

The influence of prey-scent stimuli on predatory behavior of the North American copperhead *Agkistrodon contortrix* (Serpentes: Viperidae)

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Viperid snakes strike, envenomate, and release mammalian prey to prevent being harmed by the prey; snakes must then track prey in the process of strike-induced chemosensory searching. Because rattlesnakes prefer to track and consume envenomated prey, it would seem that the scent of envenomated tissue is key to the tracking process. After striking rodents, rattlesnakes also retain a specific chemical search image of prey items. I examined this behavioral pattern in copperheads (*Agkistrodon contortrix*) from three US populations with documented dietary biases toward mammals (Kansas), lepidopteran larvae (Texas), and amphibians (Louisiana), respectively. Experiments were conducted to assess whether copperheads form a specific search image of non-envenomated mouse, hornworm, and frog prey items. Additional experiments tested the relative importance of envenomated tissue to prey scent. Results indicate that copperheads do not form a specific search image of prey items. Preference for non-envenomated prey items is in the order mouse > hornworm > frog for all three populations; therefore, the innate behavioral preference for types of prey does not match the dietary biases noted in the literature. Envenomated mice and hornworms were preferred to all nonenvenomated prey items, but most trials involving envenomated frogs did not suggest envenomated prey preference. Overall, these results suggest that when the snakes search for prey, envenomated tissue stimuli are more important to snakes than scents arising from the prey itself. Searching and consumption behaviors seem to be independent, suggesting that strike-induced chemosensory searching and consumption are more complicated behavioral processes than previously recognized. *Key words:* *Agkistrodon contortrix*, chemoreception, prey, snake, behavior, venom. [*Behav Ecol* 15:345–350 (2004)]

The senses of taste and smell, collectively or individually known as chemoreception, are nearly ubiquitous among bacteria and multicellular animals (Norris, 1981). Chemical stimuli obtained during chemoreception can be used by animals to modify numerous essential behaviors, including foraging (Bernays and Chapman, 1987; Weissburg et al., 2002), predator avoidance (Brown and Zachar, 2002; Chiussi and Diaz, 2002), reproduction (Rittschof et al., 2002; Swaisgood et al., 2002), orientation (Burghardt, 1970), and aggression (Howse et al., 1986; Mathis and Simons, 1994). Moreover, chemoreception has been linked to studies of kin recognition (Main and Bull, 1996; Olsen et al., 2002) and numerous other intraspecific and interspecific interactions (e.g., Heise and Rozenfeld, 2002). Snakes rely on chemoreception for all of these behaviors, perhaps because of relatively poor visual and hearing abilities (Burghardt, 1970). The link between chemoreception and predatory behavior is especially strong among the vipers (Kardong and Smith, 2002), which often feed in complete darkness (Greene, 1997).

Viperid snakes are noted for their stereotyped behavioral adaptations to avoid counterattacks by rodents. Typically, these snakes will strike, envenomate, and release mammalian prey in rapid succession, thereby minimizing the chance of a defensive and damaging bite from the prey (Kardong and Smith, 2002). After striking, viperids use chemoreception to trail, locate, and consume prey (Chiszar et al., 1992). These actions are

associated with strike-induced chemosensory searching (SICS), a process that includes an elevated level of tongue-flicking and searching movements by the snake (Stiles et al., 2002). Some researchers have suggested that SICS is an “innate, structural feature of rattlesnake predation” (Chiszar et al., 1992: 369), which occurs in numerous other species of viperid, elapid, and colubrid snakes, as well as in several families of lizards (Chiszar et al., 1982; Cooper, 1989, 1993; Cooper et al., 1989; De Perno and Cooper, 1993; Radcliffe et al., 1986).

Tongue-flick counts have been used as an index of chemosensory investigation in many studies of squamate predatory behavior (Cooper and Burghardt, 1990; Kardong and Smith, 2002). Specifically, many studies of viperid SICS behavior have documented that individuals tongue-flick mammalian prey envenomated by a conspecific significantly more often than prey that is not envenomated, a common phenomenon in viperids (Chiszar et al., 1992, 1999; Lavin-Murcio and Kardong, 1995). These studies suggest that vipers are more responsive to chemical stimuli from envenomated mammalian tissue than they are to chemical cues produced by the prey itself (e.g., prey scent, urine, or alarm pheromones; Chiszar et al., 1992). However, a series of experiments on rattlesnakes demonstrated that after striking, snakes obtain a specific chemical search image of individual prey items and use this information to track their prey (Kardong and Smith 2002; Melcer and Chiszar, 1989). To date, no one has examined the relative importance of these prey-scent stimuli to snakes during chemoreceptive searching. Specifically, are scents related to the chemical search image of prey items more important to snakes than envenomated tissue cues?

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Received 25 March 2003; revised 29 May 2003; accepted 2 June 2003.

The North American crotaline viper *Agkistrodon contortrix* is an ideal organism with which to examine this phenomenon because the species has stereotyped viperid SICS behavior and prefers envenomated prey (Greenbaum et al., 2003; Stiles et al., 2002). Rodents are the main prey item of *A. contortrix* throughout its range from northeastern Mexico to Massachusetts (Gloyd and Conant, 1990), but members of local populations consume other types of prey (e.g., Louisiana: frogs; Dundee and Rossman, 1989; Texas: cicadas and lepidopteran larvae; Lagesse and Ford, 1996; Kansas: mammals; Fitch, 1960). These disparate and localized dietary preferences in *A. contortrix* provide an excellent opportunity to examine several aspects of the viperid SICS process.

I tested the behavioral responses of three populations of copperheads (*A. contortrix*) to non-envenomated (NE) prey items of mice, hornworm larvae, and frogs to determine whether these snakes (1) possess an innate behavioral preference for specific prey types and (2) form a specific chemical search image of prey items. Because the snakes would not strike and release hornworms or frogs in a predatory context, all SICS behavior was initiated by strikes to mice. Based on the results of previous experiments with rattlesnakes (Kardong and Smith, 2002), I hypothesized that copperheads would form a specific search image of struck mice and seek similar prey items during SICS. Moreover, I predicted that my hypothesis would be most strongly supported by data collected from Kansas copperheads, because this population is known to eat mainly mammalian prey, whereas the other tested populations (Texas and Louisiana) prey on invertebrates and anurans, respectively.

In another series of experiments, I tested the relative importance of envenomated (E) prey to NE prey during SICS. Because envenomated tissue seems to be more important than cues from the prey itself in previous studies, I predicted that all populations of copperheads would seek E prey, regardless of the type of prey (i.e., mouse, hornworm, or frog). I also examined what prey snakes consumed during all experiments. Previous work suggested that prey consumption is a different behavioral process from chemoreceptive trailing (Greenbaum and Jorgensen, in press). I predicted that snakes would consume prey items consistent with their respective population-level preferences noted in the literature (Dundee and Rossman, 1989; Fitch, 1960; Lagesse and Ford, 1996).

MATERIALS AND METHODS

Animal collection and maintenance

Adult copperheads (*A. contortrix*) from three populations (Kansas, Texas, and Louisiana, USA) with different dietary preferences (mammal, lepidopteran larvae, and amphibian, respectively) were collected from 15 May–30 June 2000 with the “bucket method” for safely collecting venomous snakes (Greenbaum, 2003). I collected 9 snakes from the vicinity of Lawrence, Kansas; 13 from the vicinity of Whitehouse, Texas; and 8 from the vicinity of Monroe, Louisiana. Individual snakes were housed in 10-gal glass cages (26 × 31 × 51 cm) lined with newspaper bedding and with brown-paper sides to shield the animals from distractions during experiments. Bowls of water were provided, and cages and water bowls were cleaned regularly with disinfectant quaternary ammonium. All animals were housed in a limited-access room with a relatively constant temperature (27.0 ± 1.0°C), humidity (50.0 ± 5%), and fluorescent lighting set for a daily 12 h light:dark cycle. Snakes acclimated to captivity for 6 weeks before behavioral experiments, which commenced in mid-August 2000. Based on results from previous experiments with the same snakes, there were no significant differences in length, weight, or

venom yields among snakes from the three populations (Greenbaum et al., 2003). Therefore, I assumed that the average amount of venom injected during behavioral experiments did not differ significantly among populations.

Laboratory-raised mice (15–20 g) were obtained from the Animal Care Unit, The University of Kansas (Lawrence, Kansas). Wild-caught, subadult (~20 g) northern leopard frogs (*Rana pipiens*) were obtained from Kons Scientific Company (Germantown, Wisconsin) and maintained on a diet of laboratory-raised crickets. Mature (10–15 g) tobacco hornworm larvae (*Manduca sexta*) were obtained from Carolina Biological Supply (Burlington, North Carolina) and frozen until needed for experiments.

Behavioral experiments

I modified behavioral experiments from previous studies of chemoreceptive behavior in squamates (Chiszar et al., 1999; Main and Bull, 1996). Each snake's cage served as a test arena for each trial. I began a trial by removing the cage lid and placing a small, 60 watt lamp over the cage to facilitate observation of behavior. After each snake was acclimated for 1–2 min, it was allowed to strike a live mouse, which was removed immediately (Chiszar et al., 1999). Then I placed a prey-presentation device in the cage on the side farthest from the snake (≥20 cm from the snake). This device consisted of two carcasses (mouse, hornworm, or frog), each in separate nylon bags that were suspended (10 cm apart and 2 cm from floor of cage) from a wooden beam across the top of the cage. Location of each prey item in either the right or left nylon bag was determined randomly. Nylon bags were washed with detergent and allowed to air dry between trials to remove prey scent and venom residue.

Before placement in nylon bags, NE mice and frogs were killed by CO₂ overdose; frozen hornworm larvae were defrosted in lukewarm water and rolled on clean paper towels to eliminate excess moisture. For experiments involving E prey items, I observed mice and frogs for 10 min after defensive (toward frogs) or predatory (toward mice) strikes by snakes to ensure that venom had been injected and that all prey's physical movements had ceased. Copperheads would not strike frogs in a predatory context, so I elicited defensive strikes by gently prodding snakes with frogs restrained with padded forceps. Because copperheads struck and did not release hornworm larvae (Kardong, 1986), I easily could observe snake fangs puncturing the body cavities of the hornworms to ensure envenomation.

I recorded the number of tongue flicks directed toward each prey item (within 2 cm of the bottom of the nylon bag) for 10 min during trials. At the end of each trial, I removed both prey items from the bags and offered them to the snake; the purpose was to evaluate whether the initial strike was a defensive or predatory response to the prey item. If the snake ate one of the items within 5 min, I classified its behavior as “predatory” (Chiszar et al., 1999). If a snake attempted to consume a prey item through a nylon bag during the last 2 min of a trial, I also interpreted the behavior as “predatory,” the trial was terminated, and the bitten prey item was recorded as “consumed.” If a snake crawled out of the cage, or remained stationary for the first 5 min, the trial was terminated and discounted.

Experiment 1 tested whether the snakes preferred prey items resembling the struck prey item (mice) when all prey items were NE. I placed different NE prey items (mouse, hornworm, or frog) in the nylon bags of the prey-presentation device in all possible combinations (mouse vs. hornworm, mouse vs. frog, and frog vs. hornworm). I recorded the number of tongue flicks directed at two NE hornworms and

two NE frogs, respectively, in two control experiments. The results of a control experiment for two NE mice did not indicate significant differences in a previous study that used the same test subjects (Greenbaum et al., 2003). The results of this experiment served as a control for the next experiment. In experiment 2, I tested whether the snakes could distinguish between E prey items (mouse, hornworm, or frog) even-omated by conspecifics in their own population versus NE prey items (mouse, hornworm, or frog). I used different types of prey items in all possible combinations (E mouse vs. NE hornworm, E mouse vs. NE frog, E hornworm vs. NE mouse, E hornworm vs. NE frog, E frog vs. NE mouse, E frog vs. NE hornworm).

Statistical analyses

All experiments followed a randomized, complete-blocks design to minimize differences in behavior caused by time of year or other unmanipulated variables (Sokal and Rohlf, 1995). Because some individual snakes rarely cooperated for experiments, there are some small differences in sample sizes among experiments within each population. At least 10 weeks elapsed between duplicate trials for individual snakes, thus minimizing the chance of one trial affecting the outcome of another. To test this assumption, I subjected these data to runs tests to search for autocorrelations among snakes (Sokal and Rohlf, 1995).

To reduce variability between individual snakes and to facilitate comparisons on the same scale, I converted number of tongue flicks directed toward each prey item to percentages of total number of tongue flicks for each trial (Chiszar et al., 1999; Duvall et al., 1980). An arcsine transformation was performed on these percentages to ensure normality and homogeneity of variance (Duvall et al., 1980). This step was essential to the statistical analysis because some individuals tongue-flicked prey excessively (e.g., >250 times), thereby inflating tongue-flick averages. I analyzed transformed data with a one-way ANOVA to test whether individual snakes differed in preference; if the ANOVA and all runs tests did not indicate significant differences, I combined all trials (including multiple trials from individual snakes) from each population. These data were then analyzed with the Student's one-sample *t* test. Because of small sample sizes, it was not possible to make adjustments to the significance level ($\alpha = 0.05$) to account for multiple *t* tests; thus, it is possible that a small number of Type I errors were made. I analyzed data on the type of prey consumed at the end of each trial with the sign test.

RESULTS

In all experiments, the one-way ANOVA did not indicate significant differences (all $p > .25$); thus, individual snakes did not differ in preference. All runs tests did not indicate significant differences (all $p > .10$). As a result of these tests and the long duration (10 weeks) between duplicate trials of individual snakes, I treated all trials within populations as independent data points and combined them for further analysis.

Experiment 1

In both control experiments, there were no significant differences in number of tongue flicks directed at the two NE prey items (hornworm or frog) for each population (all $p > .25$). In experiment 1, Kansas and Texas snakes did not significantly differ in number of tongue flicks between any two NE prey items (all $p > .1$; Figure 1). Louisiana snakes did not significantly differ in number of tongue flicks between NE

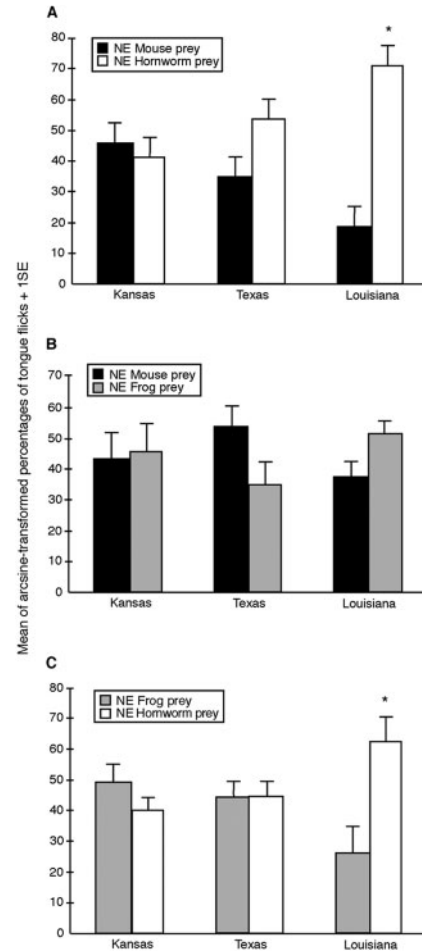


Figure 1

Mean (+ SE) of arcsine-transformed percentages of tongue flicks of three populations (Kansas, Texas, and Louisiana) of *Agkistrodon contortrix* directed at nonvenomated (NE) prey items. (A) Mouse versus hornworm trials; (B) mouse versus frog trials; (C) frog versus hornworm trials. *Significant differences in pairwise comparisons.

mice and NE frogs ($p > .2$), but there were significantly more tongue flicks directed at NE hornworms compared to NE mice ($t = 3.97$; $df = 11$; $p < .002$) and NE frogs ($t = 2.24$; $df = 11$; $p < .05$; Figure 1). Consumed prey items are summarized in Table 1; mice were preferred by all populations of snakes in five of six experiments involving mice, and hornworms were preferred by Texas and Louisiana snakes when mice were not a choice (significant sign tests: $p < .05$).

Experiment 2

The results of experiment 2 are shown in Figure 2. Snakes from Kansas preferred E mice over NE hornworms ($t = 3.02$; $df = 8$; $p < .02$) and NE frogs ($t = 5.50$; $df = 14$; $p < .000$); these snakes also preferred E hornworms over NE mice ($t = 2.64$; $df = 10$; $p < .03$) and NE frogs ($t = 3.74$; $df = 10$; $p < .004$). However, snakes from Kansas did not significantly differ in number of tongue flicks between E frogs and NE mice ($t = 1.12$; $df = 14$; $p > .28$) or NE hornworms ($t = 1.45$; $df = 7$; $p > .18$). Snakes from Texas also preferred E mice over NE hornworms ($t = 4.77$; $df = 13$; $p < .000$) and NE frogs ($t = 4.27$; $df = 11$; $p < .002$); these snakes also preferred E hornworms over NE mice ($t = 2.97$; $df = 8$; $p < .02$) and NE frogs ($t = 2.35$; $df = 11$; $p < .04$). Texas snakes did not prefer either prey item

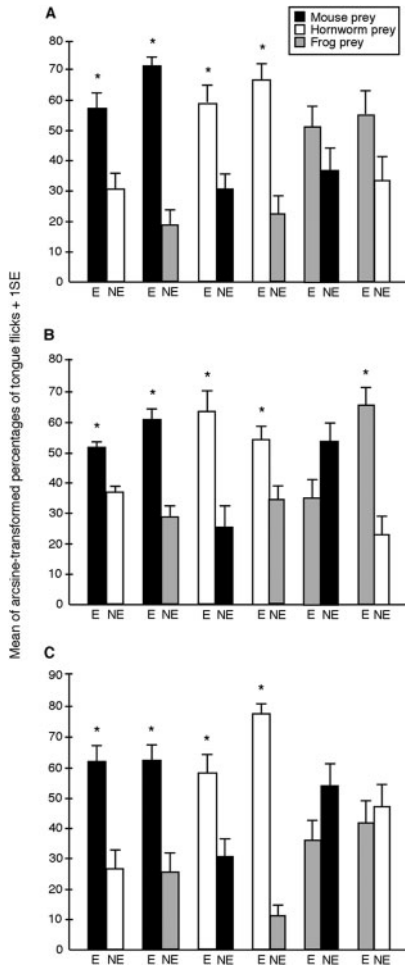


Figure 2 Mean (+ SE) of arcsine-transformed percentages of tongue flicks of three populations of *Aghkistrodon contortrix* directed at envenomated (E) and nonvenomated (NE) prey items. (A) Kansas; (B) Texas; (C) Louisiana. *Significant differences in pairwise comparisons.

in the E frog versus NE mouse trials ($t = -1.61$; $df = 11$; $p > .13$), but these snakes preferred E frogs over NE hornworms ($t = 3.94$; $df = 9$; $p < .004$). Snakes from Louisiana directed more tongue flicks at E mice than NE hornworms ($t = 3.32$; $df = 9$; $p < .01$) and NE frogs ($t = 3.61$; $df = 10$; $p < .01$); Louisiana snakes also preferred E hornworms over NE mice ($t = 2.33$; $df = 10$; $p < .05$) and NE frogs ($t = 9.00$; $df = 9$; $p < .000$). Louisiana snakes did not significantly differ in number of tongue flicks between E frogs and NE mice ($t = -1.17$; $df = 11$; $p > .26$) or NE hornworms ($t = -0.35$; $df = 11$; $p > .70$). As in experiment 1, snakes preferred to consume mice in 10 of 12 experiments that involved mice (significant sign tests: $p < .05$). Kansas snakes preferred to consume hornworms in the E hornworm versus NE frog trials, Texas snakes preferred to consume frogs in the E frog versus NE hornworm trials, and Louisiana snakes preferred to consume hornworms in both experiments that did not include mice (Table 1).

DISCUSSION

The results of experiment 1 demonstrate that copperheads from all populations directed tongue flicks at prey items randomly, or in the case of Louisiana snakes, at hornworms when given a choice between hornworms and mice or frogs

Table 1 Consumption of prey items by three populations of copperheads (*Aghkistrodon contortrix*)

Experiment	Kansas	Texas	Louisiana
NE M vs. NE H	M	ns	M
NE M vs. NE F	M	M	M
NE F vs. NE H	ns	H	H
E M vs. NE H	M	M	M
E M vs. NE F	M	M	M
E H vs. NE M	M	M	ns
E H vs. NE F	H	ns	H
E F vs. NE M	M	M	M
E F vs. NE H	ns	F	H

NE, nonvenomated prey; E, envenomated prey; M, mice; H, tobacco hornworm larvae; F, northern leopard frog; ns, not significant. Preferred prey items are listed under copperhead populations from Kansas, Texas, or Louisiana if they were statistically significant ($p < .05$) in a sign test.

(Figure 1). These results are not consistent with the hypothesis that *A. contortrix* forms a specific chemical search image of struck mice during SICS as do rattlesnakes (Kardong and Smith, 2002). Previous studies have demonstrated that rattlesnakes with lizard-biased diets (*Crotalus lepidus klauberi*; Chiszar et al., 1986; and *C. pricei*; Cruz et al., 1987) perform relatively deficiently during SICS compared with the rodent-specialist species *C. viridis*. The explanation posed by these researchers for this pattern is that rodent-specialist species have developed a more effective trailing behavior. This adaptive explanation seems feasible when one considers that rodent prey are typically struck, released, and trailed during SICS to prevent a damaging counterattack, whereas invertebrates, frogs, birds, and reptiles are struck and not released because they pose little or no threat to the predator (Fitch, 1960; Kardong, 1986). The results of experiment 1 are consistent with this adaptive explanation because *A. contortrix* is not a rodent specialist; even the Kansas population that is noted for eating mostly mammalian prey has been recorded to eat other types of prey including birds, cicadas, amphibians, and reptiles (Fitch, 1960).

The tongue-flick and consumption data in experiment 1 (Table 1) also suggest that copperheads do not seem to possess an innate behavioral preference for the types of prey they are noted to consume most in the wild; for example, Louisiana copperheads did not consume or direct more tongue flicks at frog prey, even though they are noted for eating more amphibians in the wild than any other type of prey (Dundee and Rossman, 1989). This finding is not surprising given the diversity of prey types *A. contortrix* eats in the wild (Fitch, 1960; Gloyd and Conant, 1990). Similar results have been reported for newborn *Elaphe quadrivirgata*, an Asian colubrid species that is a dietary generalist (Tanaka et al., 2001). Mainland populations of this species eat mainly frogs, whereas island populations primarily feed on lizards because frogs are not present. However, there were no significant differences in numbers of tongue flicks directed at lizard or frog prey for either population. Moreover, individuals from the island population readily ate frogs in captivity. Tanaka et al. (2001) hypothesized that some individuals of the island population retain the “ancestral” mainland ability to detect frogs as a potential prey item. For *A. contortrix*, it is likely that the many mammalian, invertebrate, and amphibian prey reported for the three copperhead populations from Kansas, Texas, and Louisiana, respectively, reflect prey availability; perceived dietary biases reported in the literature might be an effect of low sample sizes (Dundee and Rossman, 1989; Fitch, 1960;

Lagesse and Ford, 1996). It is possible that the preference for NE hornworms by Louisiana copperheads is a consequence of differences in strength of chemosensory cues among the prey items. However, this explanation is unlikely given the results of the Kansas and Texas copperheads in experiment 1, which did not indicate a preference for NE hornworms.

The prey-consumption data of experiments 1 and 2 (Table 1) suggest there may be an inherent behavioral preference in the relative order mouse > hornworm > frog. Because mice initiated all strikes by copperheads in this study, it is possible that the overall mammalian preference is linked to the initial strike. However, this explanation seems unlikely because the snakes did not prefer NE mice in experiments 1 or 2, which suggests the processes of chemoreceptive searching and consumption are independent behaviors (discussed below). A reasonable explanation of this innate consumption behavior might be that snakes are maximizing their nutritional intake; perhaps the relative nutritional value of the prey items matches the order of the consumption preference. Further studies are needed to explore all possible explanations of this interesting phenomenon.

The results of experiment 2 are mostly consistent (13 of 18 tests significant) with the hypothesis that envenomated tissue is the primary stimulus that viperids use to track their prey. This conclusion would not change even if a small number of the *t* tests contained Type I errors. Although numerous studies have documented the importance of envenomated tissue during SICS in a variety of viperid species (e.g., Baumann, 1929; Chiszar et al., 1992; Greenbaum et al., 2003; Greenbaum and Jorgensen, in press; Kardong and Smith, 2002), the results of experiment 2 demonstrate for the first time that scents of envenomated tissue override scents from the prey itself in the poststrike trailing behavior of a viper. One hypothesis to explain the nonsignificant results of the E frog experiments is that the frogs possess some resistance to the venom of copperheads (Heatwole et al., 1999). The frogs used in this study were the only prey items that were collected from the wild, and thus they are more likely to have resistance to snake venom than laboratory-raised animals. Numerous examples of an “arms race” between viperid venom and prey immunological resistance are discussed in the literature (e.g., Ovadia and Kochva, 1977; Perez et al., 1979; De Wit, 1982; Poran et al., 1987).

If envenomated tissue is the primary stimulus that copperheads use to track prey, one would predict that they would prefer to consume E prey after the completion of tracking; other studies with rattlesnakes have demonstrated a preference for E prey during tracking and consumption (Chiszar et al., 1992). However, previous studies used only one type of E or NE prey item (rodent) and noted either a strong correlation between E prey tracking and E prey consumption in highly proficient trackers (rattlesnakes: Chiszar et al., 1992), or random consumption of prey items in relatively deficient trackers (copperheads: Greenbaum et al., 2003). Before consuming prey, the snakes in the latter and present studies were observed making contact between their tongues and the integumentary surface of prospective prey items. This introduces a suite of stimuli that may not have been present through airborne chemoreception and might explain the disparity between trailing and consumption preferences noted in experiments 1 and 2. This finding suggests that chemoreceptive trailing and consumption are independent behaviors that rely on a different set of chemical stimuli, and both behavioral processes might be more complicated than previously recognized.

This work was approved by the Institutional Animal Care and Use Committee of the University of Kansas (proposal no. 76-02); I am especially grateful for the efforts of Nancy Schwarting, George Pisani,

and Eric Rundquist. For useful comments on the manuscript and grant proposals, I thank my colleagues in the Division of Herpetology, Oliver Komar, Christopher Raxworthy, Norm Slade, and John Kelly. This work was carried out with permits from the Kansas Department of Wildlife and Parks (permit no. SC-084-2000); Texas Parks and Wildlife Department (permit no. SPR0100-074); and Louisiana Department of Wildlife and Fisheries (permit no. LNHP-00-057). For field assistance, I am grateful to Hugo Alamillo, Barbara Banbury, Brett Benz, Alan Byboth, John Carr, Neil Ford, Ron Gutberlet, Mike Harrell, Steve Jensen, Chad “Leaf” Keith, Mike Monlezun, Christopher Sheil, Omar Torres, and Rod Wittenberg. Mike Jorgensen assisted me with data collection. Field equipment was generously donated by Midwest Custom Products Inc. (www.tongs.com). This work was supported by grants from the Chicago Herpetological Society, Kansas City Herpetological Society, Panorama Society (Natural History Museum, The University of Kansas), and Texas Herpetological Society (James R. Dixon Millennium Award).

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