Journal of Chemical Ecology, Vol. 30, No. 3, March 2004 (© 2004)

TIMBER RATTLESNAKES (*Crotalus horridus*) USE CHEMICAL CUES TO SELECT AMBUSH SITES

RULON W. CLARK*

Department of Neurobiology and Behavior
Cornell University
Ithaca, New York 14853, USA

(Received June 10, 2003; accepted November 12, 2003)

Abstract—Chemicals left by organisms moving through the environment are used by other organisms to mediate interspecific interactions. Most studies of chemical eavesdropping focus on prey responding to chemical cues from predators, despite the fact that chemical cues are frequently used by predators as a source of information about prey. *Crotalus horridus* uses a foraging strategy that is widespread among sedentary predators: the snake chooses a site where it is likely to encounter prey and remains immobile for many hours. I investigated this ambush hunting behavior in captive-raised timber rattlesnakes and provide evidence that sit-and-wait predators may discriminate among prey chemical cues, even when they have no prior experience with the prey. Snakes explored chemical cues with chemosensory behaviors, and more frequently adopted a stereotyped ambush foraging posture toward chemical cues from prey sympatric with their population of origin than either allopatric prey or sympatric nonprey species that are eaten by other viperids. These results support the notion that intra- and interspecific variation in diet may be mediated proximally by innate recognition of cues from particular prey items. This system also describes a bioassay that may be used in the isolation and identification of prey-derived kairomones. Studies such as this can be used to determine more realistic parameters for models of predator–prey interaction and foraging behavior that involve secretive, less active predators.

Key Words—Timber rattlesnake, *Crotalus horridus*, foraging behavior, chemical cues, prey discrimination.

INTRODUCTION

Organisms leave chemical cues on the substrate as they move through the environment. These are often used by other organisms to mediate interspecific

---

*To whom correspondence should be addressed. E-mail: rwc13@cornell.edu

0098-0331/04/0300-0607/0 © 2004 Plenum Publishing Corporation

interactions, providing prey information about their predators (Kats and Dill, 1998), and predators about their prey (Burghardt, 1990). Even though the use of chemical cues to find prey is a common hunting strategy, most work on chemical exploitation has focused on prey detecting predators (Kats and Dill, 1998).

Scent or odor trails left inadvertently by prey animals are generally assumed to be composed of chemicals released as an unavoidable consequence of excretory processes. These cues represent a reliable information source about potential prey, and are exploited by a variety of predators. Most studies of chemosensory prey recognition focus on actively foraging predators that use chemical cues to find and track prey (Burghardt, 1990; Stowe et al., 1995; Finelli et al., 2000; Koivula and Korpimaki, 2001). However, chemical cues are also used by sit-and-wait predators to locate profitable ambush sites at which to sit and wait for prey (Downes, 1999; Roth et al., 1999; Carroll, 2000; Persons and Rypstra, 2000). Many aspects of the use of prey chemical cues are likely to differ between ambush and active foragers, since they seek to derive different information.

For an ambush strategy to be effective, predators must be able to identify sites where they are likely to encounter their prey. The use of chemicals to select profitable ambush sites requires some means of identifying species-specific cues that have been left relatively recently. The extensive literature on actively foraging squamate reptiles indicates that many species are born with an ability to use chemical cues in discriminating among prey (Burghardt, 1990). These studies use similar methods to present predators with chemical cues (reviewed in Cooper, 1998): a cotton-tipped applicator is impregnated with chemicals from the integument of a potential prey species and then placed in the vicinity of the predator. The number of tongue-flicks (indicative of level of vomeronasal functioning) and the propensity to bite the applicator is then used as an index of positive responses. Studies following this methodology have found that actively foraging snakes and lizards discriminate among different prey chemical cues, and that these preferences vary geographically (Arnold, 1981). Presumably, this predisposition toward certain prey is an efficient means of focusing foraging behavior on prey that is beneficial, because it is either abundant, relatively easy to catch, or energy rich.

However, predators that typically do not actively track their prey fail to respond to chemical cues that are presented following the cotton applicator method. In particular, most iguanian and agamid lizards (Cooper, 1995) and viperid snakes (Chiszar and Scudder, 1980) exhibit no response to prey chemical cues presented on cotton-tipped applicators. It may be that for some cases the chemical cues were not presented in an ecologically relevant manner. Many snakes are primarily ambush predators, moving widely through the environment in search of chemical cues, which are then used in ambush site selection (reviewed in Greene, 1992). Prairie rattlesnakes (*Crotalus viridis*), pygmy rattlesnakes (*Sistrurus miliarius*), and broad-headed snakes (*Hoplocephalus bungaroides*) have all been shown to use chemical cues to locate suitable ambush sites (Duvall et al., 1990; Downes, 1999;

Roth et al., 1999; Theodoratus and Chiszar, 2000). Since chemosensory information is so important for snakes in general (Halpern and Kubie, 1984; Schwenk, 1995), the use of prey chemical cues exhibited by these species is probably characteristic of most snakes that ambush their prey.

In this study, I examine the selection of ambush sites by a sit-and-wait foraging viperid, the timber rattlesnake (*Crotalus horridus*), presented with chemical cues derived from various potential prey species. This study is the first to examine the ability of a sit-and-wait predator to discriminate among various chemical cues when selecting an ambush site.

METHODS AND MATERIALS

The snakes used in this experiment consisted of 24 *Crotalus horridus*, born in the laboratory to three wild-caught females that were caught on August 15, 1999, in Wyoming, Clinton, and Lycoming Counties, Pennsylvania. I conducted experiments between October 1, 2000, and May 1, 2001, during which the 24 snakes ranged from 45.5 to 66.7 cm total length and from 64 to 196 g in body mass. Snakes were housed individually in 20 gallon aquaria and reared on a diet of laboratory mice. The snakes were maintained in a Cornell University animal-holding facility at 22–26°C under a 12L:12D light cycle, with a water dish and heating pad situated at one end of each aquarium.

I tested the 24 experimental subjects once each on a series of aqueous extracts of the integument of 8 vertebrate species, some of which were known to be prey for *C. horridus* in at least some part of its range (Clark, 2002). Each subject was also tested using tap water as a control. All aqueous extracts were prepared by placing a living, intact animal into a water bath for 10 min in the proportion of 1 ml of water per gram of body mass. Extracts were refrigerated until use. All extracts were used within 8 hr.

I made extracts from green frog (*Rana clamitans*), great plains skink (*Eumeces obsoletus*), laboratory rat (*Rattus rattus*), cotton rat (*Sigmodon hispidus*), dwarf hamster (*Phodopus sungorus*), chipmunk (*Tamias striatus*), white-footed mouse (*Peromyscus leucopus*), and dog (*Canis familiaris*). All of the animals from which extracts were made were wild-caught, except the dog, laboratory rat, and dwarf hamster, which were bred in captivity. I chose species to provide chemical extracts that represent (1) species that naturally occur in the diet of the population from which the snakes were taken (white-footed mice and chipmunks); (2) species that occur in the diet of other populations of the same species (cotton rat); (3) species related to natural prey, but not sympatric with *C. horridus* (dwarf hamster and laboratory rat); (4) species sympatric with *C. horridus* that are not eaten, but that are eaten by other pitviper species (skink and green frog); and (5) a nonprey mammalian animal (dog).

The testing procedure consisted of placing a snake in a wooden, open-topped enclosure (75 × 75 × 120 cm) lined with clean construction paper and containing a water dish, a cover object, and two rectangular wooden blocks (20 × 7 × 4 cm). The snake acclimated to its new surroundings for at least 3 d before each test. At the beginning of each test, both wooden blocks were removed and paper towels were placed across the top of each. One of these paper towels, selected at random, was soaked in 10 ml of extract, while the other was soaked in tap water. Both wooden blocks were replaced in the enclosure, and the snake was allowed to respond to these chemical extracts for 120 min, after which the paper towels were removed from the wooden blocks and the trial ended. When placed back into the enclosure, the blocks were situated in an area of the arena such that each was approximately equidistant from the subject. I used this method for creating artificial chemical trails because it allows the presentation of similar chemical cues from a broad range of prey species. In pilot studies, snakes exhibited similar responses to chemical extracts made from aqueous extracts and more naturalistic trails made from allowing a small mammal to run across the substrate surface several times.

Each of the 24 subjects was tested with a different random ordering of the nine conditions (eight experimental and one control). No subject was tested more than once in a 30-d period. All tests were conducted at least 21 d after the subject had last been fed. Subjects undergoing ecdysis were not tested. Because *C. horridus* forages mainly at night (Reinert et al., 1984), all trials were conducted during the dark half of the light cycle and recorded with a video camera with low-light recording capability (Sony® Handycam CCD-TRV57).

All videotapes were coded and scored blindly. I defined the first encounter with the chemical extract as the time from the initial encounter to the time the snake removed its head from contact with the chemical extract for more than 60 sec. The snake's head did not have to be in contact with the chemical extract for the entire time of the initial encounter, so long as it was not out of contact for more than 60 sec. I recorded the latency to encounter the chemical extract and the number of tongue flicks that the snake delivered to the chemical extract during this encounter (defined as a tongue flick where the tongue actually contacted the trail or was directly above the paper towel containing the extract). Additionally, I noted whether or not the subjects adopted the stereotyped ambush posture response (Reinert et al., 1984) after encountering the chemical extract. Qualitatively, this response is a stereotyped, overt behavior, consisting of the snake coiling in a tight coil adjacent to the chemical extract, with the head and neck oriented toward the trail in a ready-to-strike position. To quantify this behavior, an ambush posture was defined as the snake not moving, with its head and anterior one third of its body in a recoiled position, oriented toward and within 15 cm of the chemical extract, adopted within 2 min of tongue flicking the chemical trail, and maintained for at least 5 min. In the majority of cases, the ambush posture was maintained for the entire duration of the trial if it was adopted.

For statistical analysis, I used a scoring system to create a composite measure of the ambush response and the number of tongue flicks, given upon first encountering a trail. This scoring system is based on a widely used measure developed for actively foraging snakes, the tongue-flick attack score, or TFAS (reviewed in Cooper and Burghardt, 1990). TFAS assumes that an attack is a stronger response than any number of tongue flicks and that the latency to attack decreases with increasing stimulus. TFAS is calculated as

$$\text{TFAS} = \text{TF}_{\text{max}} + (\text{TL} - \text{latency})$$

where TF_{max} is the maximum number of tongue flicks emitted toward the stimulus by any individual in any trial, TL is trial length in seconds, and latency is the latency in seconds to attack the stimulus. Under this scoring system, individuals that attack the stimulus receive the base unit score of TF_{max}, modified by the latency to attack. Individuals that do not attack are scored as the number of tongue flicks emitted toward the stimulus. I modified this score by substituting the ambush response for the attack response. In so doing, a tongue-flick ambush score (TFAM) is created

$$\text{TFAM} = \text{TF}_{\text{max}} + (\text{TL} - \text{latency})$$

where TF_{max} is the maximum number of tongue flicks emitted during initial encounter of the chemical extract by any individual in any trial, TL is trial length in minutes, and latency is the latency in minutes to adopt the ambush posture toward the chemical extract. This composite measure, like TFAS, assumes that an ambush posture indicates a stronger response than any number of tongue flicks, and that the latency to ambush posture decreases with increasing stimulus.

The responses of the subjects were square-root-transformed, tested for normality with Kolmogorov–Smirnov tests, and compared with a randomized block ANOVA, with snake identity as the blocking factor. Tukey's test was used to make pairwise comparisons. Statistical analysis was conducted with the software program Minitab®. All values are given as mean ± SE.

RESULTS

The number of tongue flicks toward chemical extracts during initial encounter varied markedly among treatments (Table 1) and was highest for white-footed mice (116 ± 12) and chipmunks (105 ± 13). The ambush posture was never adopted in response to the blank control treatments, nor to the skink treatment, but was adopted by at least one individual in response to all other treatments (Table 1). The ambush posture was adopted most frequently in response to chemical cues from white-footed mice (46% of trials) and chipmunks (33% of trials). In general, the mean rates of tongue flicking, latency to encounter the chemical extract, and

TABLE 1. RESPONSES OF CAPTIVE-RAISED TIMBER RATTLESNAKES DURING FIRST ENCOUNTER WITH CHEMICAL DERIVED FROM 9 DIFFERENT SOURCES

Trail	Tongue flicks	Length of encounter (min)	Latency to encounter (min)	Ambush posture occurs	TFAM
Tap water control	17 ± 5	0.6 ± 0.2	56 ± 11	0	17 ± 5
Dog	44 ± 7	1.7 ± 0.3	15 ± 7	1	52 ± 12
Green frog	42 ± 8	1.7 ± 0.3	32 ± 10	2	56 ± 15
Skink	74 ± 9	3.3 ± 0.4	18 ± 7	0	74 ± 9
Lab rat	66 ± 9	2.7 ± 0.4	27 ± 8	4	93 ± 18
Cotton rat	67 ± 11	2.8 ± 0.5	24 ± 9	5	108 ± 20
Dwarf hamster	79 ± 8	3.3 ± 0.4	11 ± 5	5	111 ± 16
Chipmunk	105 ± 13	4.0 ± 0.5	5 ± 1	8	156 ± 21
White-footed mouse	116 ± 12	5.0 ± 0.5	10 ± 4	11	164 ± 21

Note. Each snake ($N = 24$) was tested once under each treatent.

propensity to exhibit the ambush posture were correlated, indicating the usefulness of a single composite measure that takes all of these measures into account.

Comparison of the average TFAM scores with a randomized block ANOVA shows that the snakes differentiated between the treatments ($df = 8, 23$; $F = 13.2$; $P < 0.001$, Figure 1). *Post hoc* comparisons with Tukey's test reveal that (Figure 1) the response to all treatments was stronger than the response to the blank control ($P < 0.01$); the response to chemical cues from natural prey (chipmunks

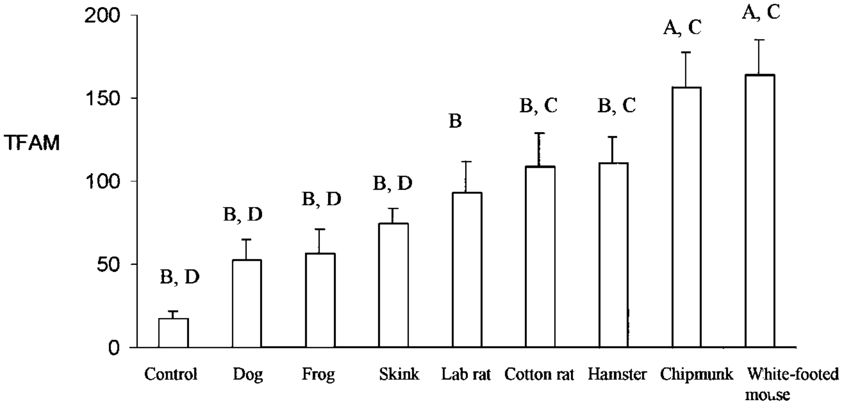

FIG. 1. Tongue flick ambush response (TFAM) of timber rattlesnakes to chemical trails from different animals ($P < 0.001$, randomized block ANOVA, $N = 24$). Tukey's test used to compare individual treatments (A > B, $P < 0.03$; C > D, $P < 0.05$).

and white-footed mice) was stronger than the response to all other treatments, including chemical cues from other small mammal species ($P < 0.03$); and the response to small mammal species was stronger than the response to trails made from nonmammal and large mammal species ($P < 0.05$).

DISCUSSION

This study illustrates the ability of *Crotalus horridus* to use chemical cues in locating suitable ambush sites. Previous studies have indicated that other ambush-foraging snake species are sensitive to chemical cues when ambushing prey. Greene (1992) reviewed field observations of venomous snakes, using chemosensory cues to locate suitable ambush sites, and coined the term "mobile ambushing" to describe that foraging strategy. Prairie rattlesnakes (*C. viridis*), in the field and in the lab, coiled near bedding soiled by potential prey (Duvall et al., 1990). Additionally, prairie rattlesnakes adopted ambush coils directed toward chemical trails left by mice (Theodoratus and Chiszar, 2000). Free-ranging pygmy rattlesnakes (*Sistrurus miliarus*) were attracted to transects that had been treated with aqueous washes from their preferred prey (Roth et al., 1999). Broad-headed snakes (*Hoplocephalus bungaroides*) were attracted to retreat sites containing odors from velvet geckos (*Oedura lesueurii*) (Downes, 1999). These studies show that the use of prey chemical cues in ambush site selection is likely an important foraging technique that is taxonomically widespread in serpents.

The use of prey kairomones (sensu Brown et al., 1970) by squamate reptiles has been the focus of several model systems in behavior and ecology (Arnold, 1981; Burghardt, 1990; Chiszar et al., 1992; Cooper, 1995); yet none of these systems have combined the ecological aspects of prey recognition and discrimination with the chemical identification of prey-derived kairomones. Identification of the kairomones used in these systems is necessary to understand the mechanisms by which predators use chemosensory information to identify and discriminate among chemical stimuli from their prey. Using bioassay-guided fractionation, proteinaceous chemoattractants that elicit predatory attacks from garter snakes in an active-foraging context have been isolated from both earthworms (Wang et al., 1993) and frogs (Wattiez et al., 1994). To date, no attempts have been made to identify kairomones used by sit-and-wait predators. Active and ambush foragers derive different types of information from prey kairomones; therefore, the nature of the kairomones used in these two contexts may differ.

Timber rattlesnakes are specialists on small mammals, and feed on almost nothing else, other than the occasional bird (Clark, 2002). The subjects from this study were taken from a north-central Pennsylvania population, where the diet consists primarily of white-footed mice, deer mice, red-backed voles, and chipmunks (Reinert et al., 1984; Clark, 2002). The only other species used in this study that regularly occurs in the diet of timber rattlesnakes is the cotton rat, which is only eaten in southern populations (Clark, 2002). The snakes responded more positively to chemical extracts from chipmunks and white-footed mice than to those of cotton rats. Chemical extracts from lizards and frogs were not as stimulating to timber rattlesnakes as those from small mammals. Other viperid species from the same dens and populations as timber rattlesnakes prey on frogs and lizards, even though timber rattlesnakes do not (Uhler et al., 1939; Savage, 1967; Keenlyne and Beer, 1973). Taken together, these results indicate that food preferences are locally adapted, and that both intra- and interspecific variations in diet are mediated in part by the recognition of prey chemical cues.

Timber rattlesnakes responded more strongly to chemical extracts from their natural prey than to chemical extracts from closely related species. This response was exhibited in spite of the fact that the subjects were born and raised in captivity and had never encountered natural prey items. However, at least one subject exhibited the ambush posture in response to all other chemical trails, except skinks, indicating that inexperienced snakes may also investigate chemical cues from animals that do not appear in their natural diet. Therefore, even though they are biased toward natural prey items, timber rattlesnakes retain the ability to respond to novel prey. Previous studies employing the cotton applicator technique have shown that active foragers using chemical cues to trail their prey also discriminate among potential prey in favor of those that occur in the natural diet (Burghardt, 1990). As with the timber rattlesnakes in this study, actively foraging snakes also exhibit mild predatory responses to a wide range of species that do not occur in their diet. In general, it seems that snakes are born with a predisposition toward chemical cues from certain prey species, which can then be strengthened or weakened by subsequent experience (e.g., Arnold, 1978; Burghardt, 1999). Subsequent experiments with timber rattlesnakes have indicated that their responses to prey chemical cues are also affected by feeding experience (Clark, unpublished data).

The snakes in this study were raised on laboratory mice (*Mus musculus*), and thus the positive responses to chemical trails from small mammals might result from this diet. However, this does not explain why sympatric small mammal species are preferred to others. Taxonomically, chipmunks are more distantly related to *M. musculus* than any of the other small rodents used in this study (Hall, 1981), so it is unlikely that the more positive response seen to natural prey was due purely to similarity between their chemical cues and those from laboratory mice.

In addition to tongue flicking and the ambush posture, mouth gaping (Graves and Duvall, 1983) was observed in these experiments. This behavior has been observed in other species, and is presumably a mechanism by which snakes can enhance chemosensory functioning by clearing the vomeronasal passage once it has become saturated with stimuli (Schwenk, 1995). In this study, it was most frequently seen either immediately after or immediately before an ambush posture was adopted.

Ambush site selection by timber rattlesnakes has the potential to address many questions about foraging behavior and predator–prey interactions. For example, it would be possible to examine how timber rattlesnakes respond to chemical trails that potentially encode information bearing on the probability of prey encounter or capture. Such a system could be used to test models of optimal giving-up time for an ambush forager (e.g., Nishimura, 1991) or game-theoretic model of habitat selection by prey (Bouskila, 2001).

Acknowledgments—The research presented here was approved by the Cornell University Institutional Animal Care and Use Committee in protocol 99-60 on May 25, 1999. For aid in the field collection of snakes, I thank C. Brennan, V. J. Clark, and D. M. Clark. For financial support, I thank the Cornell Chapter of Sigma Xi, the Kieckhefer Adirondack Fellowship, and the American Museum of Natural History Theodore Roosevelt Memorial Fund. For general support and advice, I thank K. Adler, H. W. Greene, T. Eisner, B. P. Halpern, W. B. Clark, and J. R. Garrard. For reviewing earlier drafts of this manuscript, I thank J. B. Grant, A. L. Bezzerides, K. L. Rypien, H. W. Greene, and K. Adler.

REFERENCES

ARNOLD, S. J. 1978. Some effects of early experience on feeding responses in the common garter snake, *Thamnophis sirtalis*. *Anim. Behav.* 26:455–462.

ARNOLD, S. J. 1981. The microevolution of feeding behavior, pp. 409–453, *in* A. Kamil and T. Sargent (eds.). Foraging Behavior: Ecology, Ethological, and Psychological Approaches. Garland STPM Press, New York.

BOUSKILA, A. 2001. A habitat selection game of interactions between rodents and their predators. *Ann. Zool. Fenn.* 38:55–70.

BROWN, W. L., EISNER, T., and WHITAKER, R. H. 1970. Allomones and kairomones: Transspecific chemical messengers. *Bioscience* 20:21–22.

BURGHARDT, G. M. 1990. Chemically mediated predation in vertebrates, pp. 475–499, *in* D. McDonald, D. Muller-Schwarze, and S. Natynzuk (eds.). Chemical Signals in Vertebrates 5. University Press, Oxford, UK.

BURGHARDT, G. M. 1999. Plasticity of foraging behavior in garter snakes (*Thamnophis sirtalis*) reared on different diets. *J. Comp. Psych.* 12:277–285.

CARROLL, J. F. 2000. Responses of adult *Ixodes scapularis* (Acari: Ixodidae) to urine produced by white-tailed deer of various reproductive conditions. *J. Med. Entom.* 37:472–475.

CHISZAR, D. and SCUDDER, K. M. 1980. Chemosensroy searching by rattlesnakes during predatory episodes, pp. 125–139, *in* D. Muller-Schwarze and R. M. Silverstein (eds.). Chemical Signals in Vertabrates and Aquatic Invertebrates. Plenum Press, New York.

CHISZAR, D., LEE, R., SMITH, H., and RADCLIFFE, C. 1992. Searching behaviors by rattlesnakes following predatory strikes, pp. 369–382, *in* J. A. Campbell and E. D. Brodie, Jr. (eds.). Biology of the Pitvipers. Selva, Tyler, TX.

CLARK, R. W. 2002. Dietary composition of the timber rattlesnake, *Crotalus horridus*. *J. Herpetol.* 36:494–499.

COOPER, W. E., JR. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* 50:973–985.

COOPER, W. E., JR. 1998. Evaluation of swab and related tests as a bioassay for assessing responses by squamate reptiles to chemical stimuli. *J. Chem. Ecol.* 24:841–866.

COOPER, W. E., JR. and BURGHARDT, G. M. 1990. A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *J. Chem. Ecol.* 16:45–65.

DOWNES, S. 1999. Prey odor influences retreat-site selection by naive broadheaded snakes (*Hoplocephalus bungaroides*). *J. Herpetol.* 33:156–159.

DUVALL, D., CHISZAR, D., HAYES, W. K., LEONHARDT, J. K., and GOODE, M. J. 1990. Chemical and behavioral ecology of foraging in prairie rattlesnakes (*Crotalus viridis viridis*). *J. Chem. Ecol.* 16:87–101.

FINELLI, C. M., PENTCHEFF, N. D., ZIMMER, R. K., and WETHEY, D. S. 2000. Physical constraints on ecological processes: A field test of odor-mediated foraging. *Ecology* 81:784–797.

GRAVES, B. M. and DUVALL, D. 1983. Occurrence and function of prairie rattlesnake mouth gaping in a non-feeding context. *J. Exper. Zool.* 227:471–474.

GREENE, H. W. 1992. The ecological and behavioral context for pitviper evolution, pp. 107–118, *in* J. A. Campbell and E. D. Brodie Jr. (eds.). Biology of the Pitvipers. Selva, Tyler, TX.

HALL, E. R. 1981. The Mammals of North America. Wiley, New York.

HALPERN, M. and KUBIE, J. L. 1984. The role of the ophidian vomeronasal system in species-typical behavior. *Trends Neurosci.* 7:472–477.

KATS, L. E. and DILL, L. M. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394.

KEENLYNE, K. D. and BEER, J. R. 1973. Food habits of *Sistrurus catenatus catenatus*. *J. Herpetol.* 7:382–384.

KOIVULA, M. and KORPIMAKI, E. 2001. Do scent marks increase predation risk of microtine rodents? *Oikos* 95:275–281.

NISHIMURA, K. 1991. Optimal patch residence time of a sit-and-wait forager. *Behav. Ecol.* 2:283–294

PERSONS, M. H. and RYPSTRA, A. L. 2000. Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). *Ethology* 106:27–35.

REINERT, H. K., CUNDALL, D., and BUSHAR, L. M. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.

ROTH, E. D., MAY, P. G., and FARRELL, T. M. 1999. Pigmy rattlesnakes use frog-derived chemical cues to select foraging sites. *Copeia* 1999:772–774.

SAVAGE, T. 1967. The diet of rattlesnakes and copperheads in the Great Smoky Mountains National Park. *Copeia* 1967:226–227.

SCHWENK, K. 1995. Of tongues and noses: Chemoreception in lizards and snakes. *Trends Ecol. Evol.* 10:7–12.

STOWE, M. K., TURLINGS, T. C. J., LOUGRIN, J. H., LEWIS, W. J., and TUMLINSON, J. H. 1995. The chemistry of eavesdropping, alarm, and deceit. *Proc. Natl. Acad. Sci*. U.S.A 92:23–28.

THEODORATUS, D. H. and CHISZAR, D. 2000. Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.

UHLER, F. M., COTTAM, C. and CLARKE, T. E. 1939. Food of snakes of the George Washington National Forest, Virginia. *Trans. N. Am. Wildl. Conf.* 605–622.

WANG, D., JIANG, X. C., CHEN, P., INOUCHI, J., and HALPERN, M. 1993. Chemical and immunological analysis of prey-derived vomeronasal stimulants. *Brain Behav. Evol.* 41:246–254.

WATTIEZ, R., REMY, C., FALMAGNE, P., and TOUBEAU, G. 1994. Purification and preliminary characterization of a frog-derived proteinaceous chemoattractant eliciting prey attack by checkered garter snakes (*Thamnophis marcianus*). *J. Chem. Ecol*. 20:1143–1160.