

## The Foraging Ecology of the Gray Rat Snake (*Elaphe obsoleta spiloides*)—Visual Stimuli Facilitate Location of Arboreal Prey

**ABSTRACT.**—We examined the responsiveness of adult gray rat snakes to avian prey in enclosures that simulated natural habitat conditions. Subjects searched for arboreal nest contents in the presence or absence of a bird model flown so as to simulate avian provisioning behavior. In the absence of the model, gray rat snake latency to capture prey was over 92 % greater than when searching for nest contents with the model. Snakes responded to model flight by turning their heads in the direction of its movement. We conclude that gray rat snakes perceive relatively distant visual cues from prey, and that nest provisioning (activity localized around a nest) may facilitate snakes correctly choosing to ascend trees that contain active nests and ignoring those that do not.

### INTRODUCTION

Snakes are usually alerted to the presence of their prey by either chemosensory or visual stimuli. In particular, snakes detecting volatile prey chemicals will usually respond with increased tongue-flicking and searching behavior to facilitate prey location (Drummond, 1979; Burghardt and Denny, 1983). Snakes may also orient towards visual cues from their moving prey. Studies addressing the role of prey movement in directing snake foraging behavior have been conducted primarily with laboratory-reared natricine snakes (reviewed in Ford and Burghardt, 1993), and prey are often presented within close proximity to the snake (e.g., <20 cm; Drummond, 1985; Teather, 1991). When searching for distant prey (e.g., >120 cm; Eichholz and Koenig, 1992), gopher snakes (*Pituophis catenifer*) preferentially climb trees with active nests where breeding western bluebirds (*Sialia mexicana*) provision their nestlings. If chemical cues from arboreal nests are weak or absent, foraging snakes may locate nest contents by responding to specific search images of provisioning birds (Porter and Czaplicki, 1977; Pietrewicz and Kamil, 1981).

The purpose of our study was to demonstrate the importance of a relatively distant visual stimulus (bird provisioning behavior) in orienting the foraging activity of the gray rat snake (*Elaphe obsoleta spiloides*) towards an arboreal nest cavity. This dietary generalist preys on several avian and small mammalian species (Jackson, 1974; Mullin, 1998) in a variety of habitats (usually various successional stages of deciduous or coniferous forests). Examination of snake foraging ecology in natural settings often requires extensive use of radio telemetry (Weatherhead and Hoysak, 1989; Durner and Gates, 1993) and lengthy observation periods to document rare predatory events. Therefore, we simulated a natural habitat in the laboratory, where latency to prey encounter could be accurately and precisely recorded. While unable to replicate all parameters of the natural habitat, this technique elucidated how the presence or absence of a visual stimulus affected predatory success.

### METHODS

Adult gray rat snakes (eight males and four females) were obtained from forested and semirural areas within Shelby County (Tennessee Wildlife Resources Agency Permit #684), and housed individually (Institute for Animal Care and Use Committee protocol #A-9336). Subjects were fed either northern bobwhite quail (*Colinus virginianus*) eggs or house mice (*Mus domesticus*) weekly, and provided with water ad lib. Between 17 December 1995 and 27 September 1996, subjects were individually observed foraging in each of two treatments: "no model" and "model."

Three indoor enclosures, each measuring 2.25 m<sup>2</sup> and 2 m high, were constructed to simulate conditions of a bottomland hardwood forest (specifically, the wildlife management area of Meeman Shelby Forest State Park, Shelby Co., Tennessee, where both rat snakes and arboreally nesting birds are common). Light intensity on the floor of the enclosure, temperature (26–29 C), and photoperiod (14:10 h light:dark) all approximated mean values recorded at the field site during June 1994 (Mullin, 1998). The floor of the enclosure was lined with leaf litter collected at the field site and artificial plants matching the mean ( $\pm 1$  SE) stem diam ( $6.5 \pm 0.3$  mm) and vegetation density ( $64.0 \pm 2.3$  plants m<sup>-2</sup>) recorded at the field site (Mullin, 1998). All of these parameters were measured at the field site during peak bird breeding activity, and were maintained throughout the study.

Arboreal microhabitat was provided in each enclosure by constructing a free-standing tree from a large deciduous tree branch (12–16 cm in diam) collected at the field site. Most cavity-nesting bird species construct their nests in dead trees devoid of any foliage; such trees do not occur within close proximity to one another (Eriksson and Ehrlén, 1992; pers. observ.), and intra- and interspecific territoriality among forest-dwelling birds ensures that nests are not clumped in distribution (Sherry and Holmes, 1988). Thus, using only one tree within each enclosure did not underestimate the natural nest density. Each tree contained a nest cavity positioned 120 cm above the enclosure floor. Further details concerning the construction of the simulated habitat enclosures are found in Mullin (1998).

Before its use in a foraging trial, an individual was placed on a restricted diet (water alone) for 3 wk, and acclimatized to the simulated habitat for the last 3 days during that period. Immediately preceding a trial, the subject was removed from the enclosure, and its mass determined ( $\pm 0.05$  g). During that time, three quail eggs were placed in the cavity of the constructed tree. The mass of each clutch of three eggs used in the trials was similar ( $24.1 \pm 0.6$  g;  $n = 24$ ), though the ratio of prey mass to snake mass was not fixed during the study. We placed several feathers from arboreal-nesting bird species [carolina wren (*Thryothorus ludovicianus*), northern cardinal (*Cardinalis cardinalis*), and house sparrow (*Passer domesticus*)] in the nest cavity. We assumed that the feather odors masked chemosensory cues from the quail eggs, and that placing eggs of a ground- or shrub-nesting bird species in an arboreal cavity did not bias snake foraging behavior.

During the "model" treatment foraging trials, a freeze-dried mount of a carolina wren (preserved with wings spread in flying posture) was suspended by a guy wire. The wire was secured between an upper corner of the enclosure and a point on the constructed tree directly above the nest cavity entrance. A monofilament line was attached to the legs of the bird, threaded out of the enclosure wall, and through a series of eyelets that guided the line back to an assistant (Mullin, 1998). The bird was released and retracted along the guy wire by the assistant once every 5 min, a rate matching the mean visitation rate for pairs of several forest-dwelling bird species (Grundel and Dahlsten, 1991; O'Neill, Goodbred and Holmes, 1996). In other words, though quail eggs were offered as prey, these treatment conditions depicted a pair of cavity-nesting birds provisioning hatched nestlings.

Upon reintroducing the subject into the enclosure, the time required to locate the nest (latency;  $\pm 1$  sec) was monitored by a video camera suspended above the ceiling of the enclosure (*i.e.*, foraging snakes were not disturbed by observer presence; Drummond, 1983). The order in which individuals of each sex were exposed to each treatment condition was randomized. At least 2 mo elapsed before a subject foraged in the second treatment, again preceded by 3 wk on restricted diet and a 3-day acclimatization period. The leaf litter layer and the arrangement of vegetation were always changed between trials such that individuals were not exposed to the same arrangement of plants.

Multivariate repeated-measures analyses of variance (MANOVA;  $\alpha = 0.05$ ) were used to ascertain if latency to nest location was a function of presence or absence of the provisioning model, snake gender, or an interaction between those two factors (Cohen, 1965; McCall and Appelbaum, 1973). Because trials were conducted in three different cages, we determined that there was no relationship between latency to prey capture and trial location ( $F_{2,21} = 0.72$ ,  $P = 0.49$ ). Subjects tested in one treatment condition did not gain experience which influenced their performance in the other treatment (*i.e.*, no order effect;  $F_{1,22} = 0.25$ ,  $P = 0.91$ ).

## RESULTS

Gray rat snakes used in the foraging trials ranged from 106.2–144.1 cm in SVL and from 337.3 to 799.7 g in mass ( $\bar{x} = 124.5 \pm 1.2$  cm, and  $525.1 \pm 37.2$  g, respectively). There were no significant differences in either SVL or mass as a function of the gender of the individuals tested (*t*-tests;  $P > 0.05$ ). When their view was not obscured by vegetation within the enclosure, subjects were observed abruptly turning their heads towards the model as it was released or retracted along the guy wire. Latency to successfully locate the cavity nest differed by treatment condition ( $F_{1,10} = 5.39$ ,  $P = 0.04$ ). Subjects required more time to find the nest when the model was absent ( $66.0 \pm 15.5$  min) than when it was present ( $34.3 \pm 7.8$  min). There were no differences in latency associated with subject gender or an interaction between gender and model presence ( $F_{1,10} = 0.22$ ,  $P = 0.65$ ).

## DISCUSSION

While vomeronasal cues clearly facilitate prey detection by snakes (Halpern, 1992), visual confirmation of the prey item is probably prerequisite to an attempt at capturing prey in some species (Pietrewicz and Kamil, 1981; Ford and Burghardt, 1993). Chemosensory information was present in both treatment conditions of our experimental design, and only visual cues were manipulated. Gray rat snakes required less time to locate arboreal avian prey when the provisioning model was present (the response mean with the model present was 52 % of the mean when the model was absent). Results similar to those described here have been reported for gopher snakes, another dietary generalist species that predated avian nests (Eichholz and Koenig, 1995).

Two conclusions are warranted from the present results: (1) gray rat snakes can perceive prey movement (simulated provisioning activity) over 1 m above the substrate; and (2) foraging gray rat snakes are sensitive to the visual stimulus of nest provisioning and direct their foraging maneuvers towards such movements. Additional support for the latter conclusion could be obtained from a third treatment condition involving a moving object which does not have the properties or significance of parent birds provisioning their young. If latency to prey encounter in such conditions is similar to the response in "model absent" conditions, then gray rat snakes may respond to specific search images of avian provisioning behavior. However, logistical considerations and spatial constraints within the enclosures restricted our experimental design to two treatment conditions. Goodman and Goodman's (1976) suggestion that arboreally foraging kingsnakes (*Lampropeltis zonata*) were aided in locating nests by the intensity of antipredatory response by parent birds indicates another interesting area worthy of further study.

Vomeronasal cues on the ground that might indicate the presence of an arboreal bird nest (e.g., egg shells, faeces) are generally not available to snakes because birds caring for altricial young commonly remove sources of such cues from the nest before they can be deposited on the ground below (Morton, 1979; Darveau *et al.*, 1993). As such, volatile chemosensory information from arboreal nests may stimulate searching behavior in rat snakes, while provisioning activity at the nest may facilitate nest location by foraging snakes. Subjects were responsive to the visual stimulus of the model as they would abruptly direct their head towards the model in flight. Similar directed response to prey movement has been reported in several species of natricine snakes (e.g., *Nerodia* and *Thamnophis*; Drummond, 1985; Schaeffel and Mathis, 1991; Heinen, 1995).

Radio-telemetered gray rat snakes have been frequently observed in arboreal habitats during their activity season, especially coincident with bird breeding activity (Mirarchi and Hitchcock, 1982; pers. observ.). Because snakes must enter the arboreal microhabitat to access nest contents, ascent time and energy constitute a cost that must be added to overall foraging effort for snakes seeking avian prey. The time and energy spent in ascent is presumably offset by the savings associated with the predator not having to pursue sessile prey, once it is detected. The results of this study taken together with those of Eichholz and Koenig (1992) and Neal *et al.* (1993) suggest that gray rat snakes using avian provisioning activity to locate nests in natural settings probably do not ascend trees randomly in search of their prey. By climbing only trees containing active nests, rat snakes maximize energetic benefits associated with arboreal predation (Pounds, 1991; Lillywhite and Henderson, 1993). Further work should confirm the importance of this visual cue in field settings and attempt to compare snake responses to provisioning activity at nests of cavity-nesting and cup-nesting bird species.

Bird activity at a nest typically increases following the incubation period as parents provide for their nestlings (Darveau *et al.*, 1993; O'Neill Goodbred and Holmes, 1996). Hensley and Smith (1986) reported that 90 % of eastern bluebird (*Sialia sialis*) nests predated by rat snakes contained nestlings. Gray rat snakes do not refuse eggs (Mullin, 1996), but would presumably experience greater net energetic gain from the ingestion of nestlings (Romanoff and Romanoff, 1949; Ehrlich *et al.*, 1988). Gray rat snakes may maximize energetic gain per unit foraging effort via sensitivity to the stimuli associated with parent birds provisioning nestlings (Tinbergen, 1960; Pietrewicz and Kamil, 1981).

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