

CAUDAL DISTRACTION BY RAT SNAKES (COLUBRIDAE, *ELAPHE*): A NOVEL BEHAVIOR USED WHEN CAPTURING MAMMALIAN PREY

Stephen J. Mullin¹

ABSTRACT.—Caudal movement in snakes may serve either a predatory (e.g., caudal luring) or defensive (e.g., rattling, aposematism) function. I describe a new behavioral pattern of tail movement in snakes. Gray rat snakes (*Elaphe obsoleta spiloides*) foraging on small mammals (*Mus domesticus*) moved their tails in an erratic, whiplike fashion after detecting prey in their vicinity. The thrashing movement in the horizontal plane was audibly and visually obvious, resulting in displacement of leaf litter around the tail. All subjects displayed the behavior, but not in all foraging episodes. Shorter durations of caudal distraction resulted in greater predator success during the 1st attempt at prey capture. Caudal distraction may facilitate prey capture by gray rat snakes by directing the attention of prey away from the approaching head of the snake.

Key words: caudal display, predatory behavior, deceit, *Elaphe obsoleta*, mammalian prey, rat snake, Colubridae.

Visual communication by snakes (Carpenter 1977, Carpenter and Ferguson 1977) occurs in the absence of appendages used by many other vertebrate taxa (Cullen 1972, Enquist et al. 1985). Limblessness necessitates the use of head, body, or tail for visual display. Snake defensive displays frequently involve tail movement or posturing (Greene 1988, Sazima and Abe 1991). In particular, members of the subfamily Crotalinae have evolved a specialized morphology at the tail tip, the rattle. Greene (1992) suggested that the incipient structure serves as a warning device to snake predators, a conclusion that is the subject of continued discussion (Sisk and Jackson 1997, Tiebout 1997). Several species of colubrid snakes (Greene 1988) and other elongate reptiles (Greene 1973) also perform defensive tail displays.

Another form of tail movement, termed *caudal luring*, facilitates prey capture. This behavior is described as a slow, undulatory or vermiform movement of the tail while it is held upright in close proximity to the snake's head (Heatwole and Davison 1976). Caudal luring is presumably mimetic, in that the movement is thought to resemble an insect larva or worm and thus attracts potential prey to within striking distance of the otherwise motionless snake. Caudal luring has been documented in nearly all families of snakes (Carpenter et al. 1978, Radcliffe et al. 1980, Sazima and Puerto

1993, Rabatsky and Farrell 1996) and at least 1 lizard species (Murray et al. 1991). It is typically displayed by snakes foraging from an ambush posture (Chiszar et al. 1990).

Both defensive tail vibration and caudal luring have been observed in rat snakes (*Elaphe obsoleta*; Tiebout 1997; personal observation). While observing a gray rat snake (*E. o. spiloides*) foraging for a small mammal (*Mus domesticus*), I recorded a tail display unlike that of either luring (Chiszar et al. 1990) or defensive rattling or tail vibration (Greene 1988). During subsequent observations, several individuals displayed similar tail movement when approaching their prey. The purpose of this study is to describe a heretofore undocumented predatory behavior of gray rat snakes that was displayed only in the presence of mammalian prey. Frequency and duration of this behavior and its facilitation of prey capture are also reported. Because this behavior parallels caudal luring and defensive tail vibration, I term the novel behavior *caudal distraction*.

MATERIALS AND METHODS

I first noticed caudal distraction in a 113-cm snout-vent length (SVL) female gray rat snake foraging for a mixed-strain mouse (*M. domesticus*). The snake was in an enclosure that simulated a bottomland hardwood forest

¹Department of Biology, University of Memphis, Memphis, TN 38152. Present address: Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920.

habitat (see below). Behavior was documented on videotape to permit detailed description. Several other adult snakes displayed this behavior with little departure from the original pattern. To examine possible differences in capture success and latency to prey capture that might be dependent on the use of this behavior, I recorded adult gray rat snakes ($n = 15$) involved in foraging episodes under similar conditions.

Subjects (10 males and 5 females, ≥ 100 cm SVL) were obtained from forested and semi-rural areas within Shelby County, Tennessee, and maintained in captivity at temperature and photoperiod regimes of 26–29°C and 14:10 h light:dark, respectively. Subjects had spent between 1 and 16 months in captivity prior to examination. Snakes were housed individually in cages measuring a minimum of 30 × 60 × 30 cm, provided with water ad libitum, and fed either Northern Bobwhite Quail (*Colinus virginianus*) eggs or mixed-strain mice weekly. Excepting occasional cage cleaning and monthly SVL (± 0.5 cm) measurements, subjects were handled as little as possible to minimize any behavioral modifications resulting from prolonged captivity (Warwick 1990, Ford 1995). Because recently fed snakes may exhibit shifts in behavioral pattern (Beck 1996) or alteration of locomotor performance (Martin 1996), individuals were placed on a restricted diet (water alone) for 3 wk prior to experimental trials. Between 23 April 1995 and 25 March 1996, snakes were allowed to forage individually for mice on at least 2 different occasions, each separated by a 3-wk restricted diet.

An enclosure (2.25 m² and 2 m in height), constructed to simulate bottomland hardwood forest of the wildlife management area of nearby Meeman-Shelby Forest State Park (MSFSP), Tennessee, was maintained at the photoperiod and temperature regimes described above. Artificial vegetation simulated mean recorded level of vegetation density at MSFSP (measured in June 1994; $\bar{x} \pm 1 s_{\bar{x}} = 64 \pm 2.3$ plants m⁻², $n = 144$). Leaves, obtained at field sites where snakes were collected, provided a natural substrate on the enclosure floor. Light intensity on the enclosure floor approximated levels measured at MSFSP during the vegetation sampling period (for further details on habitat sampling and enclosure construction, see Mullin 1998, Mullin et al. 1998).

Adult male mice were placed in the enclosure for a minimum of 10 min for acclimatization. Only adult male mice having dark brown pelage were used as prey during the observations to minimize visual and vomeronasal differences among prey available to snakes (Loop 1970) and provide prey visually similar to those which snakes encounter in the field. All mice had similar mass (30.7 ± 0.5 g, $n = 30$), although the ratio of prey mass to snake mass was not fixed during the study. A gray rat snake was placed in the corner of the enclosure farthest removed from the prey. Because observer presence may influence snake behavior (Drummond 1983), behaviors were recorded by a video camera on a tripod elevated over the enclosure floor. The camera was always oriented toward the snake, meaning that possible differences in prey behavior were not recorded. Occasionally, caudal distraction was initiated with the tail outside the field of view; however, tail movement was audibly discernible as leaf litter in the immediate vicinity was disturbed and could thus be recorded from its initial occurrence.

The latency to successful mouse capture may have depended, in part, on initial distances separating the snake and its prey. However, the confined, relatively small enclosure probably limited the influence of initial separation distance. Missed attempts at capturing the mouse and frequency and duration of caudal distraction were recorded from videotaped observations. A repeated-measures analysis of variance (ANOVAR; each subject was recorded on 2 occasions) was used to determine whether those snakes exhibiting caudal distraction required fewer attempts to successfully capture mice. Parametric statistics (Scheffé 1959, Cohen 1965) were also used to detect any relationships between frequency and/or duration of caudal distraction and snake gender (ANOVAR) or size (Pearson's regression). Statistical tests were conducted using SuperANOVA™ software (Abacus Concepts) at an accepted significance level of $\alpha = 0.05$.

RESULTS

Description

Caudal distraction is the use of tail movements by an elongate predator which serve to hold the attention of a prey animal while the

predator's head is moved to within striking range of the prey.

In *E. o. spiloides* caudal distraction displaced leaves near the tail, was visually conspicuous when unobscured by emergent vegetation, and was audible from a distance of several meters. Mice (*M. domesticus*) responded to caudal distraction by ceasing all movement, often after orienting their heads toward the undulating tail (Fig. 1). An erratic lateral movement of the posterior 70% of the tail characterized the tail display. Undulations of the more proximal tail portion appeared sinusoidal in form, but the tail tip moved similarly to the end of a whip, curving in a 180° arc on either side of the tail. Such movements were serially repeated with an average ($\pm 1 s_{\bar{x}}$) of 1.4 ± 0.2 sec elapsing for each whiplike pattern. Usually, but not always, caudal distraction was performed while the body was laterally bent at an obtuse angle such that tail movement was positioned to one side of the body axis with respect to the head. Differences between caudal distraction and other described tail movements are discussed below.

All 15 gray rat snakes displayed the described behavior, although not in all foraging episodes (caudal distraction was observed in 19 of 30 staged encounters and has been documented in >20 other occasions involving these and other adult subjects foraging in different enclosure conditions; Mullin 1998). The behavior, while most often displayed after snakes visually detected mice, also occurred when prey was visually obscured (possibly a response to tactile or chemosensory stimuli). Caudal distraction was always initiated before the head of the snake was within striking distance of its prey (<10 cm). Duration of the behavior always extended to the moment of striking the prey. Subjects displaying caudal distraction did not require less time (127 ± 32 sec) to capture prey than those not displaying the behavior (140 ± 36 sec; $F_{1,13} = 0.09$, $P = 0.70$). Subjects did not display caudal distraction when offered other prey types (*Colinus virginianus* and *Coturnix coturnix* eggs, *C. virginianus* chicks, *Hemidactylus turcicus* juveniles, *M. domesticus* neonates) under similar test conditions.

Displays ($n = 19$) averaged 27 ± 8 sec in duration and were usually initiated while the snakes were actively searching for prey, or less often from a stationary position (although not necessarily a coiled posture). Snakes were rarely stationary for the entire duration of a caudal

distraction display; instances of stationary caudal distraction were frequently accompanied by some time displaying the behavior while advancing toward the mouse. There was no difference in the amount of time a snake displayed caudal distraction as a function of foraging mode (ambush or pursuit) or trial order ($F_{1,13} \leq 1.93$, $P \geq 0.19$).

The ability of gray rat snakes to capture their prey on the 1st strike was influenced by the duration of caudal distraction (Table 1; Pearson's $r = 0.71$, $P = 0.003$); longer times spent performing caudal distraction were associated with fewer successful 1st strikes. Snakes failing to capture their prey on the 1st attempt typically succeeded on the 2nd or 3rd strike. Neither frequency nor duration of caudal distraction was a function of snake gender ($F_{1,13} < 0.1$, $P \geq 0.9$) or size (Pearson's $r < 0.31$, $P \geq 0.26$). There was no difference in rate of successful capture on the 1st attempt as a function of whether the snake displayed caudal distraction while moving or stationary ($F_{1,13} = 0.15$, $P = 0.71$).

DISCUSSION

Caudal distraction most closely resembles rapid tail movements that Carpenter et al. (1978) described as part of the caudal luring sequence in death adders (*Acanthophis*). However, caudal distraction differs from luring in 2 discernible features: (1) position of the tail relative to the snake's head—distance separating head and tail is greater when distracting than when luring, with the tail displaced laterally away from the head (rather than aligned in front of, or behind, the head); and (2) speed of tail movement—distraction movements are generally faster than movements described for luring (approaching 2 undulations sec^{-1} ; Carpenter et al. 1978).

Caudal distraction was always initiated before snakes were within striking distance of their prey, and mice typically directed their attention toward the tail. When using caudal distraction, snakes approached prey more slowly than when not displaying the behavior. Although striking distance in foraging episodes was not quantified in this study, the behavior may permit closer approach of snakes to their prey prior to attempting capture (Schmidt et al. 1993). Foraging attempts involving display of caudal distraction did not result in gray rat

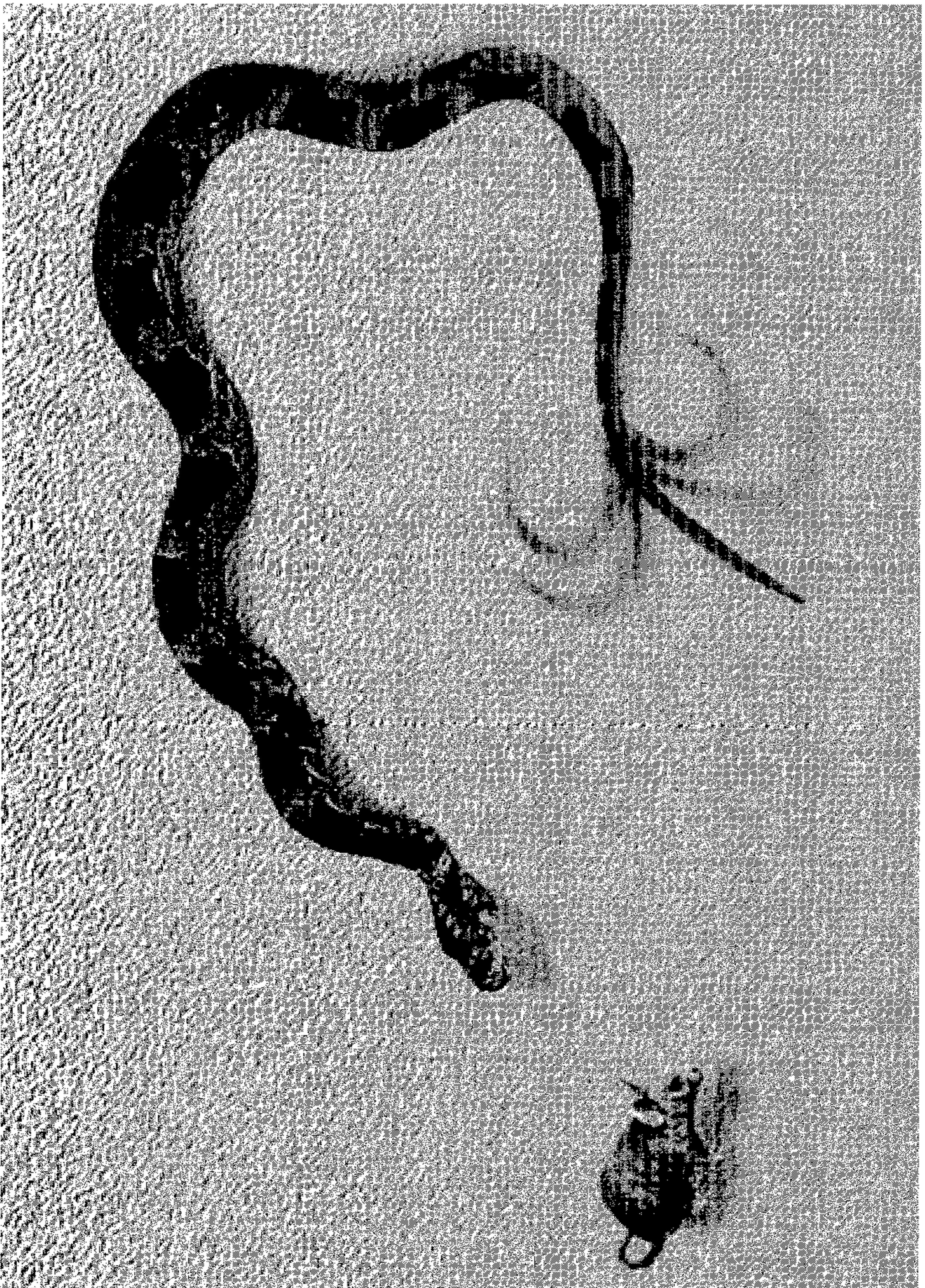


Fig. 1. Caudal distraction in *Elaphe obsoleta spiloides* (digitized from videotaped observations). Blurred silhouettes of tail indicate maximum curvature of tail during performance of behavior.

TABLE 1. Capture success as a function of the duration (sec; mean $\pm 1 s_{\bar{x}}$) of caudal distraction display in adult gray rat snakes (*Elaphe obsoleta spiloides*). Sample sizes are given in parentheses. Values in 2nd and 3rd columns are different (Pearson's $r = 0.71$, $P = 0.003$).

Duration of caudal distraction	Duration of caudal distraction when 1st strike succeeded	Duration of caudal distraction when 1st strike failed
27 \pm 8 (19)	11 \pm 7 (14)	59 \pm 14 (5)

snakes requiring less time for successful prey capture.

Two concerns are pertinent to the occurrence of caudal distraction in gray rat snakes (Wickler 1968, Greene and Campbell 1972): (1) whether prey respond to the behavior as they would to a potential food item (a deception) and therefore approach the snake, or are distracted by it (thereby facilitating approach of the snake to within striking distance); and (2) whether the behavior occurs only during periods of hunger, or as a nervous response to an unrecognized object.

In answer to the initial concern, mice directed their attention toward the tail display but never approached the area of leaf litter being disturbed by the display. The only occasions ($n = 3$) when a mouse was observed in the area of a snake's tail were before caudal distraction had been initiated, presumably because the snake had not yet detected its prey. Subjects displaying caudal distraction for a longer duration before attempting to capture their prey were less likely to succeed on their 1st strike. Although these situations could have involved mice that were inherently warier (other than excluding those with discernible physical or behavioral aberrations, mice were neither physiologically nor behaviorally tested prior to enclosure acclimatization), their perception of a nearby predator may increase following extended periods of caudal distraction. In such situations mice may increase their probability of escape at the time of the snake's 1st attempt at capture. Behavioral modification in response to increased awareness of predation risk has been demonstrated in other rodent species (Lima and Dill 1990). Subtle differences in response to snake presence by captive-bred and wild-caught mice (Dell'omo and Alleva 1994) suggest that caudal distraction would be of similar effect on small rodents in natural settings.

When performing caudal distraction, no subject ever positioned its tail close (<30 cm) to its head. Had mice been lured to the tail movement, they would not have been enticed to within striking distance of the snake. Thus, the described behavior appears to serve more as a distraction than it does as a lure to potential prey. Eckert and Karalus (1974) reported that mice may be distracted by auditory stimuli emitted by foraging owls immediately prior to their capture, suggesting that the use and effectiveness of distractive stimuli is a phenomenon worthy of further study.

In answer to the 2nd concern, gray rat snakes often responded to unfamiliar objects or a handler by rapidly vibrating their tails against the substrate, attempting to conceal themselves under leaf litter, or elevating their heads in a strike posture (all recognized defensive behaviors; Greene 1988). The duration of caudal distraction display did not differ between feeding episodes involving the same subject, as might be expected if the behavior were a response to recent handling or an unfamiliar object (in which case shorter durations would occur in successive episodes). The described behavior occurred only in moments before snakes attempted prey capture and was never displayed by subjects foraging for other prey types (e.g., avian prey) in similar enclosure conditions (Mullin 1998). These results collectively suggest that caudal distraction is elicited by visual and/or chemosensory cues that are specific not only to prey type but also to the setting in which the prey is encountered.

Observations described herein indicate that caudal distraction is a unique behavior facilitating capture of small mammals by snakes. However, an alternative explanation for the described tail movement may be that of conflict-induced displacement behavior (Krebs and Davies 1987). Such a view hinges on the assertion that predator approach toward prey is temporarily opposed by the need to remain cryptic so as to avoid detection by, and potential escape of, the prey. Rat snakes initiated caudal distraction more often when advancing toward the mouse than when stationary, however, indicating that any importance associated with crypsis or stealth that might elicit a displacement behavior was negligible. It is also worth noting that caudal distraction was repeatedly displayed by snakes maintained in captivity for durations of 1–16 months,

indicating that behavior was not suppressed by conditions of captivity (Warwick 1990).

A few other cautions warrant consideration: *M. domesticus* is not native to the geographic distribution of *Elaphe*; other small rodent taxa sympatric with gray rat snakes (e.g., *Peromyscus*, *Microtus*, *Sigmodon*, etc.) may behave differently in response to caudal distraction by snakes during a predator-prey encounter. Edge effects (a feature of noncircular enclosures; Krebs 1989) or space limitations of the enclosure may have masked a difference in ability to capture prey that was dependent upon caudal distraction frequency or duration.

The following observations suggest that much remains to be examined in the functional and ontogenetic development of, as well as the importance of specific stimuli in eliciting, caudal behaviors in *Elaphe*. (1) Whereas caudal luring has been documented in both juveniles and adults of several taxa (Chiszar et al. 1990, Sisk and Jackson 1997, Tiebout 1997, and references therein), caudal distraction has not been observed in rat snakes <2.4 yr old (Mullin 1998). (2) Two adult gray rat snakes were observed performing caudal luring, although without the tail in typical proximity to the head (Carpenter et al. 1978, Jackson and Martin 1980, Tiebout 1997). (3) Luring in gray rat snakes was recorded when foraging for mammalian and avian prey, and in both cases was elicited in response to prey movement. Differences in behavior patterns resulting from the discrimination of prey types have been demonstrated in other taxa (Arnold 1986, Ford and Burghardt 1993) and indicate an appropriate direction for further study of the described behavior. In particular, documentation of the differential display of caudal distraction in snakes exposed to different stimuli may provide evidence for consciousness or awareness to support the few cognitive ethology studies conducted with squamates (Burghardt 1991).

ACKNOWLEDGMENTS

Subjects used in this study were collected under authorization of a Tennessee Wildlife Resources Agency permit (#684) and maintained following an Institute for Animal Care and Use Committee protocol (#A-9336). Assistance during this project was provided by J. Foucault and K. May. P. Fancher deserves

special thanks for digitizing the figure of the described behavior. I am grateful for discussions with G. Burghardt and comments from E.D. Brodie, Jr., R. Cooper, M. Ferkin, N. Ford, S. Fox, W. Gutzke, A. Price, R. Reiserer, G. Rodda, and 3 anonymous reviewers that improved this manuscript. Funding was provided in part by the Department of Biology, University of Memphis.

LITERATURE CITED

- ARNOLD, S.J. 1986. Laboratory and field approaches to the study of adaptation. Pages 157–179 in M.E. Feder and G.V. Lauder, editors, *Predator-prey relationships*. University of Chicago Press, Chicago, IL.
- BECK, D.D. 1996. Effects of feeding on body temperatures of rattlesnakes: a field experiment. *Physiological Zoology* 69:1442–1455.
- BURGHARDT, G.M. 1991. Cognitive ethology and critical anthropomorphism: a snake with two heads and hog-nose snakes that play dead. Pages 53–90 in C.A. Ristau, editor, *Cognitive ethology: the minds of other animals*. Erlbaum & Assoc., Hillsdale, NJ.
- CARPENTER, C.C. 1977. Communication and displays of snakes. *American Zoologist* 12:217–223.
- CARPENTER, C.C., AND G.W. FERGUSON. 1977. Variation and evolution of stereotyped behavior in reptiles. Pages 335–554 in C. Gans and D.W. Tinkle, editors, *The biology of the Reptilia*. Volume 7. Academic Press, New York.
- CARPENTER, C.C., J.B. MURPHY, AND G.C. CARPENTER. 1978. Tail luring in the death adder, *Acanthophis antarcticus* (Reptilia, Serpentes, Elapidae). *Journal of Herpetology* 12:574–577.
- CHISZAR, D., D. BOYER, R. LEE, J.B. MURPHY, AND C.W. RADCLIFFE. 1990. Caudal luring in the southern death adder, *Acanthophis antarcticus*. *Journal of Herpetology* 24:253–260.
- COHEN, J. 1965. Some statistical issues in psychological research. Pages 95–121 in B.B. Wolman, editor, *Handbook of clinical psychology*. McGraw-Hill, New York.
- CULLEN, J.M. 1972. Some principles of animal communication. Pages 101–122 in R.A. Hinde, editor, *Non-verbal communication*. Cambridge University Press, Cambridge, U.K.
- DELI'OMO, G., AND E. ALLEVA. 1994. Snake odor alters behavior, but not pain sensitivity in mice. *Physiological Behavior* 55:125–128.
- DRUMMOND, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour* 86:1–30.
- ECKERT, A.W., AND K.E. KARALUS. 1974. *The owls of North America*. Doubleday & Company, Garden City, NY.
- ENQUIST, M., E. PLANE, AND J. ROEDITOR. 1985. Aggressive communication in fulmars (*Fulmaris glacialis*) competing for food. *Animal Behavior* 33:1107–1120.
- FORD, N.B. 1995. Experimental design in studies of snake behavior. *Herpetological Monographs* 9:130–139.
- FORD, N.B., AND G.M. BURGHARDT. 1993. Perceptual mechanisms and the behavioral ecology of snakes. Pages 117–164 in R.A. Seigel and J.T. Collins, editors, *Snakes: ecology and behavior*. McGraw-Hill, New York.

- GREENE, H.W. 1973. Defensive tail display by snakes and amphisbaenians. *Journal of Herpetology* 7:143-161.
- _____. 1988. Antipredator mechanisms in reptiles. Pages 1-152 in C. Gans and R.B. Huey, editors, *Biology of the Reptilia*. Volume 16. Allen R. Liss, New York.
- _____. 1992. The ecological and behavioral context for pitviper evolution. Pages 107-117 in J.A. Campbell and E.D. Brodie, Jr., editors, *Biology of the pitvipers*. Selva, Tyler, TX.
- GREENE, H.W., AND J.A. CAMPBELL. 1972. Notes on the use of caudal lures by arboreal green pit vipers. *Herpetologica* 28:32-34.
- HEATWOLE, H., AND E. DAVISON. 1976. A review of caudal luring in snakes with notes on its occurrence in the Saharan sand viper, *Cerastes vipera*. *Herpetologica* 32:332-336.
- JACKSON, J.F., AND D.L. MARTIN. 1980. Caudal luring in the dusky pygmy rattlesnake, *Sistrurus miliarius barbouri*. *Copeia* 1980:926-927.
- KREBS, C.J. 1989. *Ecological methodology*. Harper & Row, New York.
- KREBS, J.R., AND N.B. DAVIES. 1987. *An introduction to behavioral ecology*. Blackwell Scientific, Oxford, U.K.
- LIMA, S.L., AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- LOOP, M.S. 1970. The effects of feeding experience on the response to prey-object extracts in rat snakes. *Psychonomic Sciences* 21:189-190.
- MARTIN, J. 1996. Effects of recent feeding on locomotor performance of juvenile *Psammodromus algirus* lizards. *Functional Ecology* 10:390-395.
- MULLIN, S.J. 1998. The foraging ecology of the gray rat snake, *Elaphe obsoleta spiloides* Duméril, Bibron and Duméril. Doctoral dissertation, University of Memphis, Memphis, TN.
- MULLIN, S.J., R.J. COOPER, AND W.H.N. GUTZKE. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). III. Searching for different prey types in structurally variable habitats. *Canadian Journal of Zoology* 76:548-555.
- MURRAY, B.A., S.D. BRADSHAW, AND D.H. EDWARD. 1991. Feeding behavior and the occurrence of caudal luring in Burton's pygopodid *Lialis burtonis* (Sauria: Pygopodidae). *Copeia* 1991:509-516.
- RABATSKY, A.M., AND T.M. FARRELL. 1996. The effects of age and light level on foraging posture and frequency of caudal luring in the rattlesnake, *Sistrurus miliarius barbouri*. *Journal of Herpetology* 30:558-561.
- RADCLIFFE, C.W., D. CHISZAR, AND H.M. SMITH. 1980. Prey-induced caudal movements in boa constrictor with comments on the evolution of caudal luring. *Bulletin of the Maryland Herpetological Society* 16: 19-22.
- SAZIMA, I., AND A.S. ABE. 1991. Habits of five Brazilian snakes with coral-snake pattern, including a summary of defensive tactics. *Studies of Neotropical Fauna and Environment* 26:159-164.
- SAZIMA, I., AND G. PUERTO. 1993. Feeding technique of juvenile *Tropidodryas striaticeps*: probable caudal luring in a colubrid snake. *Copeia* 1993:222-226.
- SCHEFFÉ, H. 1959. *The analysis of variance*. John Wiley & Sons, New York.
- SCHMIDT, D.F., W.K. HAYES, AND E.E. HAYES. 1993. Influence of prey movements on the aim of predatory strikes of the western rattlesnake (*Crotalus viridis*). *Great Basin Naturalist* 53:203-206.
- SISK, N.R., AND J.F. JACKSON. 1997. Tests of two hypotheses for the origin of the crotaline rattle. *Copeia* 1997: 485-495.
- TIEBOUT, H.T., III. 1997. Caudal luring by a temperate colubrid snake, *Elaphe obsoleta*, and its implications for the evolution of the rattle among rattlesnakes. *Journal of Herpetology* 31:290-292.
- WARWICK, C. 1990. Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology. *Applied Animal Behavioral Science* 26:1-13.
- WICKLER, W. 1968. *Mimicry*. Weidenfield & Nicolson, London, U.K.

Received 1 June 1998
Accepted 19 October 1998