the four test periods, giving a total of four possible trials.

The fundamental elements of Pavlovian conditioning (reviewed by Hollis, 1982) and their specific expression as applied in our experiment consisted of: (1) an unconditioned response (UR), the species' defense reaction (specifically, retreat to a burrow when threatened by a predator); (2) an unconditioned stimulus (US), a biologically relevant event (specifically, simulated predation short of death through capture, handling, and toe-clipping); and (3) a conditioned stimulus (CS), a novel stimulus complex (specifically, the human with a pole and noose). Prior to being stalked and captured, the CS held no threat because naive lizards had never been exposed to a noose and pole; they were habituated to human activity, and only moved a short distance (<1 m) to avoid being stepped on.

Our criterion for learning was the appearance of a defense reaction (UR) to the CS. We used the following five variables to evaluate when the subjects associated the CS with the US: (1) approachability—the frequency with which a subject permitted the stalker to get within test distance (<10 m); (2) catchability—frequency of noosing a subject; (3) stalking time—elapsed time(s) from initiation of stalking (<5 m from subject) until the subject was either noosed or entered a burrow; (4) minimum noose distance—how close (m) the subject allowed the noose before the subject was either caught or entered a burrow; and (5) average distance moved—the distance (m) a subject moved away from the noose before the subject was either caught or entered a burrow, divided by the number of moves. Statistical analyses of these variables was conducted with an IBM 3801 computer and the Statistical Analysis System software program (SAS Institute, 1985).

Approachability was our primary criterion for avoidance learning. If a subject became unapproachable, it certainly could not be caught, nor was it possible to measure any of the other variables. Our sample revealed a large variance in approachability. Thirty-one lizards were caught and marked during

TABLE 1. Descriptive statistics (mean  $\pm$  standard error of the mean) for stalking time (s; ST), minimum noose distance (m; MD), and average distance moved (m; ADM) by four learning groups (defined by the number of trials before the subject became unapproachable) of free-ranging *Leiocephalus schreibersi*.

Learning groups	Trial number			
	1	2	3	4
1 (N = 7)				
ST	13.3 $\pm$ 3.01			
MD	0.0 $\pm$ 0.00		unapproachable	
ADM	0.0 $\pm$ 0.00			
2 (N = 9)				
ST	30.9 $\pm$ 7.76	11.9 $\pm$ 3.19		
MD	0.0 $\pm$ 0.00	1.5 $\pm$ 1.09		unapproachable
ADM	0.2 $\pm$ 0.12	0.8 $\pm$ 0.35		
3 (N = 7)				
ST	24.0 $\pm$ 5.87	12.4 $\pm$ 2.40	5.4 $\pm$ 2.74	
MD	0.0 $\pm$ 0.00	2.0 $\pm$ 0.15	1.9 $\pm$ 0.68	unapproachable
ADM	0.1 $\pm$ 0.09	1.1 $\pm$ 0.42	1.4 $\pm$ 0.48	
4 (N = 8)				
ST	22.1 $\pm$ 5.34	22.3 $\pm$ 6.52	8.9 $\pm$ 2.87	11.8 $\pm$ 5.66
MD	0.0 $\pm$ 0.00	0.6 $\pm$ 0.39	1.1 $\pm$ 0.45	0.6 $\pm$ 0.36
ADM	0.0 $\pm$ 0.00	1.5 $\pm$ 0.36	2.3 $\pm$ 0.90	0.4 $\pm$ 0.14

trial 1, 11 males (SVL  $\bar{x}$  = 78.9 mm  $\pm$  14.7 SD) and 20 females (SVL  $\bar{x}$  = 62.7 mm  $\pm$  3.3 SD). In each subsequent trial, however, approachable subjects decreased by about 25% of the original sample (Table 1). The marked subjects that were not approachable moved to the entrances of their burrows before the stalker came within test distance (approx. 10 m); sometimes they disappeared before the stalker entered the study area. Seven (all females) were approachable only on trial 1 (23% of marked lizards); 9 were approachable only on trials 1-2 (29%); 7 on trials 1-3 (23%), and 8 were approachable on all four trials (25%). Females became unapproachable quicker than males (Fisher Exact Probability Test,  $P$  = 0.01; Siegel, 1956); after two trials only 6 of the original 20 females (30%) could be approached, versus 9 of the original 11 males (82%).

Based on approachability, there were four subject-determined groups of avoidance learners, which ranged from those that participated in only one trial (fast learners) to those that allowed approach in all four trials (slow learners). For subsequent statistical analyses, we kept these four "learning" groups separate (see Table 1) in order to meet the pairing requirements of the Wilcoxon Test (Siegel, 1956) when performing inter-trial comparisons, and to test if any of these learning groups were behaving differently within a trial.

Catchability decreased precipitously with subsequent trials. Of the 24 subjects approachable on trial 2, only 6 were recaptured (<20% of trial 1 sample), with no difference among sexes. Thereafter, for trials 3 and 4, no approachable subjects could be noosed. Stalking time was longest in trial 1 ( $\bar{x}$  = 23.1 s  $\pm$  2.11 SE), decreasing to a mean of 15.5 s ( $\pm$ 2.66) in trial 2, 7.3 s ( $\pm$ 1.98) in trial 3, and 11.8 s ( $\pm$ 5.66) in trial 4. A comparison between learning groups of a trial showed no significant differences in stalking time within any of the four trials (Kruskal-Wallis Test: trial 1,  $df$  = 3,  $\chi^2$  = 3.82,  $P$  = 0.28; trial 2,  $df$  = 2,  $\chi^2$  = 1.24,

$P$  = 0.54; trial 3,  $df$  = 1,  $\chi^2$  = 3.07,  $P$  = 0.08). However, when comparing learning groups in common between trials, there was a significant shift to shorter stalking times in all but the trial 3 with trial 4 comparison (Table 1; Wilcoxon 2-sample Test: pooled learning groups 2-4 among trials 1 and 2,  $df$  = 1,  $z$  = 1.97,  $P$  = 0.05; pooled learning groups 3-4 among trials 2 and 3,  $df$  = 1,  $z$  = 2.21,  $P$  = 0.03; learning group 4 among trials 3 and 4,  $df$  = 1,  $z$  = 0.21,  $P$  = 0.83).

Minimum noose distance was zero ( $\bar{x}$  = 0.0 m) for all subjects during trial 1; subjects allowed the noose to touch them. In trials 2-4, most subjects moved before the noose could be brought close, making noosing impossible. The mean minimal distances between subject and noose for the last three trials were 0.8 m ( $\pm$ 0.43 SE), 1.5 m ( $\pm$ 0.40), and 0.6 m ( $\pm$ 0.14), respectively. These trial averages are minimum flight distances for the population, because noose distances could not be quantified for the unapproachable lizards that entered burrows before they could be stalked (flight distances >10 m). For the approachable subjects, the minimum noose distances did not vary significantly among the learning groups within any of the trials (Kruskal-Wallis Test: trial 1,  $df$  = 3,  $\chi^2$  = 0.00,  $P$  = 1.0; trial 2,  $df$  = 2,  $\chi^2$  = 1.24,  $P$  = 0.54; trial 3,  $df$  = 1,  $\chi^2$  = 1.16,  $P$  = 0.28). However, when comparing learning groups in common between trials, there were significantly increasing minimum noose distances in all but the trial 3 with trial 4 comparison (Table 1; Wilcoxon 2-sample Test: pooled learning groups 2-4 among trials 1 and 2,  $df$  = 1,  $z$  = 2.81,  $P$  = 0.005; pooled learning groups 3-4 among trials 2 and 3,  $df$  = 1,  $z$  = 2.07,  $P$  = 0.04; learning group 4 among trials 3 and 4;  $df$  = 1,  $z$  = 0.64,  $P$  = 0.52).

Avoidance movements were rapidly acquired after only a single trial. In trial 1, 27 of the 31 subjects never moved before being noosed, in spite of long stalking times. During trial 2, 20 of the 24 subjects moved, and all lizards moved when stalked in trials

3 and 4. The average distance of each move during trials 1-4 was 0.1 m ( $\pm 0.04$  SE), 1.1 m ( $\pm 0.22$ ), 1.9 m ( $\pm 0.53$ ), and 0.4 m ( $\pm 0.14$ ), respectively. The average distance moved did not vary significantly between learning groups within a trial (Table 1; Kruskal-Wallis Test: trial 1,  $df = 3$ ,  $\chi^2 = 5.26$ ,  $P = 0.15$ ; trial 2,  $df = 2$ ,  $\chi^2 = 3.02$ ,  $P = 0.22$ ; trial 3,  $df = 1$ ,  $\chi^2 = 0.22$ ,  $P = 0.64$ ). When common learning groups were compared between trials, there was a trend for minimum noose distance to increase (Table 1), but only the trial 1 with trial 2 comparison was significant (Wilcoxon 2-sample Test: pooled learning groups 2-4 among trials 1 and 2,  $df = 1$ ,  $z = 4.59$ ,  $P = 0.0001$ ; pooled learning groups 3-4 among trials 2 and 3,  $df = 1$ ,  $z = 0.31$ ,  $P = 0.76$ ; learning group 4 among trials 3 and 4,  $df = 1$ ,  $z = 1.80$ ,  $P = 0.07$ ).

In summary, 80% of our subjects were uncatchable by the second trial, and by the third trial all were uncatchable, with 75% having established long flight distances ( $> 10$  m). This unapproachability was developed significantly faster by females than by males. Comparisons among learning groups, defined by the number of trials a subject required before it was unapproachable, did not show significant differences in stalking time, minimum noose distance, or average distance moved during stalking within any given trial. However, in most cases of among-trial comparisons, stalking time decreased significantly, and minimum noose distance and average distance per move increased significantly with each subsequent trial. These are all predictable directional shifts with the recognition and avoidance of an aversive stimulus.

Tested within their natural habitat and within an ecologically relevant context, the curly-tailed lizard, *L. schreibersi*, unequivocally demonstrated an ability to quickly learn to avoid a previously neutral stimulus. The exceptional learning performance by *L. schreibersi* is in direct contrast to most studies on other lizard species. For example, Powell (1967, 1968) and Powell and Mantor (1969) never observed avoidance learning by *Anolis carolinensis* and *A. sagrei*, even after hundreds of trials. These studies used a shuttle box design which discouraged climbing, the innate avoidance behavior typically used by these anoles; in addition, the stimuli employed, electric shock (US), tones (CS), and/or flashing light (CS), were all of low ecological relevance to the subject species. It is implausible to conclude that anoles have little or no ability for avoidance learning. A more likely conclusion is that learning performance can be greatly affected by the test conditions.

The acquired avoidance response of *L. schreibersi* fits a model by Bolles and Fanselow (1980), who proposed that any stimulus which causes fear will elicit the subject's species-specific defense reaction unconditionally. If this unconditioned stimulus is accompanied by a neutral stimulus, then after some repetition, the neutral stimulus will become a "learned releaser" (sensu Woodruff and Williams, 1976) and will reliably elicit the unconditioned defense reaction by itself. This learning process can serve as a flexible system to augment innate mechanisms for recognizing predators. Obviously the formation of a learned releaser can only be effective if the subject is able to live through the predatory encounter. Many lizards, including *L. schreibersi* (Jenssen and Marcellini, 1986), have evolved a complex morphology for caudal au-

totomy, an adaptation which allows the escape from a predator should the lizard be grasped by its tail (Arnold, 1988). Complementing this adaptation, our study shows that a second chance is all a lizard may require to thwart future predator contacts. A single learning experience by *L. schreibersi* was sufficient to produce a learned releaser for the recognition and avoidance of a novel predator.

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### Failure of *Bufo americanus* Tadpoles to Avoid Lead-enriched Water

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A number of recent studies have documented the world-wide decline in amphibian populations (e.g., Jennings, 1987; Berger, 1989; Baringa, 1990). Reasons suggested for this decline have included habitat modification and destruction, roadway mortality, and the adverse effects of pesticides and pollutants (see Jennings, 1987, for review). The decline of amphibian populations not only in areas of industrial development, but also in agricultural areas (Berger, 1989) requires particular attention because of the steady increase over the past decade of applying sewage sludge for agricultural land use (Rappaport et al., 1987). This increased use of sewage sludge to fertilize agricultural lands has raised concerns about potential toxicological effects on exposed populations and ecological communities as a result of the cycling of toxicants in the sludge (Hall et al., 1990). A number of heavy metals, including lead, accumulate in the soils of sludge-treated lands (see Hall et al., 1990, for review). Lead (Pb) produces behavioral alterations in non-mammalian vertebrates, including amphibian larvae.

For example, Eby (1986), and Strickler-Shaw and Taylor (1990) found that exposure of green frog (*Rana clamitans*) tadpoles to 750 or 1000 µg Pb/l produces deficiencies in acquisition and retention of learned responses. Exposure to these concentrations of Pb also increases the variability of locomotor activity in green frog tadpoles (Taylor et al., 1990). Bullfrog (*R. catesbeiana*) tadpoles exposed to 625, 750, or 1000 µg Pb/l also exhibit deficiencies in learning acquisition and retention, while exposure to 500 µg Pb/l interferes with learning acquisition (Strickler-Shaw, 1988). Most importantly from an ecological perspective, Steele et al. (1989) and Taylor et al. (1990) found, respectively, that neither bullfrog nor green frog tadpoles avoid these Pb concentrations shown to produce behavioral deficiencies.

The current study is a continuation of our research on the effects of Pb, a common heavy-metal contaminant in aquatic systems, on tadpoles. Among the variety of sources introducing Pb into receiving waters is runoff from agricultural and sludge fields (Birdsall et al., 1986). Amphibian larvae can be excellent indicators of field pollution because they develop in small water bodies subject to such runoff (Berger, 1989). Berger (1989) found that toad tadpoles, including *Bufo bufo*, were much more sensitive to mercuric phylacetate and a variety of fertilizers in agricultural runoffs than were ranid tadpoles. If this observation is a general phenomenon, then perhaps *Bufo* species would more readily perceive waterborne pollutants and would be better indicators of behavioral toxicosis in laboratory behavioral bioassays. To test this hypothesis with respect to Pb, we assessed the preference-avoidance responses of American toad, *Bufo americanus*, tadpoles to several concentrations of Pb-enriched plumes of water.

A total of 112 American toad tadpoles were captured from a temporary pond near the base of the dam at Acton Lake, Hueston Woods State Park, near Oxford, Ohio, in May, 1988. The pond was formed from the retention of excess rainwater and was not subject to runoff from surrounding streams or drainages, thus we feel fairly certain that the tadpoles experienced little or no prior exposure to environmental pollutants. The tadpoles were held in community aquaria (22 ± 1.2 C) under a 12:12 LD photoperiod; lights on, 0800 h for 2 weeks prior to experimentation and were fed freshly-boiled lettuce ad libitum, except during behavioral experiments. No tadpoles had visible limb buds. All were at a comparable premetamorphic stage of development (stage 24 of Rugh, 1962).

The tadpoles were divided randomly into 7 experimental groups chosen from the community aquaria with no apparent bias (N = 4 exposure groups of 4 tadpoles each, for each experimental group). Tadpoles in each exposure group were exposed for 144 h in 1500 ml Pyrex crystallizing dishes containing 1000 ml of filtered, dechlorinated laboratory water to one of 4 concentrations of Pb: 0 µg/l (control group, C); 500 µg/l (low-exposure group, L); 750 µg/l (medium-exposure group, M); or 1000 µg/l (high-exposure group, H). No deaths occurred in the exposure groups during Pb exposure.

These concentrations of Pb and this exposure regimen were selected for comparative purposes since they were similar to those used by Strickler-Shaw (1988) and Strickler-Shaw and Taylor (1990) in their