

The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). II. Influence of habitat structural complexity when searching for arboreal avian prey

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Abstract. A predator's behavior and success when foraging can be compromised by a variety of environmental factors. We examined the effect of variation in habitat structural complexity on the predatory success of the semi-arboreal gray rat snake (*Elaphe obsoleta spiloides*) foraging for arboreal bird nest contents. Individual snakes searched for nests in enclosures containing one of five levels of vegetation density that reflected the range of structural complexity measured at a field site where predator and prey species are common. Subjects were most proficient at locating prey in enclosures having low levels of structural complexity, and experienced decreased predatory success in barren or highly-complex habitats. Ten behaviors comprised over 95% of the trial durations, and four of these occurred more often than the other six regardless of variation in structural complexity within the enclosure. We suggest that low levels of structural complexity offer snakes concealment from predation while not obscuring their view of provisioning activity at the nest.

Introduction

A predator's success at obtaining prey is central to its survival and yet typically reflects trade-offs between profits (prey detection) and costs (injury or exposure to other predators) experienced during a foraging event (Pianka, 1983). Changes in habitat structural complexity may affect predatory success (reviewed in Heck and Crowder, 1991), although results from studies documenting variation of success in response to such changes have not been consistent. Some predator species forage most successfully in an intermediate level of habitat structural complexity, above or below which success decreases (Nelson, 1979; Savino and Stein, 1982). For such species, structure may conceal their approach to prey

or may serve to reduce predation risk on the predators themselves. Other species forage most successfully in open habitats because the absence of structure increases the predator's probability of detecting prey (Nelson and Bonsdorff, 1990). This study addresses the previously reported inconsistency by examining changes in predatory success in the gray rat snake (*Elaphe obsoleta spiloides*) as a function of habitat structural complexity.

In addition to influencing predatory success, habitat structure may affect the occurrence and duration of specific foraging behaviors. Such behavioral modification may result from changes in habitat selection or prey type that influence choice of foraging substrate (Moermond, 1979a; Fragaszy and Boinski, 1995) and mode (ambush versus pursuit tactics: Moermond, 1979b; Jones, 1990; Murray et al., 1995). Variation in the expression of specific behaviors may also be associated with perceived risk of foraging in a particular habitat (Lima and Dill, 1990, and references therein). If a predatory behavior is more effective at obtaining prey in certain settings than others, then behavior duration should change when foraging in habitats of different structural complexity. We also describe, and report the duration of, behaviors exhibited by *E. o. spiloides* foraging for arboreal nest contents in habitats simulating different levels of structural complexity.

A selected habitat having a certain level of structural complexity may reflect a compromise between several factors of an organism's ecology (McCoy and Bell, 1991; Pounds, 1991). Our approach to examining the trade off between costs (concealment from predators) and benefits (prey detection) involved testing the following null hypotheses: 1. Changes in habitat structural complexity do not influence the predatory success (measured as latency to capture a single prey item: Royama, 1970) of *E. o. spiloides* foraging for the nest contents of cavity-nesting birds; and, 2. changes in habitat structural complexity do not influence the duration of behaviors exhibited by *E. o. spiloides* foraging for arboreal nest contents.

Gray rat snakes prey 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). Examining snake behavioral ecology in natural settings often requires extensive use of radio telemetry (Weatherhead and Hoysak, 1989; Durner and Gates, 1993); furthermore, lengthy observation periods are often required to document rare foraging events. We present an alternative technique of simulating the habitat in the laboratory, where observations of snake foraging can be closely monitored. This technique sacrifices realistic representation of all possible environmental parameters in the interest of precise manipulation of a single variable that was quantified in the field. Field measurements of how changes in habitat structural complexity influenced predatory success and behavior in *E. o. spiloides* would not only have been logistically problematic, but also led to decreased power of interpretation of the results.

Materials and Methods

Habitat Simulation. During June 1994, we measured the vegetation composition in randomly-selected 2.25 m² quadrats within the wildlife management area of Meeman-Shelby Forest State Park (MSFSP), Shelby County, Tennessee. The sampling period coincided with the peak in avian breeding activity (pers. obs.). We counted the number of living plants within each plot and measured the size of the plants (± 0.5 mm) comprising the annually-emergent understory at the base of each stem. The plant species at MSFSP are reported in Mullin (1998).

We constructed three enclosures (each 2.25 m², and 2 m high) simulating several habitat parameters of a bottomland hardwood forest (characterized by MSFSP), and maintained these enclosures in the laboratory. The walls and ceiling of each enclosure were comprised of a combination of aluminum flashing and fiberglass screen to prevent subjects from escaping. 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 approximated the range observed at the MSFSP forest floor during the vegetation sampling period.

Based on measurements of vegetation density obtained from MSFSP (mean $\pm 1 s_{\bar{x}} = 64.0 \pm 2.3$ 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. These treatment densities approximated the range of vegetation density recorded in the MSFSP plots (98.6% of all plots sampled). We used artificial plants matching the mean stem diameter of plants measured at MSFSP (6.5 ± 0.3 mm) to simulate the understory vegetation within each enclosure. We inserted plants randomly into a 2.5 cm layer of polystyrene foam lining the enclosure floor, covered by leaf litter collected at MSFSP. The foam layer enabled alteration of 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. We used a random dispersion of plants in all trials to simulate field conditions (Pielou, 1959).

We provided arboreal microhabitat in each enclosure by constructing a single free-standing tree from a large deciduous tree branch collected at MSFSP. Most cavity-nesting bird species construct their nests in dead trees devoid of any foliage; intra- and interspecific territoriality ensures that nests are not clumped in distribution (Sherry and Holmes, 1988). Dead trees typically do not occur within close proximity to one another (Eriksson and Ehrlén, 1992; pers. obs.) meaning that we did not underestimate potential nest site density within the enclosures. We constructed all trees with nest cavities 120 cm above ground level so that all snakes had to get their entire bodies off the ground in order to enter the nest (snake length often exceeded this height [see below], but the path of ascent was never linear).

We concede that these enclosures were probably too small to make broad generalizations about rat snake foraging behavior in a natural setting. However, we are unaware of any study of similar scope that has used enclosures larger than those described here. Furthermore, we were interested primarily in changes in predatory response resulting from quantified manipulation of known environmental variables, and took steps to minimize the influence of other features of our enclosures on snake foraging performance (e.g., use of inert materials). We do not suggest that the treatment conditions represented the full range of habitat types encountered by *E. o. spiloides*. Rather, they represented a reasonable range of variation about a mean level of structural complexity found in a bottomland hardwood forest. Of all plots measured at MSFSP, 98.6% fell within the range of treatment densities used in the enclosures.

Foraging Trials. We collected adult *E. o. spiloides* from forested and semirural areas within Shelby County, sexed them with a cloacal probe, and housed them individually in cages measuring a minimum of 30 × 60 × 30 cm. We fed subjects either *Colinus virginianus* eggs (Northern Bobwhite Quail) or *Mus musculus* weekly and provided them with unlimited access to water. All individuals accepted both prey types prior to their use in foraging trials.

Prior to its use in a foraging trial, we restricted a subject's diet (water alone) for at least three weeks, and acclimatized it to the enclosure for the last three days of that period. Immediately preceding the trial, we removed the subject from the enclosure to record its mass (± 0.05 g). With the snake out of the enclosure, we placed three quail eggs in the cavity of the constructed tree. The mass of each clutch of three eggs used in the trials was similar (26.6 ± 0.2 g; $n = 75$), although the ratio of prey mass to snake mass was not fixed during the study.

As we were interested in examining the arboreal behavior of *E. o. spiloides*, we were concerned that using quail eggs (the only avian prey type available in adequate numbers for the duration of the study) might

Table 1. Description of behaviors performed by gray rat snakes (*Elaphe obsoleta spiloides*) during foraging trials in simulated habitats of varying vegetation density between 17 December 1995 and 5 November 1996. [TFR = tongue-flick rate].

Behavior	Description
<i>Resting behaviors</i>	
Resting on litter	Snake motionless, body exposed, and TFR less than 1 flick per 2 s.
Resting under litter	Snake motionless, body concealed under leaf litter.
Resting on snag	Snake motionless, majority of body on snag, TFR less than 1 flick per 2 s; head visible outside of cavity in snag.
<i>Predatory behaviors</i>	
Ingesting prey	Behavior initiated when the snake gapes and bites down on prey (following capture) and concluded at the first tongue flick after the prey passes the mouth margin.
Slow searching	Entire body of snake in motion over leaf litter, and TFR at or exceeding 1 flick per 2 s.
Searching over foliage	Similar to slow searching or stationary searching, with head on the foliage.
Searching on snag	Majority of body on snag, anterior portion in motion, and TFR at or exceeding 1 flick per 2 s.
Stationary searching	Snake is either motionless or only anterior half of body moving, and TFR at or exceeding 1 flick per 2 s.
Searching under litter	Any movement of the anterior body underneath the leaf litter while the head is concealed.
<i>Non-predatory behaviors</i>	
Ascending	Forward movement up or around (laterally) the tree.
Gaping	Snake stationary while opening its mouth in a fashion similar to a yawn.

influence foraging behavior. Therefore, we added several stimuli to mask cues from quail eggs that might bias snake foraging patterns. First, we placed eggs in the cavity nest, meaning that chemosensory cues were stronger in the arboreal microhabitat. Second, we placed several feathers from arboreal-nesting bird species (*Thryothorus ludovicianus* [Carolina Wren], *Cardinalis cardinalis* [Northern Cardinal], and *Passer domesticus* [House Sparrow]) in the nest cavity; their odors may have masked chemosensory stimuli from the quail eggs. Gray rat snakes eat eggs of all of these species (Mullin, 1998) and did not refuse quail eggs that had been scented with feathers from other bird species. Third, we suspended a freeze-dried mount of a Carolina Wren (preserved with wings spread in flying posture) below a guy wire secured between a corner of the enclosure and the nest cavity entrance. Using a monofilament line attached to its legs, the bird was released and retracted along the guy wire once every 5 min. This rate is within the range of recorded visitation rates for pairs of several forest-dwelling bird species (Grundel and Dahlsten, 1991; Darveau et al., 1993; O'Neill Goodbred and Holmes, 1996). In other words, although quail eggs were offered as prey, the habitat simulation depicted a pair of cavity-nesting birds provisioning hatched nestlings. Because subjects readily ate quail eggs placed in arboreal nests during preliminary trials, we feel confident that use of this prey type did not alter predatory behavior.

Upon re-introducing the subject into the enclosure, we recorded foraging behaviors and the time required for encountering prey (latency; ± 1 s) on video tape. We identified and described specific behaviors (table 1) based on observations of subjects during preliminary trials and radio-telemetered individuals in the field. We labeled behaviors as foraging-type if an individual's tongue-flick rate (TFR) was greater than 1 flick per 2 s, or non-foraging type for slower TFR's. The relationship between tongue flick rate and searching behavior is well established (Halpern, 1992; Ford and Burghardt, 1993). Because we minimized disturbances during the time the subject was being weighed, we feel confident that tongue-flicking activity was a response only to cues associated with the added prey stimuli.

Between 17 December 1995 and 5 November 1996, we replicated foraging trials for each treatment density of vegetation with 15 gray rat snakes (10 males and five females). Monthly measurements of snout-vent length (SVL) were recorded for the duration during which each subject was used in the experiment and the mean of these

measurements used in all statistical analyses (see below). The order in which individuals of each sex were exposed to treatments of vegetation density was random. We changed the leaf litter layer and arrangement of vegetation between each trial. From the video taped recordings, we determined the time individuals spent performing each behavior from the initiation of each trial until prey ingestion was complete. Occasionally, subjects briefly searched the enclosure and then burrowed under the leaf litter, remaining concealed for several hours. We presumed these individuals to be uninterested in foraging (data from such trials were excluded from any analysis) and tested them again at a later date in a new arrangement of vegetation. Subjects successfully locating the nest within 2 h did not ingest nest contents on all occasions (see below); we stopped trials if subjects approached the provisioning model by climbing the guy wire, or if subjects did not attempt to ingest prey 10 min after locating the nest.

Statistical Analyses. Unless otherwise stated, we compared response means across treatment levels using multi-way repeated-measures analyses of variance (ANOVA; Cohen, 1965; McCall and Appelbaum, 1973). When statistically significant differences were attributable to either vegetation density or an interaction between independent variables, we used Tukey's honestly significant difference test (HSD, $df = 1$ in all comparisons) to detect differences between treatment means (Kirk, 1982). All statistical tests were conducted using Statistical Programs for the Social Sciences (Norusis, 1990) software with $\alpha \leq 0.05$ (adjusted to more conservative values for post hoc multiple pair-wise comparisons of response means; Dowdy and Wearden, 1991).

We expressed behavior durations as percentages of their respective trial durations (hereafter referred to as "percent time") because the durations of specific behaviors were proportional to trial length. We used an arcsine-square root transformation on timed behavior data to obtain a normal distribution (Sabin and Stafford, 1990); however, all values are reported in their 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 (ANOVA; $F_{2,72} = 0.72$, $P = 0.49$). Similarly, the number of days that snakes were starved before their respective foraging trials did not influence their latency to prey capture (Pearson's regression; $r = 0.15$, $P = 0.20$). Subjects tested at one treatment density did not gain experience that influenced their performance during subsequent trials in different treatments (ANOVA; $F_{4,56} = 0.25$, $P = 0.91$).

Results

Gray rat snakes used in this study ranged from 106.2-144.1 cm in SVL and from 338.6 to 785.8 g in mass at trial initialization (mean $\pm 1 s_{\bar{x}} = 124.5 \pm 2.7$ cm, and 487.0 ± 30.7 g, respectively). There were no reliable differences in either SVL or mass as a function of the gender of the individuals tested (table 2; unpaired t -tests; $P \geq 0.10$). Nest contents were consumed in 47 of the 75 foraging trials (63%). The time taken to ingest prey was positively correlated with the ratio of prey mass to snake mass ($r = 0.35$, $P = 0.02$).

Table 2. Snout-vent length (SVL, cm) and mass (g) of male ($n = 10$) and female ($n = 5$) gray rat snakes (*Elaphe obsoleta spiloides*) used in foraging trials in simulated habitats of varying vegetation density between 17 December 1995 and 5 November 1996. Mean values are reported $\pm 1 s_{\bar{x}}$; differences in values between gender are absent (unpaired t -tests; $P \geq 0.10$).

Dimension	Gender	
	Male	Female
SVL (cm)		
mean $\pm 1 s_{\bar{x}}$	126.8 \pm 3.5	119.9 \pm 3.8
range	109.4-144.1	106.2-129.2
mass (g)		
mean $\pm 1 s_{\bar{x}}$	520.5 \pm 41.1	420.0 \pm 24.4
range	338.6-785.8	340.0-482.8

Table 3. Latency to prey capture (mean \pm 1 $s_{\bar{x}}$, in min) for gray rat snakes (*Elaphe obsoleta spiloides*; shown for all individuals, and by sex) foraging in simulated habitats of varying vegetation density (reported as % of mean ambient density) between 17 December 1995 and 5 November 1996. Different superscripts indicate differences between mean latency as a function of treatment density (Tukey's HSD; $df = 1$, $P \leq 0.05$).

Vegetation Density	Latency (min; mean \pm 1 $s_{\bar{x}}$)		
	All individuals ($n = 15$)	Males ($n = 10$)	Females ($n = 5$)
0%	26.3 \pm 6.3 ^a	16.4 \pm 4.9	46.2 \pm 12.5
50%	12.0 \pm 2.3 ^b	8.5 \pm 1.0	19.1 \pm 5.7
100%	29.3 \pm 6.7 ^a	22.6 \pm 7.1	42.8 \pm 13.6
150%	34.8 \pm 9.6 ^a	21.1 \pm 10.6	62.4 \pm 13.4
200%	28.7 \pm 6.7 ^a	19.8 \pm 8.4	46.6 \pm 6.5

Latency to prey capture was influenced by density of vegetation ($F_{4,52} = 2.62$, $P = 0.05$). Less time was required to successfully encounter prey at the 50% mean ambient treatment than at other treatments of vegetation density (HSD = 4.0, $P = 0.05$); latency times did not differ among other treatment densities (table 3). Latency to prey capture was also influenced by snake gender ($F_{1,13} = 14.94$, $P = 0.002$); ignoring effects of vegetation density, males took less time to successfully encounter prey (17.6 \pm 3.2 min) than females (43.4 \pm 5.3 min). There was no significant interaction between gender and vegetation density ($F_{4,52} = 0.81$, $P = 0.52$).

Several behaviors were recorded in $\leq 10\%$ of the trials; these behaviors (described in Mullin [1998]) comprised less than 5% of the total trial durations and were excluded from statistical comparisons. The duration of specific behaviors did not vary as a function of snake gender ($F_{1,13} = 0.81$, $P = 0.39$), nor was there any interaction between gender and behavior type ($F_{9,117} = 0.93$, $P = 0.57$; this finding does not negate the gender-associated difference in overall latency to successful nest location, reported above). There was no interaction between snake gender and vegetation density that influenced the duration of any behavior ($F_{4,52} = 2.24$, $P = 0.14$).

The duration of certain behaviors exceeded those of others regardless of vegetation density ($F_{9,117} = 16.38$, $P = 0.003$; table 4). Individuals spent more time ascending, resting on litter, slow searching, or stationary searching compared to other specific behaviors ($F \geq 14.30$, $P \leq 0.01$). Among these four behaviors, more time was spent stationary searching than either slow searching or ascending ($F \geq 10.39$, $P \leq 0.02$), and more time was spent resting on litter than ascending ($F = 10.82$, $P = 0.02$).

The duration of certain behaviors varied as a function of vegetation density ($F_{36,234} = 5.46$, $P < 0.001$). Individuals spent more time resting on litter in the 200% density treatment than at other vegetation densities ($F \geq 14.85$, $P < 0.02$). More time was spent resting under litter at 150% density than either the 0% or 200% density treatments ($F \geq 6.02$, $P \leq 0.05$), but differences in the duration of this behavior between other treatment levels were absent. Three-way interactions between gender, vegetation density, and behavior type that may have influenced behavior duration were also absent ($F_{36,468} = 1.05$, $P = 0.40$).

Table 4. Percent durations (mean \pm 1 $s_{\bar{x}}$; $n = 15$) that gray rat snakes (*Elaphe obsoleta spiloides*) spent performing specific behaviors while foraging in simulated habitats of differing vegetation density between 17 December 1995 and 5 November 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 behavior durations pooled across all treatment densities; different superscript letters indicate differences in durations of individual behaviors between treatment densities (Tukey's HSD; $df = 1$, $P \leq 0.05$).

Behavior Code	Percent Duration (mean \pm 1 $s_{\bar{x}}$)					
	Vegetation Density					
	All trials	0%	50%	100%	150%	200%
<i>Resting behaviors</i>						
Resting on litter ^{1,2}	21.0 \pm 2.3	15.8 \pm 3.3 ^a	20.0 \pm 4.3 ^a	17.7 \pm 3.5 ^a	17.9 \pm 5.1 ^a	33.6 \pm 7.3 ^b
Resting on snake ³	1.9 \pm 0.6	1.2 \pm 0.5	1.1 \pm 0.5	3.0 \pm 0.9	3.2 \pm 2.6	0.9 \pm 0.4
Resting under litter ³	2.6 \pm 1.3	1.5 \pm 1.2 ^{a,b}	0.0 \pm 0.0 ^a	5.3 \pm 2.9 ^{a,b}	6.1 \pm 5.9 ^b	0.04 \pm 0.04 ^{a,b}
<i>Predatory behaviors</i>						
Slow searching ^{2,4}	17.8 \pm 1.2	20.7 \pm 3.6	20.8 \pm 2.7	14.6 \pm 2.7	16.0 \pm 2.5	16.8 \pm 2.2
Searching over foliage ³	2.4 \pm 0.6	0.1 \pm 0.1	2.3 \pm 1.8	2.6 \pm 0.7	3.6 \pm 1.7	3.4 \pm 1.4
Searching on snag ³	1.5 \pm 0.5	0.4 \pm 0.3	1.6 \pm 1.6	3.0 \pm 0.9	0.9 \pm 0.5	3.2 \pm 1.7
Stationary searching ¹	26.3 \pm 1.8	27.6 \pm 3.8	29.2 \pm 4.1	23.3 \pm 3.3	26.2 \pm 5.4	25.2 \pm 4.1
Searching under litter ³	1.3 \pm 0.3	1.8 \pm 0.9	0.9 \pm 0.6	2.6 \pm 1.2	0.8 \pm 0.3	0.4 \pm 0.4
<i>Non-predatory behaviors</i>						
Ascending ⁴	14.6 \pm 1.3	12.7 \pm 2.2	18.0 \pm 2.3	11.9 \pm 2.5	16.6 \pm 3.8	13.7 \pm 3.1
Gaping ³	0.1 \pm 0.03	0.02 \pm 0.02	0.03 \pm 0.03	0.1 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1

We constructed post hoc orthonormalized comparisons (Kirk, 1982) of pooled percent times of ecologically related behaviors. Less time was spent performing behaviors concealed under the leaf litter (e.g., resting under litter, searching under litter) compared to those occurring above the litter layer ($F = 88.09$, $P < 0.001$). Similarly, less time was spent performing behaviors in the arboreal microhabitat (e.g., ascending, resting on snag, searching on snag) compared to those performed on the ground ($F = 44.66$, $P < 0.001$). There was no difference between the duration of resting behaviors (resting on litter, resting on snag, resting under litter; possibly ambush postures, discussed below) and active behaviors ($F = 0.003$, $P = 0.64$).

Discussion

Predatory Success. Gray rat snakes required less time to successfully locate nests in habitats simulating low levels of structural complexity and experienced decreased predatory success in barren or highly-complex habitats. The results are consistent with studies indicating that foraging in an intermediate level of habitat complexity enhances predatory success (Vince et al., 1976; Heck and Orth, 1980; Savino and Stein, 1982), and contrast with those suggesting that success monotonically decreases with increasing habitat complexity (Nelson and Bonsdorff, 1990). Habitat structure appears to be an

important variable influencing predatory success in *E. o. spiloides* and may direct patterns of habitat selection such that snakes can maximize net energy consumption when foraging (Moermond, 1979b; Ostrand et al., 1996).

Increased predatory success at a low level of structural complexity (but not barren habitat) probably reflects more than one feature of the behavioral ecology of *E. o. spiloides*. Vegetation, regardless of its density, does not hide vomeronasal cues available to snakes searching for prey (Chiszar et al., 1990). However, provisioning birds typically remove vomeronasal cues (e.g., nestling feces) that would indicate the presence of an arboreal nest before such cues are deposited on the vegetation below (Morton, 1979; Darveau et al., 1993). Thus, *E. o. spiloides* may rely on other stimuli when foraging for arboreal nest contents. Using similar enclosures, Mullin and Cooper (1998) found that *E. o. spiloides* require twice as much time to successfully locate nests in the absence of the provisioning model as compared to foraging in the presence of a model. Snakes were responsive to the visual stimulus of the model, as they would abruptly direct their head towards the model in flight. Heinen (1995) reported similar responsiveness in garter snakes (*Thamnophis*) to visual stimuli from relatively distant prey. High vegetation densities may, therefore, obscure visual cues from snakes.

Several snake species that frequent a variety of structural environments, including *Elaphe obsoleta*, are rarely found in open habitats (Weatherhead and Charland, 1985; Durner and Gates, 1993), and may experience increased risk of their own predation in those habitats (Shine and Fitzgerald, 1996). Latency to prey capture, therefore, may increase in barren habitats because *E. o. spiloides* does not forage in habitats where risk of their own predation is high (cf. Mushinsky and Miller, 1993). Alternatively, snakes in a novel habitat may fail to respond to prey because the absence of environmental factors (e.g., a canopy background) does not provide the appropriate context for a specific search image of the prey (Tinbergen, 1960; Pietrewicz and Kamil, 1981).

Female latency times were over twice as long as those for male subjects, the latter gender occupying larger home ranges (Stickel et al., 1980; Weatherhead and Hoysak, 1989). Increased male mobility may decrease latency to prey capture because the probability of detecting sessile prey (e.g., provisioning activity centered around a nest) is higher. Willingness to incur potentially higher predation risk by male snakes is presumably offset by both increased reproductive success and prey encounter rates.

Foraging Behaviors. 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* (Fitch, 1949, 1963) and our own observations of *E. o. spiloides* in the field. Ignoring the effects of vegetation density, snakes in the simulated habitats spent more time ascending, resting on litter, slow searching, and stationary searching; among these, stationary searching duration was the greatest. When their view of the provisioning model in flight was not obscured by vegetation, several subjects oriented their heads (without advancing) towards the movement immediately following its occur-

rence, and tongue-flicked rapidly. The regularity of this response contributed to increased stationary searching duration, and indicates that *E. o. spiloides* may respond to visual and chemosensory stimuli with nearly equal vigor (Halpern, 1992). The interpretations of this conclusion are limited because we did not attempt to ascertain which stimuli (visual or vomeronasal cues) evoke particular types of response.

Gray rat snakes have been observed in arboreal habitats during the bird breeding season (Mirarchi and Hitchcock, 1982; pers. obs.). Because snakes must ascend vegetation in order to locate arboreal nests, ascent time constitutes that which must be added to overall foraging time for snakes seeking avian prey. Once ascent was initiated by snakes in this study, the time taken to reach the nest was independent of vegetation density because all nest cavities were of equal height in the tree. We suggest that: 1. costs associated with ascent are presumably offset by not having to pursue sessile prey once it is detected; and, 2. snakes may remain arboreal throughout the bird breeding season (when possible, moving within a continuous canopy: Naulleau [1987] as cited in Luiselli and Rugiero, 1993; pers. obs.), thus reducing the repeated energetic cost of ascending trees.

Gray rat snakes spent more time resting on litter in the 200% mean ambient density treatment than in other treatment levels, suggesting the use of an ambush posture foraging in habitats of limited visibility. Similar postures in complex environments were observed in radio-telemetered individuals in the field and have been noted for other snake species (Jones and Whitford, 1989; Jones, 1990; pers. obs.). Dense vegetation probably obscured the flying bird model from the view of the snake, thus preventing any perception of a visual stimulus that may trigger arboreal foraging behavior (Porter and Czaplicki, 1977; Eichholz and Koenig, 1992). While vomeronasal cues are clearly important for detecting prey presence by this and other snake species (Halpern, 1992), visual confirmation of the prey item is sometimes prerequisite to an attempt to capture the prey (Burghardt and Denny, 1983; Ford and Burghardt, 1993). Gray rat snakes may visually confirm avian prey detected from chemosensory stimuli before ascending a tree, thus elevating the probability of successful nest location.

In the described enclosures, *E. o. spiloides* exhibited foraging behaviors traditionally classified as an active strategy (e.g., slow searching and stationary searching) for durations as long as those which were characteristic of an ambush strategy (e.g., resting on litter). That subjects employed both strategies (independent of structural complexity) indicates that *E. o. spiloides* can use variable foraging modes to facilitate prey encounter. Use of, or alternation between, two foraging modes would appear adaptive for predatory generalists that do not specialize on any particular prey type (Moermond, 1979b; Helfman, 1990; Murray et al., 1995).

Conclusions. Optimization models attempt to predict the foraging choices that maximize net energetic intake per unit effort for a predator, which can increase its fitness (Stephens and Krebs, 1986); yet, a predator's optimal foraging strategy is a compromise between several selection pressures (Pianka, 1983). The dynamic vegetation landscape encountered

by *E. o. spiloides* presents a type of cost-benefit trade off that influences this species' decisions and its success when foraging in specific habitats. The increased predatory success by *E. o. spiloides* foraging for arboreal nests in a particular level of habitat structural complexity probably reflects a combination of perceived predation risk on the snake (vegetation offers protective cover) and visual stimuli from the prey (vegetation obscures nest provisioning activity).

While manipulative experiments have not been conducted in larger enclosures than those used in this study, we concede that our conclusions concerning predatory performance and behavioral patterns in *E. o. spiloides* are limited in their extrapolation to natural settings. Our results are nevertheless supported by those of Mullin and Mushinsky (1995) and Mullin et al. (1998) for snakes similarly examined in simulated habitats. Future research conducted in the larger display exhibits of zoological parks, where opportunities to forage are usually regulated, could provide improved simulations of natural conditions. Such efforts would not only increase the amount of comparative data on snake foraging ecology, but would also increase the role of zoological parks as institutions of ecologically oriented research (Chiszar et al., 1993).

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