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Responses of Naive Lizards to Predator Chemical Cues

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ABSTRACT.—The ability to recognize chemical cues from predatory snakes is congenital in the common lizard *Lacerta vivipara*. This conclusion follows from a series of experiments in which we observed the behavior of naive lab-born lizards in terraria that had previously been inhabited by predatory snakes. Chemicals from both the viper *Vipera berus* (a sympatric predator) and the smooth snake *Coronella austriaca* (an allopatric saurophagic snake) elicited a sharp increase in tongue-flick rates. The lizards, when confronted with snake chemicals, exhibited an increased number of foot shakes, tail vibrations and starts, and moved about in a strange, jerky way. In these aspects, the behavioral response of juvenile lizards resembled that of adults. The only quantitative age-related difference concerned thermoregulatory behavior: whereas juveniles refrained almost completely from basking in the presence of snake chemicals, adult lizards basked equally long in snake and control experiments.

Given the high costs of improper responding towards predators, it is not surprising that many young animals exhibit species-typical defensive behaviors, even in the absence of prior experience with threatening stimuli. Anti-predator behavior is expected to be congenital in precocious species, in particular, because their offspring cannot rely on or learn from parental protective behavior.

In reptiles, naive neonates or juveniles are known to react to natural predators by running, threatening and/or striking, in ways much like their parents (for a review see Greene, 1988). On the other hand, ontogenetic changes in squamate defensive behavior have been reported. In a number of species, juveniles and adults differ in wariness (Beebe, 1945; Schmidt and Shannon, 1947), aggressiveness (Wall, 1907; Mertens, 1952; Bustard, 1968; Branch, 1973; Sweet, 1985; Herzog et al., 1992), or their abilities and tendency to run and hide from predators (Fitch, 1956; Huey, 1982; Garland, 1985; Herzog et al., 1992). However, it is seldom clear whether these changes result from experience, social transmission, or other factors (e.g., maturation of neuromuscular control mechanisms). In addition, most of the information is based on anecdotal observations, and, with the notable exceptions of the papers by Arnold and Bennett (1984), Burger (1989, 1990), Weldon et al. (1990), Herzog et al. (1992) and Phillips and Alberts (1992), few studies have provided quantitative descriptions of complex behavioral responses towards predators in naive newborn reptiles.

An important component of anti-predator behavior is the ability to ascertain the presence of predators. Many reptiles possess a highly developed tongue-vomeronasal system (Parsons, 1970), that is involved in the detection of chemical cues of widely differing origins (for reviews see Simon, 1983; Halpern, 1992). Many species of snakes feed on lizards and other snakes. Further, snakes deposit chemical trails, composed of sex pheromones and/or other nonvolatile proteins and lipids (Crews and Garstka, 1982; Garstka et al., 1982; Burken et al., 1985), that could be detected and recognized by their prey. An increasing number of studies have indeed demonstrated the abilities of both lizards and snakes to detect chemical cues released by their snake predators (Bogert, 1941; Chiszar et al., 1978; Weldon and Burghardt, 1979; Weldon, 1982; Thoen et al., 1986; Burger, 1989, 1990; Dial et al., 1989; Cooper, 1990)

Common lizards (*Lacerta vivipara*) can detect chemicals that are left on the substrate by the predatory snakes *Vipera berus* and *Coronella austriaca* (Thoen et al., 1986). This capacity is manifested through an elevated rate of tongue flicking, indexing an increased usage of the vomeronasal system. Detection of the snake odors elicited an alteration of the movements patterns: lizards moved more slowly and exhibited sudden quick runs, tail vibrations and foot shaking (Thoen et al., 1986). These findings were based on observations of adult male lizards that came from an area where they lived syntopically with the lizard eating snake *Vipera berus*. Hence, it did not provide information on whether the lizards' ability to detect snake chemicals is congenital or, alternatively, acquired through experience. We address this issue through examining the responses by naive hatchling lizards, that were born and raised in the laboratory, towards predator-derived chemicals. We evaluate ontogenetic changes by comparing the chemoreceptive and behavioral responses of hatchling and adult lizards.

Materials and Methods

Animals and Their Maintenance.—*Lacerta vivipara* is a small diurnal lizard that inhabits large parts of Europe and Central Asia. It is a ground-dwelling species that feeds on a variety of small invertebrates and prefers well-vegetated and rather humid habitats. Adults weigh 3–4 g and have snout-vent lengths (SVL) that typically range between 50 and 65 mm. In most populations, embryonic development is completed within the maternal body, and hatchlings have SVLs of 18–22 mm, and weigh between 0.15 and 0.20 g. There is no parental care of any sort.

Both the adder *Vipera berus* and the smooth snake *Coronella austriaca* are frequent predators of *Lacerta vivipara*. The adder is a heavy set (adult SVL 60–75 cm) diurnal snake that feeds on mice, young birds, frogs, and lizards (Pielowski, 1962; Prestt, 1971), and kills its prey by injecting a cytotoxic venom. The smooth snake is a small, slender, secretive snake (adult SVL 50–70 cm), that predominantly feeds on small rodents and lizards (Spellerberg and Phelps, 1977). Lacking poison-glands, it constricts its prey before eating it. Both snakes have geographic distributions and habitat preferences that overlap extensively with those of *Lacerta vivipara*.

During June 1984, we collected five gravid female *L. vivipara* and one adult male viper from a small heather field within the military property 'het Groot Schietveld,' Brasschaat (51°20'N, 4°30'E), in Antwerp, Belgium. The site is known to lodge a dense population of *Vipera berus*, but although herpetologists have been scanning the area frequently for the past 15 years, not a single *Coronella austriaca* was observed. An adult female smooth snake was caught near Spontin (50°18'N-5°00'E), in Namur, Belgium.

In the laboratory, the gravid lizards were kept individually in soil-filled plastic terraria (60 × 35 × 22 cm) containing some heather and mosses. House crickets (*Acheta domestica*), periodically dusted with a vitamin and mineral supplement, and water were provided ad libitum. Heat and light (8 h/d) came from a 75-W bulb, suspended ca. 30 cm above the substrate of each cage. This allowed lizards to select temperatures within their preferred range (Van Damme et al., 1986). At the end of July, the females gave birth to a total of 17 juveniles, which were marked individually and put in similar terraria, with no more than three juveniles together. Siblings were kept apart. The juveniles were given small crickets and a variety of small arthropods caught by sweep-netting in or near lizard habitats. Snakes were housed in glass terraria (40 × 40 × 20 cm) that were placed in a different room. Like the lizard cages, the snake terraria contained some heather and mosses. The home cages of the snakes were used as experimental terraria. We took care that lizards did not have contact with snake stimuli before they were tested.

Experimental Procedure.—We used the experimental protocol of Thoen et al. (1986), where each of the 17 juveniles was consecutively introduced in three types of experimental terraria; (1) Control: an unfamiliar, untreated terrarium; (2) Viper: a cage chemically labelled by the viper; (3) Smooth snake: a cage chemically labelled by the smooth snake.

The snakes were removed from their home cages 5 min before each test and replaced after its termination; thus lizards were only exposed to chemicals that the snakes left on the substrate, not to visual or auditory snake stimuli. Snakes were kept in the respective cages overnight and for at least one hour between successive tests. Although test cages differed slightly from those used by Thoen et al. (1986), special care was taken to make the appearance of the three terraria used in each series as similar as possible. During the tests, terraria were heated by two 75-W bulbs, suspended 22 cm above the substrate, allowing lizards to attain preferred body temperatures.

Each lizard was tested once in each experimental cage, and returned to his or her home cage for at least 24 h between consecutive experiments. The order in which juveniles were confronted with the three experimental situations was randomized for each individual lizard. Juveniles were tested at an age of 40–50 d.

Observations.—Observations started ca. 10 sec after the lizard's introduction into the test terrarium and lasted for 20 min. The lizard's behavior was monitored continuously from behind a one-way mirror. This mirror does not seem to affect the behavior of common lizards. We distinguished between the following behavioral acts and locomotor patterns (see also Thoen et al., 1986; Van Damme et al., 1990).

(1) Tongue flick: the lizard extrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or is 'waved' in the air.
(2) Walk: continuous, relatively fast, forward movement. This locomotor pattern is typically observed in unrestrained lizards.
(3) Slow motion: slow stalking movements, most often accompanied by jerky or waving movements of the forelimbs.
(4) Run: very fast movement, often over only a short distance.
(5) Bask: the lizard rests under the heat bulb with the ribs spread laterally.
(6) No move: the lizard does not move and does not spread its ribs laterally as when it is basking.
(7) Stand up: the lizard stands in an upright position against the glass wall of the terrarium and performs scratching movements with the forelegs.
(8) Start: sudden jump, most often followed by a quick, short run.
(9) Foot shake: the raised forelimbs are alternatively and rapidly moved up and down.
(10) Tail vibration: the entire tail, or its posterior portion, is moved briskly from side to side.

Tongue flicks were counted by a hand held counter; the total number was recorded at the end of each test. The occurrence of Starts, Foot shakes, Tail vibrations (frequency) and the other behavioral acts (duration) were recorded continuously by use of an event recorder (Esterline Angus, 20 channels).

Data Analysis.—We checked for possible family effects on the behavior of juveniles by analyzing the frequency or duration of each behavioral act by a repeated measurements analysis of variance (ANOVA) design with family entered as a between subjects factor, and experimental situation as the within subjects factor. Significant family or family × treatment effects were found for none of the behavioral acts (all $P > 0.10$). Therefore, we considered the juvenile scores as independent data points to facilitate subsequent statistical analyses. We tested for differences between experimental treatments in the frequency of tongue flicks, and the frequency or duration of other behavioral acts using repeated measurements ANOVA. Univariate F-tests showed which individual contrasts contributed to the overall differences found among treatments. If Mauchly's test indicated violation of the assumption of sphericity of the covariance matrix of transformed variables, we multiplied both denominator and numerator degrees of freedom with the Huynh-Feldt epsilon before calculating the significance of the F-ratios (Norusis, 1988). Bartlett's F-tests were used to check the homogeneity of variances of mean responses within treatments.

RESULTS

Responses of Neonates.—Tongue flick rates (TFR) of juveniles differed among test situations (ANOVA, $F = 4.58$, $df = 2,32$, $P = 0.02$), and were higher in the cages that had previously held snakes ($F = 7.6$, $df = 1,16$, $P = 0.01$). Tongue-flick rates were comparably high in the viper and smooth snake tests ($F = 2.5$, $df = 1,16$, $P = 0.3$). With the sole exception of Stand up, all behavioral acts recorded varied in frequency or duration among test situations (Table 1). The juvenile lizards reacted to chemicals of both snakes with an increased number of Starts ($P = 0.02$), Tail vibrations ($P < 0.001$), and Foot shakes ($P = 0.06$). The total duration of Slow Motion ($P < 0.001$), Run ($P = 0.001$), and No move ($P = 0.001$) was higher in the snake cages, whereas the duration of Walk ($P < 0.001$) and Bask ($P < 0.001$) was higher in the control situation. Behavior in both snake situations was similar, although the viper chemicals seemed to elicit a higher number of Tail vibrations than the smooth snake chemicals ($P = 0.03$). Also, the duration of Walk was shorter ($P = 0.002$) and that of Slow motion longer ($P = 0.001$) in the viper cages than in the smooth snake cages.

Comparing Neonates with Adult Lizards.—A detailed account of the responses of adult male lizards to analogous experimental treatments is given in Thoen et al. (1986).

Tongue-flick rates of juvenile lizards closely resembled those of adult lizards in all three test situations (Fig. 1). Although the young lizards in the snake cages shifted their locomotory pattern from Walk to Slow motion in a way that closely paralleled the reaction of the adult lizards, their behavioral response differed somewhat in other aspects. Snake odors, especially the viper chemicals, elicited many more Starts and Food shakes in adult lizards than they did in juveniles (the difference in the number of Foot shakes is probably underrated because not all adult Foot shakes were registered). Juvenile lizards were infrequently seen basking in the

TABLE 1. Mean (±1 SD) duration or frequency of distinct behavioural acts displayed by naive juvenile common lizards in three experimental situations. F- and *P*-values (repeated measurements analyses of variance with 2 and 32 df) measure the overall effect of treatment; superscripts common in a row denote values that do not differ significantly.

	Control	Smooth snake	Viper	F	*P*
Tongue flicks*	392.1 ± 135.2	480.4 ± 118.9^a	532.2 ± 186.4^a	4.58	0.02
Walk†	614.0 ± 156.2	361.5 ± 125.2	208.1 ± 213.4	34.38	<0.001
Slow motion†	7.3 ± 14.6	106.9 ± 87.1	350.6 ± 188.4	39.79	<0.001
Run†	1.0 ± 2.3	7.5 ± 9.1	1.5 ± 2.5	8.11	0.001
No move†	497.1 ± 208.8	715.6 ± 101.1^a	639.1 ± 184.9^a	9.07	0.001
Bask†	78.06 ± 91.5	6.0 ± 17.2^a	0.0 ± 0.0^a	11.05	<0.001
Stand up†	2.5 ± 5.2^a	2.4 ± 3.1^a	0.6 ± 2.0^a	1.37	0.3
Starts*	0.1 ± 0.3	0.8 ± 0.8^a	1.9 ± 3.0^a	4.30	0.02
Foot shakes*	0.06 ± 0.2	1.2 ± 2.5^a	1.6 ± 2.4^a	3.06	0.06
Tail vibrations*	0.6 ± 1.2	6.2 ± 4.7	3.1 ± 4.6	10.46	<0.001

* Frequency/20 min.

† Duration (sec/20 min).

control experiments, and almost never in the viper and smooth snake cages; adults basked more than juveniles in the control situation, and the presence of snake chemicals did not alter the duration of basking. In all three test situations, young lizards spent more time performing the Run behavior, but engaged less in Stand up than adults.

DISCUSSION

Juvenile *Lacerta vivipara* that were born in the laboratory and that had not experienced prior contacts with natural predators have the ability to detect chemicals deposited by two species of predatory snakes. As evidenced by the elevated number of tongue-flicks, naive juvenile lizards intensively examined substrates that were labelled with predator-derived chemicals. The intense chemosensory (or vomerolfactory—Cooper and Burghardt, 1990) exploration of predator odors elicited a shift in general behavior: lizards moved more slowly and displayed Tail vibrations, Foot shakes, and Starts. These chemoreceptive and behavioral responses are highly similar to that observed in adult male common lizards (Thoen et al., 1986; Van Damme et al., 1990). We therefore conclude that both the chemosensory capacities to detect odors of two predatory snakes, and the subsequently induced suite of behavioral shifts, are congenital in this lizard species.

The adaptive significance of the innate ability to recognize viper chemicals seems apparent in this particular population of lizards, as their natural home site is inhabited by a relatively dense population of this predatory snake. Moreover, as the common lizard is highly precocious and asocial, learning from parents or other conspecifics seems an improbable way of developing a predator recognition system. Also, although we have no exact data on the success rate of vipers attacking common lizards, the predatory skills of the venomenous *Vipera berus* may be too high to allow lizards to develop an aversion for it via personal experience learning. It is less clear why the lizards under study should be able to detect *Coronella austriaca* chemicals as well, because this snake, although clearly a predator of common lizards in other areas, is allopatric to this particular population. Possibly, (1) lizards react to (a range of) chemicals that are shared by a variety of snake species, or (2) the ability to recognize smooth snakes is vestigial in this population, stemming from a time when lizards were sympatric with *C. aus-*

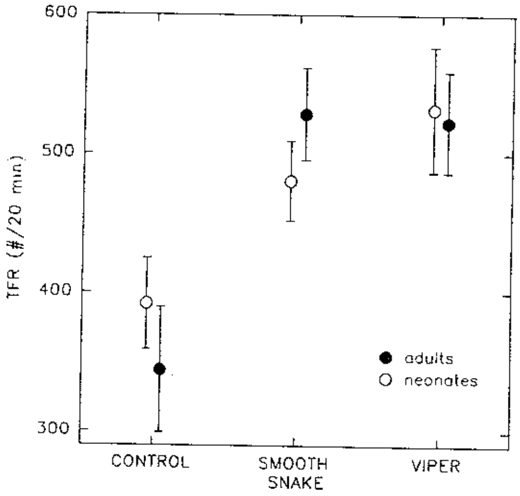

FIG 1. Mean (±1 SE) number of tongue flicks exhibited by adult (closed circles, data from Thoen et al., 1986) and naive juvenile (open circles) common lizards during a 20 min stay in an unfamiliar but otherwise clean terrarium (control), and in terraria with chemical cues from predatory snakes (smooth snake and viper).

triaca We are currently investigating geographical variation in *Lacerta vivipara*'s chemoreceptive abilities to elucidate this problem.

Our observations demonstrate only minor age-related differences in the behavioral responses following detection of predator chemicals. In both juveniles and adults, the presence of snake chemicals restricted the overall mobility of the lizards, and induced a characteristic change from the normal type of locomotion (Walk) to a jerky, hesitating kind of movement (Slow motion). Nevertheless, juveniles and adults differed in the number of Foot shakes and Starts displayed in the presence of snake chemicals: the frequency of both acts was higher in adults than in juveniles. Although the exact function of both behaviors remains to be clarified, they are typically exhibited in conflict situations (Verbeek, 1972; Thoen et al., 1986), and might therefore be indicative for stress. One possible interpretation of the observed age-related difference in the frequency of Foot shakes and Starts could therefore be that adult lizards, through prior experience or as a result of selection, are more aware of predatory risks associated with the presence of snake chemicals. However, this interpretation is not supported by our results for other behavioral acts: the increase in the number of Tail vibrations and the duration of Slow motion, presumably also indicative of extreme awareness or stress (Thoen et al., 1986), was highly similar in adults and juveniles.

The most important quantitative difference in response between adults and juveniles concerned the thermoregulatory behavior: in the presence of snake chemicals, juveniles almost completely refrained from basking, whereas adults basked equally long in all three test situations. These differences in basking patterns might arise from age-related variation in thermal preferences (Van Damme et al., 1986) or heating rate (Porter and Gates, 1969; Porter et al., 1973; Porter and James, 1979). However, although we took great care to mimic the set-up and procedures used by Thoen et al (1986), we cannot rule out the possibility that minor deviations in experimental treatment, rather than ontogenetic factors, are responsible for the behavioral differences observed here. The difference in time spent in captivity (adults: 14 d, juveniles: 40–50 d) prior to behavioral testing is one such source of variation. Earlier testing of juveniles was not practical however, because of the difficulty of handling the small animals.

Our data demonstrate that the capacity of chemosensory detection of snake chemicals is congenital in the common lizard. The behavioral response that follows identification of the deposits seems subject to minor ontogenetic changes. This finding raises new, interesting questions on both the proximal mechanism of recognition and on its evolution. Potential future research topics include the characterization and identification of the chemicals involved, analysis of the interindividual and interpopulational variation in behavior and its genetic basis, and assessing its survival value in natural conditions.

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