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Stimulus Control of Predatory Behavior by the Iberian Wall Lizard (*Podarcis hispanica*, Sauria, Lacertidae): Effects of Familiarity With Prey

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The authors examine the relative roles of vision and chemoreception and the influence of previous experience with prey on the predatory behavior of Iberian wall lizards (*Podarcis hispanica*). Experiment 1 compared the responses to visual, chemical, and a combination of visual and chemical cues of a familiar prey by 2 groups of lizards that had been kept in captivity for either 3 months or 21 days. Experiment 2 assessed the responses of lizards kept in the laboratory for more than 3 months to a novel prey species. The results reveal that feeding on a prey species affects the lizards' responses to chemical stimuli from that prey. The response to chemical cues of a novel prey requires a 1st-feeding experience with that prey. Lizards that have been fed the same prey species for several months cease responding to the chemical stimuli of that particular prey.

Predators use different sensory modalities to detect and recognize prey; indeed, every known sensory modality has been shown to be used by some predator for this purpose (Curio, 1976). Many predators do not rely on a single sensory modality for predation. Research on the stimulus control of prey detection and recognition in squamate reptiles has attributed a predominant role to chemical and visual stimuli (Burghardt, 1970, 1990; Simon, 1983). When several senses are involved in prey detection and recognition, the question arises as to how the different sensory modalities interact. Early work with amphibians suggested that predatory behavior in this group is almost exclusively controlled by visual stimuli (Eibl-Eibesfeldt, 1952; Ingle, 1968; for a review, see Ewert, 1987). However, more recent studies have demonstrated that some anurans and urodeles detect, localize, and capture prey more efficiently when visual stimuli are combined with chemical stimuli (Lindquist & Bachmann, 1982; Luthardt & Roth, 1983; Uiblein, 1992). Similarly, studies with snakes have suggested a synergistic effect of visual and chemical prey stimuli: In colubrid snakes, chemical prey stimuli are necessary and sufficient to elicit a predatory attack, but a combination of chemical and visual stimuli results in a more intense predatory response (Burghardt & Denny, 1983; Chiszar, 1990; Drummond, 1985; Shivik, 1998). In contrast, the interaction of different sensory modalities on the control of predatory behavior in lizards has been relatively neglected. However, work on skinks (Hasegawa & Taniguchi, 1993; Nicoletto, 1985a, 1985b) and varanids (Kaufman, Burghardt, & Phillips, 1996) has suggested that predatory behavior in lizards may depend on a complex interaction of different sensory stimuli.

There is ample evidence that experience and learning can affect the behavior of predators (e.g., Krebs & Inman, 1994). However, the influence of a predator's experience on the interaction between different sensory modalities used to detect and recognize prey remains largely unexplored. Few studies have investigated the ontogeny of prey-chemical discrimination in lizards (Burghardt, 1973; Brockhusen-Holzer & Curio, 1990; Cooper & Hartdegen, 2000; Cooper & Lemos-Espinal, 2001; Garrett & Card, 1993; Loop & Scoville, 1972), and evidence concerning the influence of feeding experience on chemoreception is very scarce (Cruz-Neto & Andrade, 1993). In contrast, there are several studies dealing with the ontogeny of prey-chemical discrimination in snakes (for reviews, see Burghardt, 1990, 1993). Some snakes show congenital preferences for certain prey extracts, and such preferences can to some extent be altered by experience. In particular, the response to prey-chemical stimuli presented on cotton-tipped applicators can be modified by previous experience with prey extracts (Burghardt, 1969), habituation (Burghardt, 1977; Czaplicki, 1975), avoidance learning (Burghardt, Wilcoxon, & Czaplicki, 1973; Terrick, Mumme, & Burghardt, 1995), and diet (Burghardt, 1990; Fuchs & Burghardt, 1971). These studies have suggested that experience plays a crucial role in the predatory behavior of snakes, particularly in generalist species. A similar conclusion has been reached through research on generalist species belonging to other taxa, such as fish (e.g., Croy & Hughes, 1991).

The aim of this study was to investigate the relative importance of chemical and visual prey stimuli in eliciting predatory behavior

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in the Iberian wall lizard (*Podarcis hispanica*, Sauria, Lacertidae). Like other lacertid lizards, *P. hispanica* is capable of detecting and identifying prey odors presented in cotton-tipped applicators (Cooper, 1990; Font, 1996). Conversely, laboratory observations of feeding in *P. hispanica* suggest that visual stimuli are sufficient to elicit a predatory attack, as lizards attack familiar prey without previous tongue-flicking. However, the same lizards direct tongue-flicks to unfamiliar prey (Desfilis, 1999; Desfilis, Font, & Gómez, 1993). These observations indicate that previous experience with prey is an important factor in relation to the sensory stimuli used for prey recognition. Thus, a second aim of this study was to examine the effects of feeding experience on the stimulus control of predatory behavior in *P. hispanica*.

General Method

Subjects

Subjects were adult male Iberian wall lizards (*Podarcis hispanica*) wild caught by noosing in Burjasot, Valencia, Spain. In the laboratory, the lizards were housed individually in glass or Plexiglas terraria (25 × 30 × 50 cm) kept in a temperature-controlled room (21–28 °C). Each terrarium was equipped with a 40-W bulb that supplied light and a thermal gradient for behavioral thermoregulation 14 hr daily. The floor was covered with an artificial turf substrate. A small rock for shelter and basking and a water dish were also available inside the terrarium. From their arrival in the laboratory, the lizards were fed 2–3 times per week with mealworms. This diet was supplemented with a vitamin complex (A+D3; Solvay Duphar BV; Weesp, the Netherlands) added periodically to the water dish. All subjects were fed as described until 5 days prior to the first experimental day and were not fed again until completion of the study to ensure adequate motivation to respond to prey stimuli.

After completion of the study, all the lizards were released at their site of capture. No general deterioration in condition was observed during the time that the lizards remained in captivity. The lizards stayed healthy and their body mass at the time of release was typical of wild lizards of similar size.

Prey Types

Mealworms (*Tenebrio molitor* larvae, Coleoptera, Tenebrionidae) and waxmoth larvae (*Galleria mellonella*, Lepidoptera, Pyralidae) of similar size (22–26 mm in length) were the prey types used in the experiments. Both prey types were obtained from our own breeding colonies maintained in the Ethology Laboratory at the Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia. In the laboratory, lizards readily attack and eat both prey types. Although coleopteran and lepidopteran larvae are part of the natural diet of *P. hispanica* (for a review, see Desfilis, 1999), mealworms and waxmoth larvae are not easily available prey in the field. Therefore, the lizards used in these experiments probably did not have any previous experience with these particular prey species.

Experimental Procedure

During the experiments, we tested each lizard with four stimulus conditions (see Figure 1). In the visual plus chemical cues condition (Condition V+C), there were two live prey items inside an air-tight glass vial (5 ml) with a plastic cap. The glass vial was secured with a piece of sticky material (blue tack or sticky tack) on top of a circular section of filter paper 5 cm in diameter to prevent the lizards from knocking the vial over. The filter paper had been previously impregnated with prey odor by placing it in a flask that contained 30 live prey items for 1 hr prior to the experiment. In the visual cues condition (Condition V), a vial containing prey was placed on top of a circle of clean filter paper. In the chemical cues condition (Condition C), an empty vial was placed on a circle of filter paper impregnated with prey odor as in the first condition. In the blank condition (Condition B), an empty vial was placed on a circle of clean filter paper.

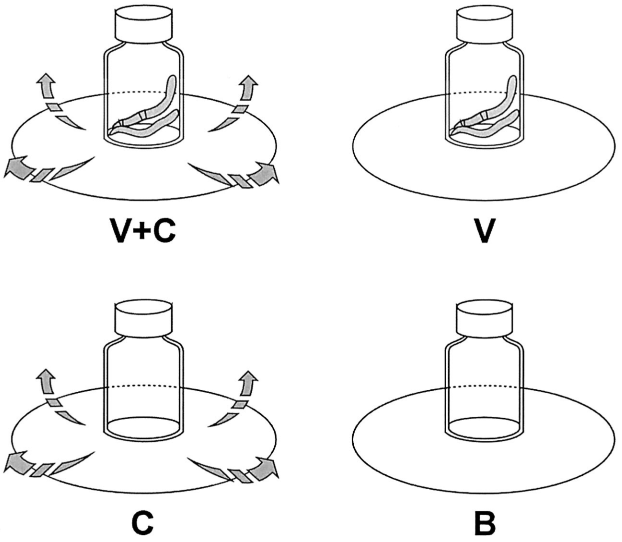

Figure 1. Schematic representation of the setup used for testing lizards' responses in the control (B), visual (V), chemical (C), and visual plus chemical (V+C) conditions. Visual stimuli were provided by two live prey items. Chemical stimuli were added to the circle of filter paper by placing it in a flask containing 30 live prey items.

Each lizard was tested by introducing one of the stimulus combinations in its home terrarium, one per day, on 4 consecutive days. The order of presentation was counterbalanced. One hour before testing, we removed the rock and the water dish from the lizard's terrarium. During testing, the room lights were dimmed and a radio receiver was turned on to provide a uniform acoustic background. Ambient air temperature at the time of testing was 25 ± 1 °C. All testing took place between 11:30 a.m. and 3:30 p.m., local time. The trial began when the experimenter placed the appropriate stimulus in the center of the lizard's terrarium, directly underneath the light bulb. The lizard was observed for 1 min; if during this time the lizard did not respond (i.e., did not walk or perform any of the behaviors listed below), the trial was terminated and the lizard was assigned a response latency of 60 s. If the lizard responded, we recorded its response latency in seconds and observed its behavior during a further 3-min period. During this period, we recorded the following behaviors using a portable computer equipped with event-recording software (slightly modified from Unwin & Martin, 1987): (a) latency to the first tongue-flick; (b) directed tongue-flicks, that is, number of tongue-flicks directed at the stimulus (glass vial and/or paper circle)—a tongue-flick was considered to be directed at the stimulus if the tongue actually touched the vial or the paper or came within 1 cm of it with the lizard facing the stimulus; (c) undirected tongue-flicks, that is, number of tongue-flicks directed away from the stimulus (at the substrate, air, or terrarium walls); (d) contacts, that is, number of times the lizard touched the vial with its mouth closed; (e) attacks, that is, number of times the lizard touched the vial with an open mouth or bit the filter paper; and (f) lip-licks, that is, number of times the lizard wrapped its tongue around the rims of the mouth (see Figure 2C in Desfilis et al., 1993).

Because of the presence of several zero values, we could not assume that the data follow a normal distribution, and therefore, we used nonparametric statistical tests (Siegel & Castellan, 1988; Zar, 1999). We used Friedman tests followed by nonparametric comparisons of control (Condition B) with other conditions (Dunnett's procedure) to test for differences between the four conditions. We used Wilcoxon–Mann–Whitney tests to compare two independent samples (see below) and Wilcoxon signed-ranks tests to analyze the difference between two related samples (e.g., comparisons between two conditions). We corrected for multiple comparisons using the sequential Bonferroni procedure of Holm (1979; see also Wright, 1992). Although unadjusted probabilities are given in the results, individual tests reported as significant were significant after adjusting to maintain a 5% experimentwise error rate.

Experiment 1

The purpose of this experiment was to determine the relative importance of visual and chemical stimuli in eliciting chemosensory exploration (i.e., tongue-flicking) and prey attack in *P. hispanica* lizards that differed in their prior feeding experience (i.e., time in captivity).

Method

The subjects were 23 adult male *P. hispanica* (45–60 mm snout–vent length). These lizards differed in the time they had been kept in the laboratory and, therefore, in their feeding experience with mealworms. Eleven lizards that had been in the laboratory for 21 days prior to the experiment formed the 21-days group (prior to the experiment, they ate 5–9 mealworms). The 3-months group comprised 12 lizards that had been kept in the laboratory between 3 and 5 months during which time they were fed two or three times per week with mealworms (they ate a minimum of 36 mealworms). Trials followed the procedure previously described using mealworms as prey.

Results

Three lizards did not respond in any of the four trials and were not included in the analysis. In Condition B, 8 lizards did not respond (3 in the 21-days group and 5 in the 3-months group), and 12 walked around the terrarium tongue-flicking at the substrate and the terrarium walls but paid little attention to the stimulus (vial plus paper). In contrast, the conditions that included visual prey cues stimulated investigatory behavior directed at the stimulus such as approach and tongue-flicking. However, the two groups of lizards differed in their responses to the chemical cues when these were presented alone (Condition C). In the 3-months group, only 2 lizards out of 10 approached and directed tongue-flicks at the chemical stimulus. In contrast, 7 lizards out of 10 in the 21-days group approached and directed tongue-flicks at the stimulus in this condition. When the condition included prey chemical cues, the lizards often performed intense upward and downward movements of the floor of the mouth before moving ("buccal pulsing"; Dial & Schwenk, 1996). The lizards then approached the stimulus, directing tongue-flicks at the air and substrate. To test if the lizards were capable of detecting chemical prey cues from a distance, we compared the latency to the first tongue-flick in the two conditions lacking visual prey stimuli (Condition C vs. Condition B). The latency to the first tongue-flick was lower in Condition C than in Condition B: Wilcoxon signed-ranks test, $T(N = 10) = 50.5$, $p < .01$. Lip-licks are not included in the results because they occurred at a very low rate.

Response latency. Figure 2A presents mean response latency data for both groups of lizards. In the 3-months group the response latency in the conditions increased in the order $\mathrm{V+C} < \mathrm{V} < \mathrm{C} < \mathrm{B}$, but the differences between conditions were not significant: Friedman test, $\chi^2(3, N = 10) = 2.75$, *ns*. In the 21-days group, the response latency was similar in the three conditions including prey cues and higher in Condition B, although these differences were again not significant: $\chi^2(3, N = 10) = 7.00$, *ns*.

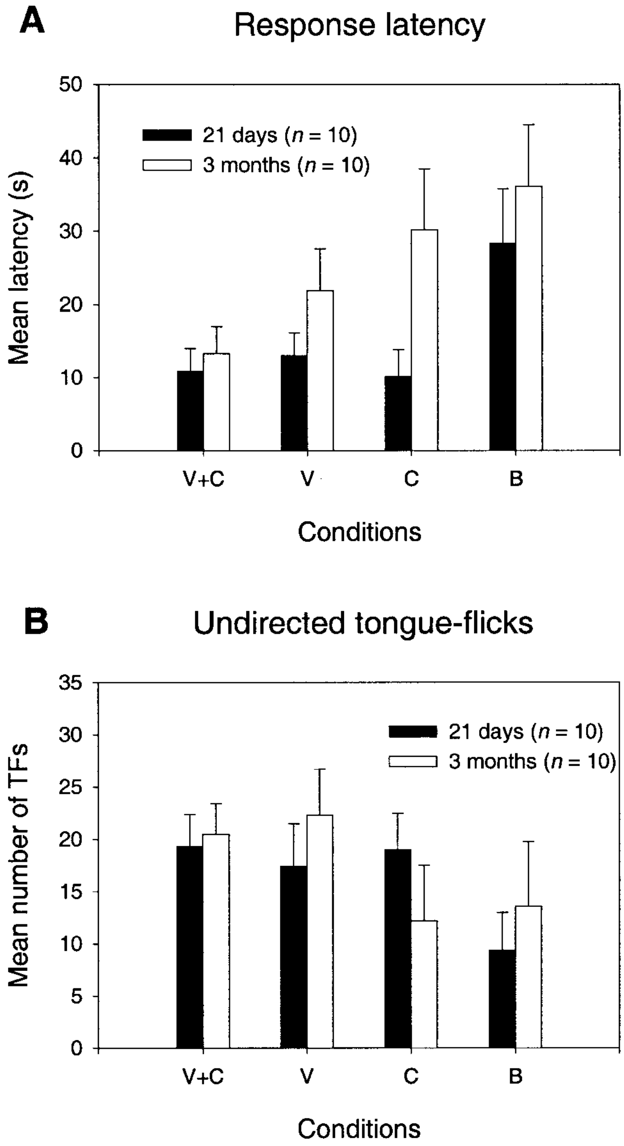

Figure 2. A: Mean (+ *SE*) response latency to a familiar prey for the lizards in Experiment 1. The two groups of lizards differed in the time that they had been kept in captivity: 21 days for one group and 3 months for the other. There were no statistically significant differences among conditions (Friedman tests). B: Mean (+ *SE*) number of undirected tongue-flicks (TFs) emitted in each of the four conditions by the two groups of lizards in Experiment 1. There were no statistically significant differences between conditions (Friedman tests). V+C = visual plus chemical cues; V = visual cues; C = chemical cues; B = blank (control).

Tongue-flicks. The mean number of tongue-flicks directed at the air or terrarium was similar in the four conditions for both groups of lizards: 21-days group, $\chi^2(3, N = 10) = 4.48$, *ns*; 3-months group, $\chi^2(3, N = 10) = 7.62$, *ns* (see Figure 2B). In contrast, there were statistically significant differences between conditions in the number of tongue-flicks directed at the stimulus: 21-days group, $\chi^2(3, N = 10) = 19.41, p < .001$; 3-months group, $\chi^2(3, N = 10) = 25.41, p < .001$. Multiple comparisons of the experimental conditions (V+C, V, and C) with Condition B showed that lizards in the 21-days group directed more tongue-flicks at the stimulus in the conditions in which visual and/or chemical cues were present ($p < .05$, for each comparison). Conversely, lizards from the 3-months group showed increased tongue-flicking only in Conditions V and V+C ($p < .05$) and not in Condition C. Lizards from the 21-days group emitted more tongue-flicks in Condition C than those from the 3-months group: Wilcoxon–Mann–Whitney test, $W_x(n_1 = 10, n_2 = 10) = 68, p < .004$ (see Figure 3A).

Attacks and contacts. Three lizards from each group did not attack the stimulus in any condition. No lizard attacked in Condition B, and only 2 lizards from the 21-days group attacked (bit the paper) in Condition C. Visual cues elicited attack behavior in some lizards from both groups. Lizards performed more attacks in Condition V+C than in Condition V (because their attack response was similar, we pooled the data from both groups for statistical analysis): $T(N = 13) = 85.5, p < .002$ (see Figure 3B).

There was considerable variation among individuals in the rate with which they performed closed mouth contacts with the vial. Lizards from both groups performed contacts only when visual prey cues were present.

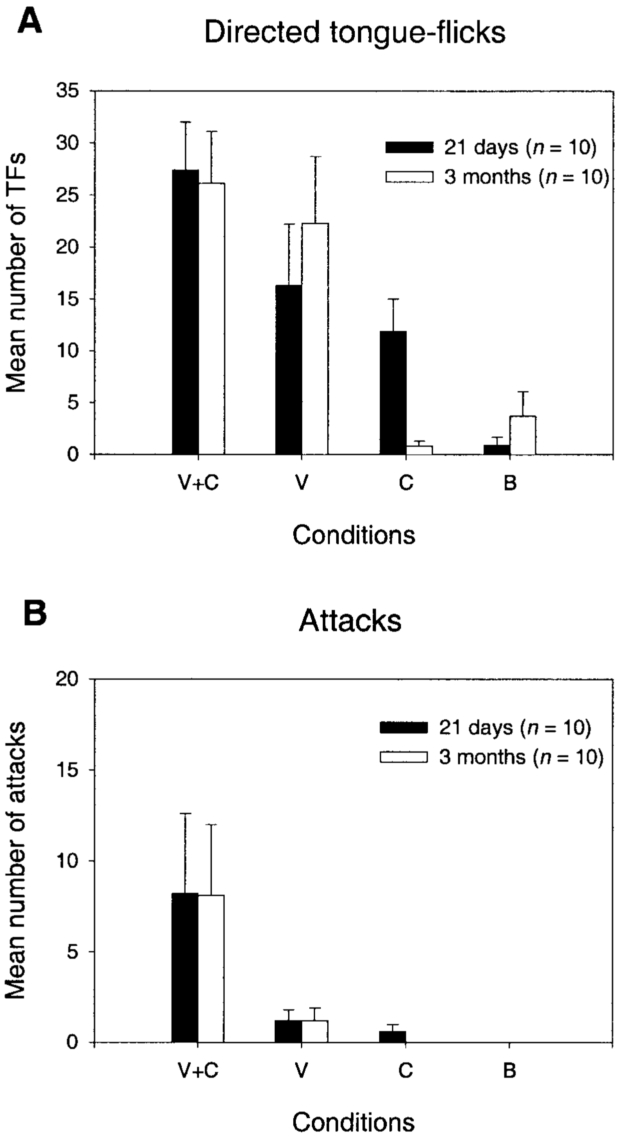

Figure 3. A: Mean (+ *SE*) number of tongue-flicks (TFs) directed at the stimulus (vial plus paper) by the two groups of lizards in Experiment 1. The two groups of lizards differed in the time that they had been kept in captivity: 21 days for one group and 3 months for the other. There were statistically significant differences among conditions for both groups of lizards (Friedman test for each group, $p < .001$). B: Mean (+ *SE*) number of attacks in response to a familiar prey for the two groups of lizards in Experiment 1. V+C = visual plus chemical cues; V = visual cues; C = chemical cues; B = blank (control).

Experiment 2

Results from Experiment 1 show a lower rate of tongue-flicking directed to prey chemical cues in the 3-months group. Because the two groups of lizards differed not only in their feeding experience but also in the length of their captivity, the lower responsiveness of the 3-months group could be explained in two ways. Captivity conditions could affect the lizards' behavior by reducing their responsiveness to chemical stimuli of any kind. Alternatively, the stimulus control of predatory behavior in these lizards could be affected by their familiarity with prey. That is, lizards that are confronted repeatedly with a prey type may end up losing interest in the chemical cues of that particular prey, perhaps because they learn (through prolonged or frequent exposure to prey chemicals) that chemical cues alone do not lead to food in the laboratory environment. To discriminate between these two explanations, we performed an experiment with a group of lizards that had been kept in the laboratory for more than 3 months, but this time we used a prey type that was novel to them. In generalist lizards such as *P. hispanica*, a single contact with prey could be necessary (and perhaps sufficient) to learn the visual and/or chemical cues of that particular prey type. Therefore, in this experiment, each lizard was tested twice: once before and once following their first experience with the novel prey.

Method

Fifteen experimentally naive, adult males of *P. hispanica* were used. They had been maintained in the laboratory for more than 3 months prior to this experiment, during which time they were fed mealworms two or three times weekly. The basic procedures for this experiment were identical to those of Experiment 1 except that each lizard was tested twice using waxmoth larvae as prey. In the first test (naive test), the lizards did not have any previous experience with this prey species. Following the last trial of the first test, the lizards were fed two waxmoth larvae, and 5 days later they were tested again (experienced test).

Results

Only lizards that responded in at least one condition in each of the two tests were included in the analysis, bringing the sample size down to 10 lizards. In general, the results were similar to those of Experiment 1. In both tests, there were differences among conditions in the number of tongue-flicks directed at the stimulus: naive test, $\chi^2(3, N = 10) = 12.76, p < .01$; experienced test, $\chi^2(3, N = 10) = 12.26, p < .01$ (see Figure 4A). In the naive test, lizards directed more tongue-flicks at the stimulus in the two conditions including visual cues than in the control condition ($p < .05$). However, there was no statistically significant difference in the number of tongue-flicks between Conditions C and B. In contrast, in the experienced test (after a single exposure to waxmoth larvae), lizards emitted more tongue-flicks directed at the stimulus in all three conditions bearing prey stimuli (V+C, V, and C) than in Condition B ($p < .05$, for each comparison). The number of tongue-flicks directed at the stimulus in Condition V was lower in the experienced test than in the naive test: $T(N = 9) = 41.0, p < .015$.

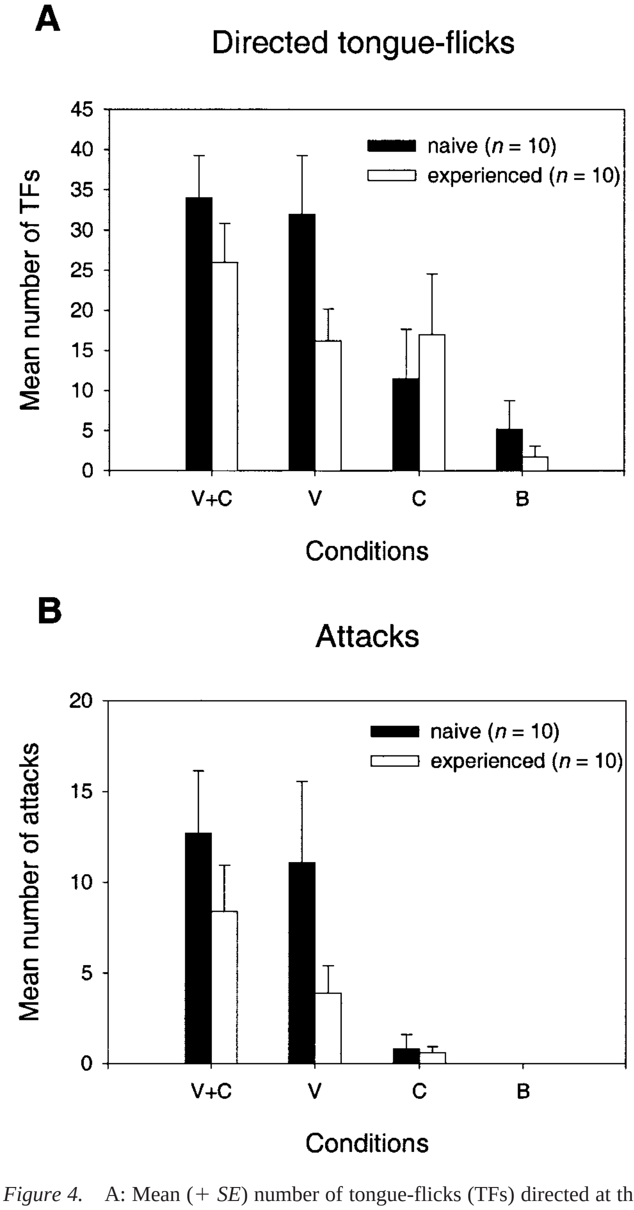

Figure 4. A: Mean (+ *SE*) number of tongue-flicks (TFs) directed at the stimulus in the four conditions used in Experiment 2. The lizards had been kept in the laboratory for more than 3 months. Lizards were tested twice: before (naive) and after (experienced) their first experience with a novel prey. Friedman tests revealed statistically significant differences among conditions in the two tests ($p < .01$, for each test). B: Mean (+ *SE*) number of attacks in the four stimulus conditions for the two tests (naive and experienced) in Experiment 2. V+C = visual plus chemical cues; V = visual cues; C = chemical cues; B = blank (control).

One lizard did not attack in any test, and another attacked only in the naive test. Most lizards attacked in the conditions including visual cues, but 1 lizard in the naive test and 3 in the experienced test bit the filter paper impregnated with chemical prey stimuli in the absence of visual prey stimuli (Condition C). In the naive test, there were no significant differences in the number of attacks between Conditions V and V+C: $T(N = 9) = 26.0$, *ns*. In this case, the lizards performed more attacks in the first presentation of any condition including visual cues: $T(N = 9) = 45.0, p = .004$. In contrast, in the experienced test, the number of attacks was, as in Experiment 1, higher in Condition V+C than in Condition V: $T(N = 7) = 28.0, p < .016$ (see Figure 4B).

General Discussion

The Role of Visual and Chemical Prey Cues in Predatory Behavior

The results of the present experiments reveal that visual cues from both familiar and novel prey trigger chemosensory exploration (i.e., tongue-flicking) and attack behavior, even in the absence of chemical prey cues. This suggests that *P. hispanica* lizards are capable of detecting and discriminating prey by visual stimuli alone. Several authors have stressed the importance of visual stimuli on predatory behavior in lizards belonging to other families. In general, visual cues appear to be important in locating prey and orienting predatory attacks in three-dimensional space (Cooper, 1981), in prey discrimination and selection (Askew, Musimeci, Sloane, & Stephan, 1970; Brockhusen-Holzer & Curio, 1990; Burghardt, 1964; Díaz & Carrascal, 1993; Kaufman et al., 1996; Reznick, Sexton, & Mantis, 1981), and in rejection of distasteful prey (Boyden, 1976; Hasegawa & Taniguchi, 1994; Sexton, 1964).

Our results further suggest a synergistic effect of visual and chemical cues, as lizards attacked more often when visual and chemical cues were combined than when only visual cues were available. Nicoletto (1985a) reported similar results in a study of the response of skinks (*Scincella lateralis*) to different combinations of chemical and visual prey cues. His study demonstrated that these lizards respond primarily to visual prey cues and that these are sufficient to elicit a predatory attack. However, tongue-flick rate increased in the order control < chemical < visual < visual plus chemical, suggesting an additive effect of chemical and visual cues. Some studies of the stimulus control of predatory behavior in snakes also suggest a synergistic effect of visual and chemical prey cues similar to that observed in our experiments (Burghardt & Denny, 1983; Chiszar, 1990; Drummond, 1985; Shivik, 1998). Similarly, Terrick et al. (1995) have demonstrated that aversive learning in *Thamnophis radix* is stronger when chemical prey cues are associated to aposematic visual cues.

Using cotton-tipped applicators, Cooper (1990, 1991) demonstrated that *P. hispanica* and *Podarcis muralis* lizards are capable of discriminating prey from nonprey odors. However, in his experiments with lacertid lizards, few animals attacked the applicator (only 1 of 5 *P. hispanica* and 3 of 9 *P. muralis*). Cooper (1994) noted that lizards initially tongue-flicked applicators bearing prey chemicals and then began tongue-flicking away from the applicators as if searching for prey. As Cooper (1994) pointed out, chemical stimuli may serve to identify prey, but other cues may be necessary to induce a predatory attack in these species. The results of our experiments using a different experimental design confirm that in the absence of visual prey cues, chemical cues are capable of eliciting predatory attacks in *P. hispanica*. However, attacks in the chemical cue condition were infrequent: Only 2 lizards in Experiment 1 and 4 in Experiment 2 attacked in this condition. It is possible that in our experiments neither the paper nor the vial provided an adequate visual stimulus to which lizards could direct attacks (although occasionally a lizard would bite the filter paper). In experiments using cotton-tipped applicators, the visual stimulus provided by the swab impregnated with prey chemical cues is probably sufficient to evoke the attack behavior. However, the effectiveness of the visual stimuli provided by the cotton swab (size, shape, contrast, and movement) in eliciting attack could show interspecific variability and/or be affected by the lizards' prior experience. These factors have not been considered in the numerous studies that have used this experimental approach.

In our experiments, lizards may have detected the chemical prey cues impregnating the filter paper using several chemosensory systems. Although olfaction and vomerolfaction are the most likely candidates for detection of prey chemicals, a possible involvement of taste can not be discarded because *P. hispanica* has abundant taste buds in its oral cavity (Font, 1996; Schwenk, 1985). Therefore, chemicals that the tongue introduces into the oral cavity during tongue-flicking could, in principle, stimulate both vomeronasal and gustatory systems. The intense buccal pulsing that preceded tongue-flicking in our experiments (which presumably functions in the chemoreception of volatile compounds; Dial & Schwenk, 1996) and the lower latency to the first tongue-flick in the chemical condition compared with the control condition together suggest that lizards may be able to detect chemical prey stimuli at a distance by nasal olfaction. Following a period of buccal pulsing, most lizards approached and investigated the stimulus using the tongue–vomeronasal organ system. These results provide indirect support for Cowles and Phelan's (1958) hypothesis of the different functions of the olfactory and vomeronasal systems.

Effects of Feeding Experience on the Response to Prey Stimuli

Our results reveal that feeding on a prey species affects the lizards' responses to chemical stimuli from that prey. The results of Experiment 1 show that lizards that have extended experience with a prey type do not approach and tongue-flick the paper with chemical stimuli of that particular prey. However, because a combination of visual and chemical cues elicits more attacks than visual cues alone, this result cannot be attributed to sensory adaptation or to the lizards' inability to detect and recognize chemical prey cues. Furthermore, lizards that have been in captivity for more than 3 months approach and explore the chemical cues of a new prey type (Experiment 2). The decrease in tongue-flicking to chemical cues from familiar prey could be caused by a mechanism of learned laziness (Engberg, Hansen, Welker, & Thomas, 1972) or learned irrelevance (Shettleworth, 1998). The lizard's terrarium could accumulate chemicals of a particular prey type (that which the lizard usually eats), so that to the lizard prey odor would not be a good predictor of the presence of prey. Lizards would therefore learn not to search when they detected chemical cues of familiar prey that were not accompanied by a visual stimulus because of the repeated lack of reward. Burghardt (1992) obtained similar results with newborn *Thamnophis sirtalis* snakes exposed for some days to chemical cues of fish or earthworm. In Burghardt's experiment, prey items were placed inside an opaque ceramic bowl covered with plastic screening, so that the snakes were exposed to chemical cues from prey but could not capture them. After a day in a clean cage without prey odors, each snake was tested with cotton-tipped applicators impregnated with chemical stimuli of worm or fish. Snakes responded less to the chemical stimuli of prey to which they had been exposed previously as did the lizards in the 3-months group in our experiment. As Burghardt (1992) pointed out, these results have important implications for the design and interpretation of experiments concerned with responses to chemical prey stimuli. The slight response of lizards to chemical prey stimuli observed in some experiments (e.g., Nicoletto, 1985a) could be caused by previous feeding experience with this prey or mere exposure to prey odors present in the laboratory.

The results of Experiment 2 suggest that the first time that *P. hispanica* lizards encounter a prey type, their response is likely based on perception of visual stimuli such as shape, size, contrast, and movement. After a successful predatory attack, lizards would associate chemical and visual stimuli of a particular prey type that they could later use for detecting, localizing, or discriminating other individuals of the same prey species. Feeding experiments with another lacertid (*Lacerta agilis*) suggest a similar interplay of visual and chemical cues (Svoboda, 1969, as cited in Curio, 1976).

Most reptiles are precocial species that do not exhibit parental feeding; so that after hatching, the young must find food for themselves. Therefore, it is generally expected that prey recognition should occur with the first encounter with prey, without the need for previous learning (Suboski, 1992). As a result, research on the ontogeny of predatory behavior in reptiles has mainly focused on innate prey recognition, and few studies have investigated the influence of previous experience or learning. Experimental work with colubrid snakes has demonstrated that newborn snakes recognize and attack chemical stimuli of prey that are part of their usual diet in the wild (for reviews, see Burghardt, 1990, 1993) and that these innate responses can be modified by dietary experience. In some species, experience with a prey increases the snakes' responses to chemical stimuli from that prey (Burghardt, 1990; Fuchs & Burghardt, 1971; Loop, 1970; Lyman-Henley & Burghardt, 1995). However, experiments with other snakes did not find an effect of diet on the response to prey chemical stimuli (Arnold, 1978; Dunbar, 1979; Ford & Burghardt, 1993; Gove & Burghardt, 1975; Mushinsky & Lotz, 1980). In lizards, Cruz-Neto and Andrade (1993) studied the effects of diet on the response to chemical prey cues in juvenile *Tupinambis teguixin* (Teiidae). Lizards fed with crickets responded more to the chemical cues of this prey, but lizards fed cattle or chicken meat responded equally to chemical cues of the three types of prey. However, care must be taken when interpreting this result because cattle and chicken are not part of the natural diet of these lizards.

Taken together, the results of our experiments reveal that previous feeding experience is a critical factor in the stimulus control of predatory behavior in *P. hispanica* lizards. The importance of this finding to natural foraging behavior in this species and the extension of this research to other reptiles are interesting areas for future investigation.

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