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Source: *Herpetologica*, Vol. 55, No. 1 (Mar., 1999), pp. 18-28

Published by: Herpetologists' League

Stable URL: <http://www.jstor.org/stable/3893065>

Accessed: 20/05/2009 13:16

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THE FORAGING ECOLOGY OF THE GRAY RAT SNAKE (*ELAPHE OBSOLETA SPILOIDES*). I. INFLUENCE OF HABITAT STRUCTURAL COMPLEXITY WHEN SEARCHING FOR MAMMALIAN PREY

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ABSTRACT: The habitat in which a predator experiences the highest level of foraging success may depend on the complexity of the structure within that habitat. Visual perception of prey may increase in an open habitat where structure is absent, whereas a predator's cryptic in an ambush posture may increase in a highly complex habitat. We examined the effect of variation in habitat structural complexity on the predatory success of the semi-arboreal snake *Elaphe obsoleta spiloides* foraging for small mammals (*Mus domesticus*). Individual snakes searched for mice in large enclosures containing one of five levels of vegetation density. Latency to prey capture and snake behaviors were recorded on video tape for each foraging episode. Gray rat snakes were least proficient at capturing prey in enclosures devoid of vegetation, but latency to prey capture was not reliably affected by variation in the density of vegetation within the enclosures. Subjects spent over 95% of foraging time performing 10 of the 20 described behaviors; three behaviors occurred more often than the other seven regardless of variation in structural complexity of habitat. Experimental manipulation of structural complexity within simulated habitats did not influence predatory success or behavioral expression in gray rat snakes foraging for small rodents.

Key words: *Elaphe obsoleta spiloides*; Foraging behavior; Gray rat snake; Habitat simulation; Predatory success; Structural complexity

VARIATION in habitat structural complexity may affect predatory success (reviewed in Heck and Crowder, 1991), although many studies examining this phenomenon have been conducted only in aquatic habitats (Anderson, 1984; Vince et al., 1976) and results have not been consistent. The optimal level of habitat structural complexity for some predatory species is an open habitat (Nelson and Bonsdorff, 1990), because the absence of vegetation can increase the predator's probability of visually or aurally detecting prey. Conversely, foraging by other species is most successful when structure is present at a particular level (Nelson, 1979; Savino and Stein, 1982), above or below which success decreases. For such species, structure may conceal their approach to prey or may serve to reduce predation risk on the predators themselves. A selected habitat may therefore reflect a compromise between several factors of an organ-

ism's ecology that are influenced by habitat structure (McCoy and Bell, 1991).

In addition to the effects on predatory success, habitats having different structural regimes may manifest effects on the specific behaviors used to acquire prey. Such behavioral modification may result from changes in habitat selection that influence choice of foraging substrate (Fragaszy and Boinski, 1995), foraging mode (pursuit versus ambush tactics) (Moermond, 1979; Murray et al., 1995), or prey type and its behavior that affects the associated predatory behaviors (Jones, 1990). Variation in the expression of specific behaviors may be also associated with perceived risk of foraging in a particular habitat (Lima and Dill, 1990, and references therein). Changes in behavioral expression in response to different microhabitat conditions may alter levels of predatory success unless the different behaviors are equally effective at finding and capturing prey in the respective microhabitats.

Examinations of predatory success as a function of habitat structural complexity in

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snakes have considered only semi-aquatic species (Mullin and Mushinsky, 1995, 1997). In aquatic habitats, snakes are surrounded by a vegetational structure that is relatively uniform (aquatic macrophytes or littoral plants) compared to the heterogeneous vegetational landscape possibly encountered by a terrestrial species of snake. Examination of snake foraging ecology in habitats of differing structural complexity often requires extensive use of radio telemetry (Weatherhead and Hoysak, 1989) and lengthy observation periods to document rare predatory events. In this study, we present an alternative technique of simulating the habitat in a laboratory setting where observations of snake foraging can be closely monitored. While unable to replicate all parameters of the natural habitat accurately, this research was designed to illustrate how alterations of closely controlled variables manifest changes in foraging behavior or success.

The gray rat snake (*Elaphe obsoleta spiloides*) preys upon several avian and small mammalian species (Cink, 1991; Fitch, 1963; Hensley and Smith, 1986; Jackson, 1974; Mirarchi and Hitchcock, 1982) in a variety of habitats (Durner and Gates, 1993). We examined the influence of habitat structural complexity on the success (measured as latency to capture a single prey item: Royama, 1970) of gray rat snakes foraging for small mammals. Additionally, we quantified differences in snake behaviors at different levels of structural complexity that may indicate shifts in foraging mode for this generalist predator.

MATERIALS AND METHODS

Habitat Simulation

During June 1994, the vegetation composition in randomly selected 2.25 m² quadrats was measured within the wildlife management area of Meeman-Shelby Forest State Park (MSFSP), Shelby County, Tennessee. The number of living plants within each plot was counted, and plant size of the annually emergent understory was measured at each stem base (± 0.5 mm) using calipers. Enclosure size limitations (described below) did not permit

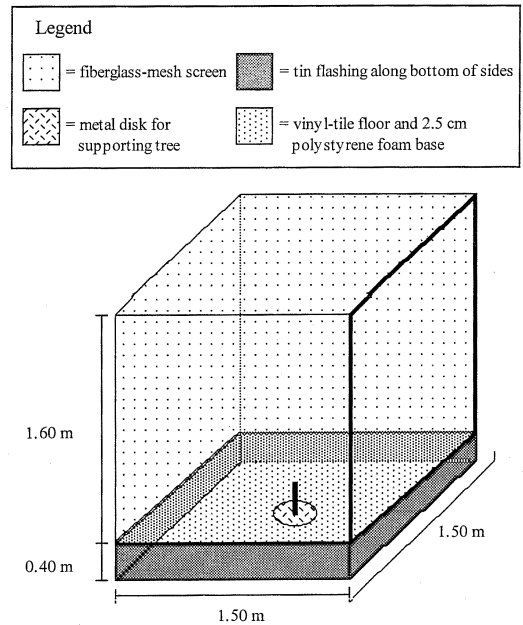


FIG. 1.—Diagram of simulated habitat enclosures used for foraging trials with gray rat snakes (*Elaphe obsoleta spiloides*) between 19 August 1994 and 10 December 1996. Enclosure depicted in absence of vegetation. The bold-faced edges along the right side denote a detachable section for introduction of predator and prey species.

simulation of large plants, so vegetation simulation was restricted to the understory vegetation. The plant species at MSFSP are reported in Mullin (1998).

Three enclosures (each 2.25 m² and 2 m in height), simulating several habitat parameters of a bottomland hardwood forest (characterized by MSFSP), were constructed and maintained in the laboratory. We are unaware of any study of similar scope that has used larger enclosures. The walls and ceiling of each enclosure were comprised of a combination of tin flashing and fiberglass-mesh screen to prevent subject escape (Fig. 1). Temperature and photoperiod in the enclosures were 26–29 C and 14:10 h light:dark, respectively. Light intensity on the floor of the enclosures was within the range measured under the canopy at MSFSP during the vegetation sampling period. The conditions were held constant for the duration of the study; logistical considerations prevented us from determining how within-season changes in

the floristic composition may affect snake predatory performance.

Based on measurements of vegetation density obtained from MSFSP ($\bar{x} \pm 1$ SE = 64.0 ± 2.3 plants m^{-2} ; $n = 144$), we chose five treatments of habitat structural complexity for the foraging trials: 200%, 150%, 100%, 50%, and 0% of the mean ambient vegetation density. We used artificial plants matching the mean stem diameter of understory plants measured at MSFSP (6.5 ± 0.3 mm) to simulate the vegetation within each enclosure. We randomly inserted plants into a foam base lining the enclosure floor that was covered by leaf litter collected at MSFSP. An inert substrate, the foam layer enabled us to change the arrangement of plants between successive trials within the same treatment density, such that individual snakes were not exposed to the same arrangement of plants.

Arboreal microhabitat was provided in the enclosures by constructing free-standing trees from large branches of deciduous trees collected at MSFSP [although examined elsewhere (Mullin, 1998), use of trees by snakes and their prey in this study was rare]. To prevent simulated trees from tipping over inside the enclosures, as well as prey escape, branches were not added to trees. Gray rat snakes are excellent climbers (Jackson, 1976) and easily ascended the constructed trees in the absence of branches or vines. While these treatment conditions may not represent the full range of habitat types encountered by gray rat snakes, they do represent a reasonable range of variation about a mean level of structural complexity found in a bottomland hardwood forest.

Foraging Trials

Adult gray rat snakes were obtained from MSFSP and other forested and semi-rural areas within Shelby County (Tennessee Wildlife Resources Agency Permit 684), and they were maintained in captivity (Institute for Animal Care and Use Committee protocol A-9336) at temperature and photoperiod levels identical to those for the enclosures. Snakes were housed individually in cages measuring a

minimum of $30 \times 60 \times 30$ cm, provided with water ad libitum, and fed either Northern Bobwhite Quail (*Colinus virginianus*) eggs or mice (*Mus domesticus*) weekly. Before their use in foraging trials, we measured the snout-vent length (SVL: ± 0.5 cm) and determined the sex of each snake using a cloacal probe.

Prior to its use in a foraging trial, a subject was placed on a restricted diet (water alone) for 3 wk and was acclimatized to the enclosure for the last three days of that period. Immediately preceding the trial, the individual was removed from the enclosure and its mass was determined (± 0.05 g). During that time (a minimum of 15 min was allowed), a mouse was acclimatized to the enclosure. We used only adult male mice having dark brown pelage as prey in the trials to minimize differences in the predator's perception of behavioral, visual, and vomeronasal characteristics of prey, and to provide prey visually similar to those that snakes encounter in the field. We used mice having similar mass ($\bar{x} = 30.7 \pm 0.5$ g, $n = 70$), although the ratio of prey mass to snake mass was not fixed during the study. Behavior of prey in enclosures having different vegetation densities did not change noticeably, and any unperceived changes in prey behavior were assumed to have a negligible effect on snake predatory success.

Upon re-introducing the individual into the enclosure (in the corner farthest removed from the mouse at that time), the snake's foraging behavior was recorded on video tape, and the time required for successful capture (latency: ± 1 s) and ingestion of prey was monitored by a timer on the video cassette recorder. Specific behaviors were identified and described (Table 1) following Mullin and Mushinsky (1995). Based on observations during preliminary trials and radio-telemetered individuals in the field, behaviors were categorized as foraging-type if an individual's tongue-flick rate (TFR) exceeded one flick/2 s, or non-foraging type for slower TFR's. Because steps were taken to minimize other disturbances during the time that the subject was being weighed, we are confident that tongue-flicking activity was

TABLE 1.—Description of behaviors performed by gray rat snakes during foraging trials in simulated habitats of varying vegetation density between 19 August 1994 and 10 December 1996. Those behaviors occurring in $\leq 10\%$ of all trials (indicated with an asterisk, *) were not included in statistical analyses.

Code	Behavior
Resting behaviors	
ROL	Resting on litter—snake motionless, body exposed, and TFR < 1 flick/2 s.
RUL	Resting under litter—snake motionless, body concealed under leaf litter.
ROS*	Resting on snag—snake motionless, majority of body on snag, TFR < 1 flick/2 s, and head visible outside of cavity in snag.
Predatory behaviors	
IOP	Ingesting prey—from when the snake gapes and bites down on prey (following capture) to the first tongue flick after the prey passes the mouth margin.
POS	Prey orientation searching—following constriction of mammalian prey, when snake searches for site of initial ingestion.
SLS	Slow searching—entire body of snake in motion over leaf litter, and TFR ≥ 1 flick/2 s.
SNC	Strike and coil—snake successfully strikes and constricts mammalian prey.
SOF*	Searching over foliage—similar to SLS or STS with head on the vegetation.
SOS*	Searching on snag—majority of body on snag, anterior portion in motion, and TFR ≥ 1 flick/2 s.
STR	Striking—a strike at prey which misses; this code is also used for a strike which captures prey, which then escapes from snake's grasp.
STS	Stationary searching—snake is either motionless or only anterior half of body moving, and TFR ≥ 1 flick/2 s.
SUL	Searching under litter—any movement of the anterior body underneath the leaf litter while the head is concealed.
Non-predatory behaviors	
ADP*	Anterior defensive posture—immediately follows frontal encounter between snake and object, resulting in a recoil of the anterior half of snake.
ASC*	Ascending—forward movement up or around (laterally) the tree.
DSC*	Descending—forward movement down or around (laterally) with the head directed downward towards the leaf litter.
EFS*	Extndng from snag—snake extends body up or away from snag, while remainder of body contacts the snag.
FML	Fast movement over litter—entire body of snake in motion at ≥ 1.0 m sec ⁻¹ ; TFR ≤ 1 flick/2 s; not a strike directed at prey.
GAPE	Snake stationary while opening its mouth in a fashion similar to a yawn.
SML*	Slow movement over litter—similar to FML except that rate of movement is < 1.0 m s ⁻¹ .
Caudal behaviors (modifiers of predatory behaviors, above)	
TR	Tail rattling—agitated snake rapidly shaking tail tip in leaf litter; accompanies SLS or STS while in proximity of prey, or ADP.
CD	Caudal distraction—majority of tail whipped erratically across leaf litter, while snake approaches prey item; accompanies SLS or STS.

a response only to cues associated with added prey stimuli. From the video taped recordings, we determined the time that individuals spent performing each behavior from the initiation of each trial until successful capture of prey.

Between 19 August 1994 and 10 December 1996, foraging trials for each treatment density of vegetation were replicated with 14 gray rat snakes. The order in which individuals of each sex were exposed to different treatment densities was chosen haphazardly. We presumed that

snakes not responding to the presence of prey 2 h after initiation of a trial were unresponsive, and we re-tested them at a later date (in a new arrangement of vegetation). Mice did not have the opportunity to escape in this study, meaning that we could not examine the effect of prey wariness on potential predation.

Statistical Analyses

The independent variables (snake gender and vegetation density) were both considered fixed effects in our experimental

TABLE 2.—Latency to prey capture ($\bar{x} \pm 1$ SE, in seconds) for gray rat snakes (shown for all individuals, and by sex) foraging in simulated habitats of varying vegetation density (reported as % of mean ambient density) between 19 August 1994 and 10 December 1996.

Vegetation density	Latency ($\bar{x} \pm 1$ SE)		
	All individuals ($n = 14$)	Males ($n = 10$)	Females ($n = 4$)
0%	591.8 \pm 252.0	691.0 \pm 346.8	343.8 \pm 180.8
50%	251.5 \pm 83.8	219.5 \pm 73.3	331.5 \pm 251.2
100%	151.7 \pm 33.2	144.0 \pm 41.2	171.0 \pm 61.6
150%	357.1 \pm 114.0	425.7 \pm 149.6	185.8 \pm 124.5
200%	211.4 \pm 51.1	200.1 \pm 63.9	239.5 \pm 92.8

design (Martindale, 1978) because we were interested in ascertaining only the effects of known levels of habitat structural complexity on predatory success. Comparisons of response mean values across treatment levels of the independent variables were conducted using multivariate repeated-measures analyses of variance (MANOVA) or analyses of covariance (MANCOVAR), the latter controlling for differences in snake size (Cohen, 1965; McCall and Appelbaum, 1973). The means of monthly SVL measurements taken during the period that each individual was used in the experiment were used as covariate values (i.e., SVL was fixed over time as the covariate: Huitema, 1980). When statistically significant differences were attributable to vegetation density (having five levels), or for any interaction between independent variables, we used Tukey's honestly significant difference test (HSD: $df = 1$ in all comparisons) as the follow-up test to detect differences between treatment means (Kirk, 1982).

Statistical tests were conducted using Statistical Programs for the Social Sciences (Norusis, 1990) software at $\alpha = 0.05$. Behavioral times were expressed as percentages of their respective trial durations, because the durations of specific behaviors are directly proportional to trial length. Relationships among variables that might be dependent on snake size (e.g., the duration of behaviors associated with prey handling time: see Table 1) were tested using the ratio of prey mass to predator mass as the independent variable; data are otherwise reported in raw form.

Because trials were conducted in three different cages, we ensured that there was

no relationship between latency to prey capture and trial location (MANOVA: $F_{2,67} = 0.56$, $P = 0.58$). Individuals tested at one treatment density did not gain experience that influenced their performance during subsequent trials in different treatments (MANOVA: $F_{4,52} = 0.78$, $P = 0.56$).

RESULTS

Subjects ranged from 101.6–148.4 cm in SVL and from 252.1–771.6 g in mass ($\bar{x} = 123.9 \pm 1.8$ cm and 475.5 ± 17.4 g, respectively). There were no reliable differences in subject SVL or mass as a function of gender (t -test; $P \geq 0.50$). The time taken to ingest the prey (IOP: Table 1) was positively correlated with the ratio of prey mass to snake mass ($r = 0.66$, $n = 70$, $P < 0.001$).

As a covariate, SVL did not affect the outcome of any analysis (MANCOVAR: $F_{1,11} = 2.37$, $P = 0.15$); it is hereafter ignored and MANOVA results are reported. The time required by subjects to capture prey did not differ reliably among treatments of vegetation density (Table 2: $F_{4,9} = 1.71$, $P = 0.23$). There were no reliable differences in latency to prey capture as a function of snake gender ($F_{1,11} = 0.76$, $P = 0.40$), nor was there any significant interaction between gender and vegetation density ($F_{4,9} = 0.68$, $P = 0.63$).

Several of the described behaviors were recorded in $\leq 10\%$ of the trials. Because the summed durations of these behaviors comprised $< 5\%$ of the total trial durations, they were excluded from statistical comparisons of duration as a function of vegetation density. The three behaviors associated with handling the prey (Table 3)

TABLE 3.—Handling time (seconds) for *Mus domesticus* prey ($n = 70$), following successful capture, required by gray rat snakes foraging in simulated habitat enclosures between 19 August 1994 and 10 December 1996. See Table 1 for an explanation of behavioral codes.

Behavior	\bar{x}	SE
SNC	107.5	11.1
POS	48.3	9.1
IOP	282.7	15.3

also were excluded because prey were captured in all trials, and durations of these behaviors may have been influenced by snake size.

Among those behaviors occurring in >10% of the trials (Table 4), certain behaviors occurred more often than others regardless of vegetation density ($F_{9,108} = 1.99, P = 0.05$). Individuals spent more time slow searching (SLS), stationary searching (STS), or resting on litter (ROL) compared to other behaviors (Tukey's HSD: $F \geq 33.15, P < 0.001$). Similarly, individuals spent more time resting under litter (RUL) than striking (STR) regardless of vegetation density ($F = 5.61, P = 0.05$); the duration of the latter behavior, when expressed, was always <2 s. Behavioral frequency and duration did not vary as a

function of snake gender ($F_{1,12} = 0.10, P = 0.76$), nor were there any interactions between gender and behavior type ($F_{9,108} = 0.78, P = 0.64$).

The duration of certain behaviors varied as a function vegetation density ($F_{36,432} = 3.15, P < 0.001$). Individuals spent more time performing RUL in the 150% density treatment than at other vegetation densities (Tukey's HSD: $F \geq 8.96, P < 0.03$). More time was spent performing ROL at 100% density than at 0% density ($F = 9.07, P = 0.03$), but differences in durations of this behavior between other treatment levels were absent. Similarly, snakes spent more time performing SLS at 0% density than either the 150% or 200% treatment levels ($F \geq 5.79, P \leq 0.05$), but there were no differences in SLS duration between other treatments. Three-way interactions between gender, vegetation density, and behavior duration were absent ($F_{36,432} = 1.30, P = 0.12$).

We constructed post hoc orthonormalized comparisons (Kirk, 1982) of pooled percent times of ecologically related behaviors (Table 1). Behaviors occurring while snakes were concealed under the leaf litter [e.g., RUL, searching under litter (SUL)] did not occur as often as those

TABLE 4.—Percent times ($\bar{x} \pm 1$ SE, $n = 14$) which gray rat snakes spent performing specific behaviors while foraging in simulated habitats of differing vegetation density between 19 August 1994 and 10 December 1996. See Table 1 for an explanation of behavioral codes. Totals do not equal 100% because behaviors occurring in $\leq 10\%$ of the trials were not included. Different superscript numbers indicate differences between behaviors pooled across all treatment densities; different superscript letters indicate differences in behavioral durations between treatment densities (Tukey's HSD: $df = 1, P \leq 0.05$).

Behavior code	All trials	Percent duration ($\bar{x} \pm 1$ SE)				
		Vegetation density				
		0%	50%	100%	150%	200%
Resting behaviors						
ROL ¹	25.8 \pm 2.6	15.2 \pm 3.4 ^a	24.3 \pm 5.1 ^{a,b}	35.8 \pm 6.7 ^b	30.4 \pm 6.4 ^{a,b}	23.4 \pm 6.5 ^{a,b}
RUL ²	5.8 \pm 2.3	1.6 \pm 1.1 ^a	4.6 \pm 4.5 ^a	0.6 \pm 0.6 ^a	19.0 \pm 9.5 ^b	3.1 \pm 2.6 ^a
Predatory behaviors						
SLS ¹	27.3 \pm 2.8	41.6 \pm 8.6 ^a	30.1 \pm 7.1 ^{a,b}	19.7 \pm 5.5 ^{a,b}	19.1 \pm 3.4 ^b	26.2 \pm 4.5 ^b
SLS-CD ^{2,3}	2.5 \pm 0.6	1.9 \pm 1.1	2.3 \pm 1.3	1.6 \pm 1.1	3.6 \pm 2.1	3.2 \pm 1.4
STR ³	0.1 \pm 0.03	0.2 \pm 0.1	0.03 \pm 0.03	0.0 \pm 0.0	0.1 \pm 0.1	0.1 \pm 0.1
STS ¹	28.2 \pm 2.7	21.0 \pm 5.4	29.1 \pm 6.3	34.3 \pm 6.0	20.5 \pm 5.5	36.1 \pm 6.0
STS-CD ^{2,3}	0.8 \pm 0.3	1.7 \pm 1.2	0.6 \pm 0.5	1.4 \pm 0.9	0.1 \pm 0.1	0.5 \pm 0.3
SUL ^{2,3}	3.8 \pm 1.1	1.4 \pm 0.9	4.7 \pm 2.7	5.1 \pm 3.5	3.8 \pm 1.9	3.8 \pm 2.2
Non-predatory behaviors						
FML ^{2,3}	1.0 \pm 0.7	0.1 \pm 0.1	3.6 \pm 3.6	0.5 \pm 0.2	1.1 \pm 0.8	0.0 \pm 0.0
GAPE ^{2,3}	0.5 \pm 0.2	0.2 \pm 0.2	0.2 \pm 0.1	1.0 \pm 0.9	0.6 \pm 0.5	0.3 \pm 0.2

occurring above the litter layer (Tukey's HSD: $F = 7.64$, $P = 0.03$). Use of the tail as a modifier of described behaviors [e.g., slow searching with caudal distraction (SLS-CD), stationary searching with caudal distraction (STS-CD)] did not occur as often as those behaviors lacking simultaneous tail movement ($F = 131.54$, $P < 0.001$); when observed, use of the tail occurred usually immediately prior to prey capture. Behaviors considered as pursuit foraging occurred more often than behaviors classified as ambush foraging ($F = 35.29$, $P < 0.001$).

DISCUSSION

Predatory Success

The time required for gray rat snakes to capture mice did not differ in habitats that simulated different levels of vegetation density. Unlike other studies (Heck and Orth, 1980; Nelson, 1979; Nelson and Bonsdorff, 1990), this species may perform equally well over a wide range of habitat structural complexities when foraging for small mammals. The absence of a narrow optimal level of complexity should not imply, however, that gray rat snakes are suboptimal foragers in all levels of habitat structure (Pierce and Ollason, 1987). As dietary generalists, gray rat snakes may be adept at not only ingesting different types of prey (Mullin, 1996), but searching for them in different structural settings as well. Generalist garter snakes (*Thamnophis*) can be highly successful predators under certain conditions whilst inadequate in others, a conclusion that Drummond (1983) attributed to behavioral pattern. Gray rat snake predatory success may be independent of habitat structural complexity, because their foraging behaviors are sufficiently diverse to capture prey successfully in a variety of microhabitats.

Gray rat snakes appeared responsive to visual stimuli as they would abruptly direct their head towards moving prey on the opposite side of the enclosure. Similar reaction to visual stimuli from relatively distant prey has been reported in garter snakes (*Thamnophis*: Drummond, 1985; Heinen,

1995; Schaeffel and Mathis, 1991) as well as for gray rat snakes foraging for avian prey (Mullin et al., 1998). The acute responsiveness to both visual and chemosensory stimuli probably facilitates gray rat snakes locating and capturing prey in an array of structural regimes. For example, while visual perception may be important when foraging in sparsely vegetated habitats (where mobile prey can be seen and followed with relative ease), vomeronasal cues may play a more important role for snakes seeking small rodents in highly complex environments (in part, because an increased amount of structure provides more substrate for chemical deposition). Further manipulative experiments in habitat enclosures similar to those used in this study may identify the conditions in which specific visual or chemosensory cues are most important.

There are several alternative (and as yet untested) explanations why, when foraging for small rodents, gray rat snake predatory success is unaffected by changes in habitat structural complexity.

(1) As with other dietary generalists, gray rat snakes may switch foraging modes (ambush versus pursuit) even when foraging in similar habitats (Helfman, 1990; Jones and Whitford, 1989). Impartial use of both foraging modes in all habitat types would obscure differences in latency to prey capture as a function of habitat complexity, because lower latency values generally associated with pursuit foraging would presumably be offset by higher values associated with an ambush strategy.

(2) Vegetation, regardless of its density, does not hide vomeronasal cues available to snakes searching for prey (Chiszar et al., 1990). Thus, gray rat snakes following recent scent trails from rodents moving across the forest floor may experience equal levels of predatory success at all densities of vegetation.

(3) The escape and, or, avoidance behaviors of mice may be sufficiently variable to minimize the differences in time required to capture prey in different levels of structural complexity. Use of a dual video recording system may illustrate prey behavioral variation in response changes in

habitat complexity (possibly dependent on predator behavior as well).

Alternatives to these hypotheses are features of the experimental design that could not be improved. Being square in shape, edge effects (Krebs, 1989) within the enclosure may have reduced the prey's ability to avoid the predator. Secondly, chemical identification of snakes by rodents has been documented in several species (Dell'omo and Alleva, 1994; Hennessey and Owings, 1978; Randall et al., 1995). Because mice were allowed to acclimatize within the enclosures only after snakes had been provided with a similar opportunity, the prey might have detected recent predator presence. Either of these factors may have masked differences in latency to capture in the different structural regimes. It is worth restating that we examined changes in predatory response resulting from quantified manipulation of a known environmental variable. We do not suggest that the habitat enclosures used in our study simulated the full range of features encountered by gray rat snakes. Rather, they did attempt to match characteristics that we believe are important to the success of foraging snakes and, in the case of habitat structural complexity, represent a reasonable range of variation about a mean level measured in a bottomland hardwood forest.

Foraging Behaviors

Gray rat snakes spent more time resting under the litter in the 150% density treatment than in other treatment levels of vegetation density, suggesting preferential use of ambush postures when foraging in habitats of limited lateral visibility. The litter effectively concealed the snakes from their prey, and strikes from such a position were generally more frequent in habitats of high complexity. Use of similar ambush postures in structured environments has been noted for other species of snakes (Jones, 1990; Jones and Whitford, 1989). While vomeronasal cues are clearly important for detecting prey presence by this and other species of snakes (Halpern, 1992), visual confirmation of prey is sometimes prerequisite to attempting capture (Ford and

Burghardt, 1993). Gray rat snakes waiting to confirm the presence of prey chemicals visually may spend more time foraging in ambush, but they may also elevate their probability of successful capture.

Tail movement in what has herein been described as caudal distraction appears to facilitate prey capture by drawing the attention of the prey away from the snake's head (Mullin, 1998). Gray rat snakes spent more time slow searching and stationary searching than those same behaviors modified with caudal distraction. The short durations of behaviors that included tail movement were not unexpected, however, because when used to facilitate prey capture, tail displays occurred in the seconds immediately preceding a strike at the prey. The absence of this behavior in gray rat snakes foraging for avian prey (Mullin, 1998) suggests that predatory behaviors may be mediated by the prey type sought (possibly through a cognitive mechanism: Burghardt, 1991).

General behavioral trends documented in this study (i.e., comparisons of pooled groups of functionally similar behaviors) do not differ markedly from species trophically similar to *Elaphe*. More time was spent above the leaf litter layer than concealed by it. Gray rat snakes are generally not fossorial, and they seek extended (>24 h) refuge under cover objects only during oviposition or periods of over-wintering (Fitch, 1963; Reinert, 1993; Weatherhead, 1989). Subjects also spent more time slow searching, stationary searching, and resting on litter. The two search behaviors were classified as a pursuit foraging mode, while the resting posture occurred when snakes either were uninterested in foraging or used an ambush foraging strategy. These results indicate that gray rat snakes can switch between foraging modes (Helfman, 1990), an ability that would promote effective foraging in a variety of structural complexities in the habitat (discussed above).

CONCLUSIONS

A quantified environmental variable was precisely manipulated to assess its effects on predatory success—a technique em-

ployed in few other studies concerning snake foraging ecology (Mullin et al., 1998; Mullin and Mushinsky, 1995, 1997). Latency to prey capture in gray rat snakes foraging for small mammals was not influenced by variation in habitat structural complexity, and several foraging behaviors were exhibited in all tested levels of complexity. Although alternative hypotheses are also plausible, phenotypic plasticity in foraging mode may allow this dietary generalist species to seek and capture small mammals effectively in a wide range of habitat types. Because environmental determinants of the compromise could result in a continuous change in the optimal foraging strategy, generalist predators should be flexible in their strategies such that net energetic intake is maximized (Helfman, 1990; Stephens and Krebs, 1986). Such flexibility may be achieved simply through effective use of a few foraging behaviors in a variety of habitat types.

The measure of habitat structural complexity simulated in the laboratory enclosures was based solely upon vegetation measurements taken at MSFSP. Conclusions concerning predatory performance and behavioral patterns in gray rat snakes, therefore, should not be generalized outside of the field locality. Increasing the available comparative data on snake foraging ecology through further manipulative studies in large simulated habitats could increase the role of zoological parks as institutions of ecologically oriented research (Chiszar et al., 1993) and establish stronger relationships between foraging behavior, predatory success, and characteristics of the predator's habitat.

Acknowledgments.—Many people contributed to this study. In particular, we thank our research assistants K. May, T. Norman, and N. Steiner. T. Moxley helped capture some of the snakes. J. Berman and G. Relyea provided valuable statistical advice. Comments from R. Cooper, G. Gale, D. Green, P. Gregory, D. Good, R. Howard, R. Jaeger, S. Reichling, H. Teibout, and two anonymous reviewers were invaluable in improving this manuscript. Partial funding for this research was provided by the Department of Biology, a Sigma Xi Grant-in-Aid of Research, and a Faculty Research Grant (2-20081) from The University of Memphis.

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Accepted: 22 January 1998

Associate Editor: Richard Howard

Herpetologica, 55(1), 1999, 28–42
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PHYLOGENY, TAXONOMY, AND BIOGEOGRAPHY OF *CNEMIDOPHORUS HYPERYTHRUS* AND *C. CERALBENSIS* (SQUAMATA: TEIIDAE) IN BAJA CALIFORNIA, MÉXICO

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ABSTRACT: A cladistic analysis of *Cnemidophorus ceralbensis* and the six allopatric subspecies of *C. hyperythrus* based on morphology, color pattern, and karyotype data supports the following hypothesis: (*espiritensis*, *hyperythrus*), (*danheimae*), (*franciscensis*), (*carmenensis*, *pictus*). This polytomy is consistent with the geological origin of the islands upon which the species occur. Evidence is presented for the specific recognition of the subspecies of *Cnemidophorus hyperythrus*.

Key words: *Cnemidophorus hyperythrus*; *Cnemidophorus ceralbensis*; *Cnemidophorus carmenensis*; *Cnemidophorus pictus*; *Cnemidophorus danheimae*; *Cnemidophorus franciscensis*; *Cnemidophorus espiritensis*; Phylogeny; Taxonomy; Biogeography; Baja California, México

CNEMIDOPHORUS ceralbensis is endemic to Isla Cerralvo in the Gulf of California, México and is considered to be most closely related to *C. hyperythrus* which currently contains six subspecies (Walker and Taylor, 1968; Welsh, 1988). [I elect not to follow the subspecies arrangement of Wright (1993) because it was proposed without comment]. *Cnemidophorus h. hyperythrus* is the only continental taxon (Welsh, 1988) and ranges from cismontane southern California, southward throughout Baja California (Fig. 1). It also occurs on the Pacific islands of Magdalena and Santa Margarita and the islands of San Marcos and Coronados in the Gulf of California. The remaining five subspecies are insular endemics in the Gulf of California: *C. h.*

carmenensis [formerly *caeruleus* (Maslin and Secoy, 1986)] from Isla Carmen; *C. h. pictus* from Isla Monserrate; *C. h. danheimae* from Isla San José; *C. h. franciscensis* from Isla San Francisco; and *C. h. espiritensis* from Islas Partida Sur and Espíritu Santo (Fig. 1).

Welsh (1988) demonstrated the poor diagnosability and clinal nature among the peninsular subspecies *Cnemidophorus hyperythrus beldingi*, *C. h. schmidtii*, and *C. h. hyperythrus* and synonymized the former two with the latter. Walker and Taylor (1968) demonstrated the distinctive and diagnostic nature of each of the insular subspecies of *Cnemidophorus hyperythrus* based on various combinations of characteristics involving color pattern and squamation. They noted that this extreme variation was more characteristic of the variation found between species within other

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