Anim. Behav., 1996, **52,** 775–781

Post-prandial chemosensory searching in black rat snakes

JAMES H. WITHGOTT
Department of Biological Sciences, University of Arkansas

*(Received 17 July 1995; initial acceptance 11 October 1995;
final acceptance 23 January 1996; MS. number:* A7365*)*

Abstract. In a laboratory experiment, black rat snakes, *Elaphe o. obsoleta*, increased rates of tongue flicking following ingestion of prey. This post-prandial tongue-flick increase, in combination with searching behaviour, represented post-prandial chemosensory searching (PPCS). Such chemosensory searching enabled rat snakes to locate subsequent prey more quickly than initial prey, which may prove beneficial in the wild. Single snakes of five other colubrid species also showed post-prandial tongue flick increases in similar experiments. Field observations are described that support inferences drawn from experimental results. Strike-induced chemosensory searching (SICS) is well known in venomous snakes, and was thought to have evolved as an adaptation for chemically trailing envenomated prey after voluntary release. This study adds to a growing list of non-venomous squamates that appear to show SICS, suggesting that the trait may instead be widespread and ancestral. The data are consistent with the view that SICS arose in a snake–lizard ancestor and may now serve different functions in different lineages. The emerging scenario for the evolution of chemosensory searching is a complex mix of adaptation and exaptation, underscoring the need to distinguish historical origin from current utility in the study of behavioural traits.

Predator adaptations for prey capture are numerous and varied, and existing behavioural traits are sometimes co-opted for new functions in evolutionarily novel contexts. Among snakes, many venomous species that hunt with vision or thermoreception release prey after striking to avoid injury, and then flick their tongues to relocate it via chemical perception once the prey succumbs to the venom. A number of studies have addressed such 'strike-induced chemosensory searching' (SICS) (e.g. Chiszar & Radcliffe 1976; Chiszar et al. 1979, 1982, 1983a, b; O'Connell et al. 1985) and have suggested that SICS evolved in viperid and elapid snakes as part of the strike–release–trail strategy (Chiszar et al. 1982). Recent work has shown, however, that SICS exists in some non-venomous snakes that use chemoreception to locate prey and that hold prey after striking. Increase of tongue-flick rate (TFR) following a strike has been documented in bullsnakes, *Pituophis melanoleucus* (Chiszar et al. 1980); corn snakes, *Elaphe g. guttata* (Cooper et al. 1989); eastern garter snakes, *Thamnophis sirtalis* (Cooper et al. 1989; Burghardt & Chmura 1993); ball pythons, *Python regius* (Cooper 1991a); and plains garter snakes, *Thamnophis radix* (Cooper 1992c). The phenomenon has also recently been demonstrated in several lizard families (Cooper 1989, 1991b, 1992a, b, 1993; Cooper & Alberts 1993). The induction of chemosensory searching by oral contact with prey may thus be an ancestral trait, retained in different squamate lineages for different functions (Cooper 1989; Burghardt & Chmura 1993; Cooper & Alberts 1993). In venomous snakes, it may represent an exaptation (sensu Gould & Vrba 1982) for the strike–release–trail strategy.

Non-venomous snakes that normally do not release prey after striking might benefit from SICS in at least two ways. First, rapid tongue flicking may allow efficient chemical trailing of prey that has escaped a snake's grasp (Cooper et al. 1989; Burghardt & Chmura 1993). Second, a TFR increase that continues after prey is swallowed may enable snakes to locate prey dispersing from aggregations (such as nests of young rodents or birds) after one of such a group is devoured (Chiszar et al. 1980; Cooper et al. 1989).

Correspondence: J. H. Withgott, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, U.S.A. (email: jhw@u.arizona.edu).

0003–3472/96/100775+07 $25.00/0

The experiment presented here tested for TFR increase and searching behaviour following ingestion of a meal in the black rat snake, *E. o. obsoleta*, a non-venomous colubrid snake of eastern North America. I use the term post-prandial chemosensory searching (PPCS) to describe the response, because I focused on TFR increase after prey is swallowed and did not explicitly test whether striking triggered the behaviour. Thus PPCS may or may not be equivalent to SICS. The experiment tested whether TFR rises after prey is swallowed and whether such an increase enables rat snakes to locate subsequent prey more efficiently. The experiment followed one described in Withgott (1994) with a number of methodological improvements. In addition, I tested single individuals of five other colubrid species for PPCS using similar methods. Finally, I describe two observations on free-ranging snakes in the wild that support inferences drawn from results of the laboratory experiment.

METHODS

I used 11 male and 11 female black rat snakes ranging in snout–vent length from 76.5 cm to 160.0 cm. I conducted the experiment on 9–11 October 1994. These snakes had been captured under permit in Arkansas between June 1991 and July 1993 and housed individually in 10-gallon terraria. Prey used in the experiment were live adult white laboratory mice, *Mus musculus*. All methods were IACUC-approved (University of Arkansas, Fayetteville), and snakes were released at site of capture following the experiment and related research. Rather than transferring snakes into experimental arenas unfamiliar to them, I conducted trials within each snake's own terrarium after removing leaf litter and water bowls and allowing snakes to acclimate to this change.

I tested snakes individually in randomly determined sequence. For each trial, I placed a terrarium containing a snake on a 44-cm stand 1.5 m in front of a table behind which sat an observer. Barriers shielded the observer from the snake's vision. Each snake was allowed 5 min to acclimate to its position on the stand. Tongue-flicking behaviour was then monitored in each of six sequential stages of the experiment. In each stage, tongue flicks were counted with hand tally meters and recorded in consecutive 30-s blocks of time. Count and time data were later converted into a tongue-flick rate (TFR) of tongue flicks per min. If a snake's head was angled so that tongue flicks were not visible, I counted and deducted seconds from the time observed and calculated TFR based on the reduced time total. Ambient temperature was 20.0–25.7°C for all trials.

During the first of the six experimental stages, a 5-min 'Rest stage', I counted the snake's tongue flicks before doing any manipulations. Next came a 'Disturbance stage' designed to control for possible agitating effects of human movement accompanying introduction of mice. The observer approached the terrarium, presented the snake with a cotton swab the size and shape of a mouse and thumped once on the terrarium (to mimic the tactile stimulus of a mouse landing inside). The observer then returned to position and counted tongue flicks for 5 min. Next, I dropped the first of two live mice into the terrarium. During this 'Mouse 1 stage' I recorded the following: (1) time until the snake became aware of the mouse; (2) time until the snake first struck at the mouse; (3) time until subsequent strikes (if the first was unsuccessful); and (4) number of tongue flicks during each of these three periods. Thus I subdivided the Mouse 1 stage into up to three periods of varying length and calculated TFR separately for each. Most snakes became aware of the mouse immediately upon its introduction and required only one strike to subdue it. Once a snake had captured the mouse, I measured time until it was swallowed. After swallowing, the fourth stage commenced. During this 'Post-mouse 1 stage' I counted tongue flicks for 5 min. Finally I presented a second mouse and repeated the steps described for Mouse 1 stage and Post-mouse 1 stage, making up the last two stages, 'Mouse 2' and 'Post-mouse 2'.

I calculated TFRs for all stages for all snakes and used a Friedman two-way analysis of variance by ranks with multiple comparisons (Siegel & Castellan 1988, pp. 174–183) to test for differences in median TFR between the six stages. Nonparametric methods were necessary because data from stages containing many zeros could not be normalized. Two comparisons were of particular interest. First, the comparison between the Disturbance stage and the Mouse 1 stage tested whether snakes increased TFR in response to sensory cueing on prey, without striking. Second, the comparison between Mouse 1 stage and

Post-mouse 1 stage tested whether a post-prandial TFR increase occurred.

Prior to running the Friedman test, I compared TFRs between the three subdivisions of the Mouse 1 and Mouse 2 stages to determine whether data from all subdivisions should contribute to overall TFR values for these stages.

I carefully noted tongue-flick behaviour as snakes approached prey and determined whether TFR accelerated or decelerated during approach. Determination was based both on holistic perception and by comparing TFRs of consecutive 30-s time blocks. In addition, I noted any searching activity or vigorous or unusual motions by snakes at any time during the experiment.

To test for differences in latency to strike between first and second mice and in swallowing time between first and second mice, data were log-transformed and subjected to paired *t*-tests. I measured latency to strike from the time snakes noticed mice to the time of first strike attempt.

To determine approximate duration of post-prandial TFR elevation, I made three 1-min tongue-flick counts on 16 snakes at varying intervals within 2 h after their trials. Data were plotted, and for each snake I estimated the time at which TFR decreased to the rate measured for that individual during its Rest stage.

I tested wild-caught snakes of five additional species for post-prandial TFR increase. These included an eastern hognose snake, *Heterodon platirhinos*, a great plains rat snake, *Elaphe guttata emoryi*, an eastern coachwhip, *Masticophis flagellum*, a southern black racer, *Coluber constrictor priapus*, an adult eastern garter snake and a neonate eastern garter snake born in captivity to a wild-caught snake. Methods were similar to those detailed above, but prey items varied with species. I ran trials between 30 May and 28 August 1993 at temperatures of 23.2–27.2°C.

RESULTS

All 22 snakes devoured both mice offered and all showed rapid tongue flicking after swallowing mice. Mean ± SE TFR was 13.0 ± 3.4 during the Rest stage and 12.2 ± 3.5 during the Disturbance stage. TFR rose from 32.7 ± 3.2 during the Mouse 1 stage to 60.8 ± 2.1 in the Mouse 1 Post-swallow stage. In the Mouse 2 and Post-mouse 2 stages, mean TFR was 44.9 ± 4.0 and 60.4 ± 2.2, respectively (Fig. 1). The Friedman test was significant (F_r=78.82, *df*=5, P<0.0001), and multiple comparisons showed significant differences between stages (Fig. 1). Mean TFR of the Mouse 1 stage was not significantly different from that of the Disturbance stage (P=0.33). A significant difference in TFR existed between the Mouse 1 and Post-mouse 1 stages (P=0.0015).

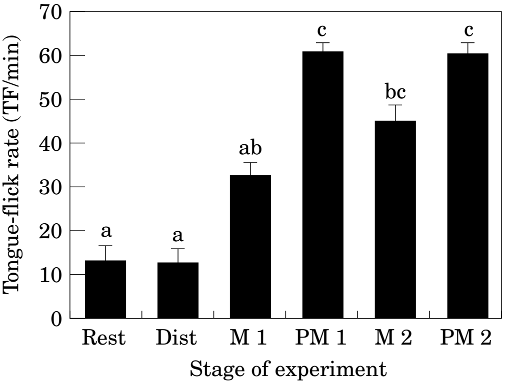

Figure 1. Mean+SE tongue-flick rates of 22 black rat snakes for each of the six sequential stages of the experiment. Letters above bars indicate significant differences after a Friedman test with multiple comparisons. The difference between the third and fourth stages represents a post-prandial increase in tongue-flick rate. Rest=Rest stage, Dist=Disturbance stage, M 1=Mouse 1 stage, PM 1=Post-mouse 1 stage, M 2=Mouse 2 stage, PM 2=Post-mouse 2 stage.

Data included in the Mouse 1 and 2 stages for analysis in the Friedman test were determined by comparing TFR variation between the three subdivisions of these stages. In the Mouse 1 stage, nine snakes failed to notice mice immediately upon their introduction. For these snakes, mean TFR before becoming aware of mice was 10.6. In contrast, mean TFR for all snakes (N=22) during prey approach (time between noticing mice and first striking at them) was 32.7. Five snakes required multiple strikes to capture prey, and these showed a mean TFR of 30.7 between first and last strikes. Seven of the nine snakes with delayed awareness of mice showed higher TFRs after noticing prey, a significant difference by the sign test (P=0.035, with one tie). Because of this result, I did not include TFR data taken before snakes noticed mice in the Mouse 1 stage values. Mouse 2 data showed a similar trend (seven of nine higher during approach; P=0.09), and I similarly excluded TFR data before noticing mice from Mouse 2 values. Three of five snakes showed increased TFRs after failed first strikes at Mouse 1, and two of six showed increases after failed strikes at Mouse 2. Post-strike Mouse 2 mean TFR was 27.6, compared to mean TFR of 44.9 during approach. I chose not to include TFR data following failed strikes in either Mouse 1 or Mouse 2 stage values, because TFRs were not significantly different from TFRs during prey approach, and because for many strikes it was not ascertained whether a snake made oral contact with prey. Thus TFR values for Mouse 1 and Mouse 2 stages included only data recorded between the time a snake became aware of the prey's presence and the time of its initial strike. These choices had the effect of maximizing TFR values for both Mouse 1 and Mouse 2 stages.

During prey approach, 17 of 44 approaches were lengthy enough to allow reliable gauging of TFR acceleration or deceleration. TFR increased during six approaches, decreased during three, and stayed roughly the same during eight (sign test, $P=0.25$).

Latency to strike for the second mouse was significantly less than that for the first mouse ($t=2.86$, $df=21$, $P=0.009$). Snakes struck at first mice 35.2 ± 12.7 s after their presentation, but struck at second mice after only 9.3 ± 1.5 s. Swallowing times for the two mice were not significantly different ($t=1.20$, $df=21$, $P=0.24$). Snakes swallowed first mice in 329.0 ± 18.8 s and second mice in 308.5 ± 16.3 s.

Regarding duration of post-prandial TFR elevation, post-trial observations produced an estimated duration of 82.6 ± 11.3 min after swallowing the second mouse. This is considerably longer than most chemosensory responses yet induced in non-venomous squamates.

Snakes showed several types of vigorous chemosensory searching behaviour (while tongue flicking) after eating mice. These included mouth-gaping (Graves & Duvall 1983, 1985), pressing snouts against terraria floors, searching in their coils (where prey chemical cues no doubt remained) and even biting segments of their bodies where mice had been constricted. These activities were all accompanied by energetic body movement and visual alertness. Sixteen of 22 snakes vigorously searched their own coils for additional prey after swallowing mice. Snakes showed none of these behaviour patterns prior to eating mice.

Two snakes released mice after constricting them and searched their terraria, apparently for more prey, before returning to eat the dead mice. On both occasions TFRs were rapid (>60) and comparable to those witnessed after swallowing. (In pilot studies, several snakes had shown this behaviour pattern, and in every case post-strike release of prey was accompanied by rapid tongue flicking.)

All six individuals of the five additional species tested increased TFR between Prey 1 stage and Post-prey 1 stage. TFR rose from 15.0 to 40.9 in the *H. platirhinos*, from 25.2 to 69.3 in the *C. constrictor*, from 45.8 to 129.9 in the *M. flagellum*, from 14.8 to 47.6 in the *E. guttata* and from 25.6 to 63.3 in the neonate *T. sirtalis*. The adult *T. sirtalis* was fed seven prey items in succession, each of which produced post-prandial TFR increases; mean pre-strike TFR was 12.5 and mean post-swallow TFR was 42.8.

DISCUSSION

Post-prandial chemosensory searching was quantitatively demonstrated in a sample of black rat snakes and was suggested in individuals of five other colubrid species. Although the experiment did not strictly test for SICS, observations on snakes that voluntarily released prey before swallowing suggested that the post-prandial tongue-flick rate increase was induced by oral contact following striking. Thus post-prandial chemosensory searching in black rat snakes may be equivalent to strike-induced chemosensory searching, although this need not be the case in other species. Results support the view that SICS is widespread in colubrids and may be ancestral in squamates (Cooper 1989; Cooper et al. 1989; Burghardt & Chmura 1993). The behaviour in pit vipers thus may be an exaptation for the strike–release–trail strategy rather than a derived adaptive trait. Perhaps SICS in pit vipers may be best viewed as an elaborated or ritualized form of a more general ancestral behavioural trait.

In the present study, the significant difference in TFR between Mouse 1 stage and Post-mouse 1 stage demonstrated a post-prandial tongue-flick rate increase. The increase could have been induced by either the action of striking, oral contact with prey, constriction or swallowing. Anecdotal observations suggested that oral contact induced the TFR increase, because individuals that released prey before swallowing showed TFRs more rapid than pre-strike rates. The action of striking itself did not seem to affect TFR, because TFR did not increase in snakes ($N=11$) that struck unsuccessfully at mice. Constriction cannot be ruled out as a mechanism for elevating TFR, but in a pilot study one snake pressed prey against the terrarium floor without constricting and still showed a typical post-prandial TFR increase. A major effect of swallowing seems unlikely because those snakes that released prey prior to ingestion showed TFRs typical of post-prandial rates. These inferences are consistent with findings (Chiszar et al. 1980; Cooper et al. 1989) that oral contact with prey in some colubrids may result in increased tongue flicking, and contrast with the finding (Burghardt & Chmura 1993) that the act of striking itself triggers increased TFR in *T. sirtalis*.

A final possibility is that accelerating tongue flicking during prey approach might result shortly before a strike in high TFR, which might then be maintained after swallowing. The present results showed no evidence of this, however; the trend of TFR acceleration during approach was weak and non-significant, and could not explain the post-prandial jump in TFR.

The lack of significant difference between the Disturbance stage and the Mouse 1 stage was surprising, given the large difference (>20) in TFR means. This result suggests that sensory cueing on prey has no effect on tongue-flick behaviour. The lack of significance, however, may simply result from reduction of alpha values in the multiple comparison method. I isolated these two stages and applied a Wilcoxon signed-ranks test to their data; Mouse 1 stage TFR was significantly greater than Disturbance stage TFR ($T^{+}=216$, $P=0.0002$, $N=21$). Differences in TFR within the Mouse 1 and Mouse 2 stages before and after snakes became aware of mice further suggest that sensory cueing on prey does induce elevation of TFR. Such 'cue-induced chemosensory searching' (Burghardt & Chmura 1993) has been found in other species (e.g. Chiszar et al. 1980; O'Connell et al. 1985), and is the basis for studies using prey extract to elicit predatory behaviour (Burghardt 1993).

The lack of significant differences between the final three stages of the experiment may indicate that TFR is maximized after a snake eats a prey item, and that consumption of subsequent prey shortly thereafter does not alter this rate.

In black rat snakes and in the five other species tested, post-prandial TFR increases were accompanied without exception by intense searching activity and vigorous body movement. The five additional species were not selectively chosen for the experiment, but represented a sample of snakes readily captured at a nearby research site, suggesting that PPCS may be widespread among colubrid snakes.

In non-venomous colubrids, SICS could help snakes to relocate prey that escapes their grasp, especially if the prey is injured and unable to move quickly. In genera such as *Elaphe*, which commonly feed on aggregated prey of limited mobility such as nest-bound young birds and rodents (Fitch 1963; Ernst & Barbour 1989), PPCS may help maximize foraging efficiency by enabling snakes to locate multiple slowly dispersing individuals. As shown in this study, PPCS permits efficient location of subsequent prey and generally lasts more than an hour after a predation event.

Two field observations on *Elaphe* species were recently made in Arkansas that lend credence to these ideas (Withgott 1994). In the first, a rodent escaped from the grasp of a radiotagged *E. o. obsoleta* after an attack in an abandoned armadillo hole. The snake, which did not emerge from the hole in time to see the rodent's direction of escape, was able to follow the rodent's path accurately for at least 9 m, while flicking its tongue at an extremely rapid rate.

In the second observation, an *E. guttata emoryi* attacked a nest containing well grown nestling indigo buntings, *Passerina cyanea*, at dusk. The snake ingested one nestling while the others tumbled out and crawled feebly through the leaf litter. Forty-five minutes after the snake had descended from the nest, I heard the squeal of a nestling in the darkness several metres from the nest site, followed immediately by the rustle of constricting snake body motions in leaf litter. I concluded that the snake had been able to locate prey that had dispersed from the site of an attack.

Comparative study of PPCS and SICS in squamates in a phylogenetic framework may reveal that evolutionary retention or loss of these behaviour patterns are correlated with behavioural, ecological, physiological or morphological factors (Burghardt & Chmura 1993; Cooper &

Alberts 1993). For example, the retention of SICS might be favoured in squamate groups that (1) have adequate chemoreceptive abilities and (2) are either venomous or able to move quickly enough to overtake escaping prey. PPCS might be favoured in squamate groups that (1) have adequate chemoreceptive abilities and (2) hunt prey that is often aggregated, and slow-moving and vulnerable once discovered. Snakes of genera such as *Elaphe*, which are active foragers and use chemical as well as visual cues in hunting (de Cock Buning 1983; personal observation), may be expected to benefit from PPCS and SICS. Further laboratory studies will be useful in testing for these behaviour patterns in different taxa, and field experimentation with radiotagged animals may permit us to test the utility of these behaviour patterns in the wild.

ACKNOWLEDGMENTS

M. Fangmeyer, P. Lewis, J. Montejo-Diaz and J. Scharp provided assistance in pilot experiments. Staff of the Poteau Ranger District of the Ouachita National Forest and students at the University of Arkansas helped capture snakes. A. Badyaev, G. Burghardt, D. Chiszar, W. Cooper, M. Waters and two referees provided thorough and insightful comments on versions of the manuscript. I thank J. Baker, E. Gbur and J. Walker for assistance, and particularly W. Montague for kindly providing space for experiments. I gratefully acknowledge C. Amlaner for his constant and dedicated support and encouragement. The Indiana State University Department of Life Sciences provided facilities for completing the manuscript. Research was funded by the Ouachita National Forest, Hot Springs, AR; the Southern Forest Experiment Station, Nacogdoches, TX; the Poteau Ranger District; and the Arkansas Audubon Society Trust.

REFERENCES

Burghardt, G. M. 1993. The comparative imperative: genetics and ontogeny of chemoreceptive prey responses in natricine snakes. *Brain Behav. Evol.*, **41,** 138–146.

Burghardt, G. M. & Chmura, P. J. 1993. Strike-induced chemosensory searching by ingestively naive garter snakes (*Thamnophis sirtalis*). *J. comp. Psychol.*, **107,** 116–121.

Chiszar, D. & Radcliffe, C. W. 1976. Rate of tongue-flicking by rattlesnakes during successive stages of feeding on rodent prey. *Bull. Psychon. Soc.*, **7,** 485–486.

Chiszar, D., Simonsen, L., Radcliffe, C. & Smith, H. M. 1979. Rate of tongue-flicking by cottonmouths (*Agkistrodon piscivorus*) during prolonged exposure to various food odors, and strike-induced chemosensory searching by the cantil (*Agkistrodon bilineatus*). *Trans. Kans. Acad. Sci.*, **82,** 49–54.

Chiszar, D., Radcliffe, C. W. & Scudder, K. 1980. Use of the vomeronasal system during predatory episodes by bull snakes (*Pituophis melanoleucus*). *Bull. Psychon. Soc.*, **15,** 35–36.

Chiszar, D., Andren, C., Nilson, G., O'Connell, B., Mestas J. S. Jr & Smith, H. M. 1982. Strike-induced chemosensory searching in Old World vipers and New World pit vipers. *Anim. Learn. Behav.*, **10,** 121–125.

Chiszar, D., Radcliffe, C. W. & Scudder, K. 1983a. Strike-induced chemosensory searching by rattlesnakes: the role of envenomation-related chemical cues in the post-strike environment. In: *Chemical Signals in Vertebrates 3* (Ed. by D. Müller-Schwarze & R. M. Silverstein), pp. 1–24. New York: Plenum Press.

Chiszar, D., Stimac, K., Poole, T., Miller, T., Radcliffe, C. W. & Smith, H. M. 1983b. Strike induced chemosensory searching in cobras (*Naja naja kaouthia*, *N. mossambica pallida*). *Z. Tierpsychol.*, **63,** 51–62.

de Cock Buning, T. 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Am. Zool.*, **23,** 363–375.

Cooper, W. E. Jr. 1989. Strike-induced chemosensory searching occurs in lizards. *J. chem. Ecol.*, **15,** 1311–1320.

Cooper, W. E. Jr. 1991a. Discriminations of integumentary prey chemicals and strike-induced chemosensory searching in the ball python, *Python regius. J. Ethol.*, **9,** 9–23.

Cooper, W. E. Jr. 1991b. Responses to prey chemicals by a lacertid lizard, *Podarcis muralis*: prey chemical discrimination and poststrike elevation in tongue-flick rate. *J. chem. Ecol.*, **17,** 849–863.

Cooper, W. E. Jr. 1992a. Prey odor discrimination and poststrike elevation in tongue flicking by a cordylid lizard, *Gerrhosaurus nigrolineatus. Copeia*, **1992,** 146–154.

Cooper, W. E. Jr. 1992b. Elevation in tongue-flick rate after biting prey in the broad-headed skink, *Eumeces laticeps. J. chem. Ecol.*, **18,** 455–467.

Cooper, W. E. Jr. 1992c. Post-bite elevation in tongue-flick rate by neonatal garter snakes (*Thamnophis radix*). *Ethology*, **91,** 339–345.

Cooper, W. E. Jr. 1993. Duration of poststrike elevation in tongue-flicking rate in the savannah monitor lizard, *Varanus exanthematicus. Ethol. Ecol. Evol.*, **5,** 1–18.

Cooper, W. E. Jr & Alberts, A. C. 1993. Postbite elevation in tongue-flicking rate by an iguanian lizard, *Dipsosaurus dorsalis. J. chem. Ecol.*, **19,** 2329–2336.

Cooper, W. E. Jr, McDowell, S. G. & Ruffer, J. 1989. Strike-induced chemosensory searching in the colubrid snakes *Elaphe g. guttata* and *Thamnophis sirtalis. Ethology*, **81,** 19–28.

Ernst, C. H. & Barbour, R. W. 1989. *Snakes of Eastern North America.* Fairfax, Virginia: George Mason University Press.

Fitch, H. S. 1963. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia*, **1963,** 649–658.

Gould, S. J. & Vrba, E. S. 1982. Exaptation—a missing term in the science of form. *Paleobiology*, **8,** 4–15.

Graves, B. M. & Duvall, D. 1983. Occurrence and function of prairie rattlesnake mouth gaping in a non-feeding context. *J. exp. Zool.*, **227,** 471–474.

Graves, B. M. & Duvall, D. 1985. Mouth gaping and head shaking by prairie rattlesnakes are associated with vomeronasal organ olfaction. *Copeia*, **1985,** 496–497.

O'Connell, B., Greenlee, R., Bacon, J., Smith, H. M. & Chiszar, D. 1985. Strike-induced chemosensory searching in elapid snakes (cobras, taipans, tiger snakes, and death adders) at San Diego Zoo. *Psychol. Rec.*, **35,** 431–436.

Siegel, S. & Castellan, N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences.* 2nd edn. New York: McGraw-Hill.

Withgott, J. H. 1994. Behavior and ecology of the black rat snake, *Elaphe o. obsoleta*, and its predation on birds' nests. M.S. thesis, University of Arkansas, Fayetteville.