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Habitat Utilization, Diet and Movements of a Temperate Arboreal Snake (Opheodrys aestivus)

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ABSTRACT—Certain niche characteristics were quantified for Opheodrys aestivus in a forest habitat surrounding a central Arkansas lake. Preferred microhabitat for this diurnal, arboreal, forest edge species was dense, highly-branched vegetation. There was no preference for plant taxon, but selection of perch height, perch diameter, perch angle and position on branch was restricted. Diel variation in some perch parameters was seen. Intraspecific class differences (sex, snout-vent length) were slight. More than 85% of the diet consisted of caterpillars, spiders, grasshoppers and crickets, and odonates. These prey were most abundant at the forest edge and were consumed by snakes in disproportion to the abundance of prey in the habitat. Distances between recaptures and size of activity range were markedly restricted compared to other snakes.

* * *

INTRODUCTION

Habitat and movement ecology of arboreal snakes is poorly known despite a recent proliferation of field and laboratory studies (Henderson, 1974; Henderson, et al., 1976, 1976a, 1976b, 1977, 1978, 1979, 1980). As noted by Henderson and his co-workers most arboreal snakes are tropical and their crypticity, secretiveness, and/or existence in low population densities render shorter-term mark-recapture studies inefficient for obtaining field data. Even when utilizing radiotelemetry, relocating arboreal animals is difficult (Henderson, et al., 1976; Montgomery, et al., 1973). However, in temperate North America, *Opheodrys aestivus*, a diurnal, cryptic, arboreal snake, is widespread and abundant in suitable habitat throughout much of the eastern United States (Wright and Wright, 1957). This species exploits an adaptive zone that is essentially unique from any other temperate North American snake. This paper describes some aspects of the species' unusual ophidian spatial and trophic niche.

STUDY AREA AND METHODS

The study area was the forest bordering a narrow (ca 50 m) channel (700 m in length) where Overflow Creek entered Bald Knob Lake in White County, Arkansas. The lake was impounded in 1961 and has developed dense, continuous vegetation at the shoreline. Common plants include Alder (*Alnus rugosa*), Hickory (*Carya* spp.), Ironwood (*Carpinus rugosa*), Oak (*Quercus* spp.), Black Willow (*Salix nigra*), Sweetgum (*Liquidamber styraciflua*), Maple (*Acer* spp.), Blackgum (*Nyssa sylvatica*), Elm (*Ulmus* spp.), Red Cedar (*Juniperus virginiana*), Dogwood (*Cornus florida*), Buttonbush (*Cephalanthus occidentalis*), Honeysuckle (*Lonicera japonica*), and Greenbrier (*Smilax* spp.). Water willow (*Justicia* sp.) formed dense mats of emergent vegetation about .5–.75 m in height and from 1–20 m in width which bordered much of the shoreline. Alder and Ironwood, comprising about 50% of the shoreline vegetation, often formed a distinct stratum 3–4 m in height. Maximum height of the vegetation was about 15–25 m.

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The study area was visited at night from 1-3 times per week Jun-Sep in 1977 and Apr-Sep in 1978 and 1979. Initially the area was searched on foot but this method was soon abandoned in favor of the much more productive search from a boat cruising the shoreline. Data recorded for snakes included snake number, sex, snout-vent length (SVL), location, perch height, perch diameter, perch angle, longitudinal position on branch, distance from shoreline, and perch taxon. It was not always possible to obtain each datum for every snake. Studies on perch taxa were discontinued early whereas movement data were collected longer than data on perch parameters. Each snake was marked upon initial capture by clipping a unique combination of the ventrals (Brown & Parker, 1976) and then released. The length of the study area was marked in 10 m increments to facilitate determining horizontal location. In order to obtain data in the daytime, snakes were captured in the hours before daybreak, marked with a narrow band of rapid-drying fluorescent orange spray paint, and released at the site of capture. These snakes subsequently coiled up in a typical sleeping posture. Thirty-one marked snakes (15 3 3, 16 9 9) were observed for a total of 72 snake-hours. Perch characteristics were recorded for each snake every 15 minutes, if possible. Observations were made through binoculars from behind a blind fitted on a boat which was anchored about 10 m from the shoreline.

For dietary analyses snakes (n = 148) were collected in similar habitat from the opposite end of the lake about 0.8 km distant and preserved. Volumes of stomach contents from preserved snakes were measured by volumetric displacement using a narrow-necked graduated cylinder. Stomach contents were identified and counted. Approximate percentage composition by volume of each prey item category in each stomach was estimated by visual inspection (Pianka & Pianka, 1976). The distribution and relative abundance of potential prey items in various areas of the vegetation was determined by sampling 1 m² plots with a beating net. The percent of shoreline area comprised by each perch taxon was estimated by visually sampling a random series of 10 m length stretches of shoreline.

RESULTS

General behavior.—In their arboreal retreats, cryptic *O. aestivus* were difficult to detect during the day. At night, however, the whitish venter of a snake could easily be seen as it reflected light from a 200,000 candlepower spotlight. Only 0.4 snake/man-hour was found during the day as compared to 3.7 snakes/man-hour during the night. Snakes were strictly diurnal and they spent most of the day in activity. Activity began soon after first light and terminated about .5–1 h before dark. Snakes appeared to be visually-oriented, active predators. Foraging often entailed searching leaves and small branches on a limb as the snake very slowly moved distally on the limb. If a bridge to another limb could not be made once reaching the tip, the snake moved proximally until a bridge could be made. When approached, *O. aestivus* ceased all movement, however, when touched these snakes glided rapidly with great agility through the vegetation. After rapid movement of several m snakes stopped suddenly and resumed slow movement after a time. Most often the sleeping posture was a loose horizontal coil with the head resting on top of the coil or on a branch, however, postures varied greatly. Although decidedly arboreal, *O. aestivus* was occasionally found on the ground.

Perch characteristics.—On some extensive areas of the lake maximum height of the vegetation did not exceed 3 m; snakes seemed to be as abundant in these areas as they were in areas of higher vegetation. However, snakes were rarely found in areas of sparce or widely-spaced vegetation, regardless of height. Snakes were found perched at night in various plant taxa (living or dead and leafless) according to the abundance of each taxon (Table 1). Most snakes (> 85%) were captured or observed at the vegetation edge within 3 m of the shoreline (Table 2). The collections at night for these data resulted from searching on foot transects parallel to the shoreline. Daytime observations on individual snakes revealed that most movement was near the edge but occasional, brief sallies of < 5 m into the forest occurred. Additionally, observations from the boat in early spring before the vegetation was fully leafed out so TABLE 1. Distribution of 90 O. aestivus captured at night that vision into the forest was little impaired re- according to perch taxa. Emergent vegetation is excluded. vealed snakes concentrated near the edge. The frequency distributions of collections or observations according to distance from the shoreline in the day and in the night are not significantly different (Table 2, P > .50, Mann-Whitney U Test).

Sixty-one percent of snakes selected a perch at night between 1-3 m in height (Fig. 1A). Mean nighttime perch height (2.3 \pm 0.11 m) did not differ between the sexes [$\delta \delta = 2.5 \pm 0.17$ (n = 84); $Q Q = 2.2 \pm 0.15$ (n = 116); P > .20, t-test]. Less than 2% of the variation in perch height at night is frequencies of < 5. explained by body size (Fig. 2). There is little variation in perch height according to time (Table 2, P > .20, Mann-Whitney U Test). Vegetation height

affects perch height primarily by restricting maximum perch height in the lowermost vegetation (Table 3).

Perch diameter and position on perch are selected narrowly (Fig. 1B, Table 2) regardless of time, but the selections are more restricted at night compared to day (P < .001 in each, Mann-Whitney U Tests). Trends are similar for perch angle (Table 2) although the time difference is not as great (P > .20). No sexual or size class differences were noted in selection of perch diameter, position or angle.

Diet .--- One hundred and four of 126 snakes (82.5%) had recently fed, as had 26 of 30 (86.7%) gravid females. The mean number of food items in stomachs was 3.1 ± .14 (excluding those snakes with empty stomachs). Caterpillars, spiders, grasshoppers and crickets, and odonates constituted more than 85% of the diet according to numbers and to volume (Table 4). Sexual differences in diet were slight. Males tended to eat more caterpillars (47.7% vs 38.6%) and fewer odonates (3.9% vs 13.2%) than females. Of the spiders, 54% were hunt-

The X^2 value is not significant (P > .10).

Perch taxon	% of area	Snakes (n)	Expected no. of snakes	х ²
Alder	41.0	39	36.9	.12
Ironwood	12.0	16	10.8	2.50
Oaks	9.5	6	8.6	.79
Willow	9.0	4	8.1	2.08
Other ¹	28.5	25	25.7	.02
				5.51 ^{ns}

¹Lumped data from 10 taxa each of which had expected

TABLE 2. Distribution of O. aestivus according to distance from shoreline, perch height, perch diameter, position on branch, and perch angle. Sample size at night is the number of individual snakes whereas sample size in the day is the number of observations on 31 snakes. Variables at night were measured whereas variables in the day were estimated.

		% of s or obse	
Perch variables		Night	Day
Distance from shoreline (m)	0–1.0	52	57
	1.1–3.0	36	29
	3.1–5.0	9	10
	> 5.0	3	4
	n =	33	129
Perch height (m)	0–1.0	14	15
	1.1-2.0	40	27
	2.1-3.0	21	29
	3.1-4.0	12	18
	4.1–5.0	7	8
	> 5.0	6	3
	n =	200	132
Perch diameter (mm)	0–5	90	66
	6-10	9	17
	11–15	0	8
	16-20	1	1
	> 20	0	8
	n =	189	132
Branch position	distal .25	87	63
	proximal .75	13	37
	n =	185	128
Perch angle (degrees)	0–30	73	65
	31–60	19	23
	61–90	8	12
	n =	182	132

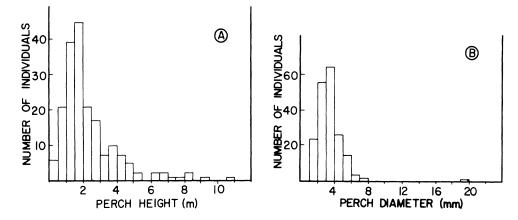


FIGURE 1. A. Frequency distribution of 200 O. aestivus captured at night according to perch height. B. Frequency distribution of 189 O. aestivus captured at night according to perch diameter.

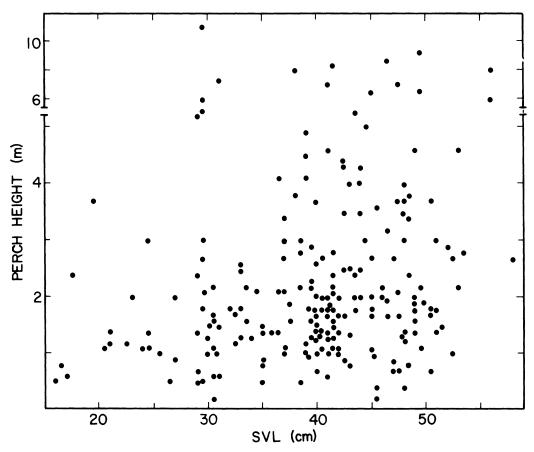


FIGURE 2. The relationship of nighttime perch height of 64 O. aestivus and SVL (r = .14, P > .05).

TABLE 3. Distribution of perch heights of *O. aestivus* captured at night according to height of vegetation (potential perch height). Mean perch heights are significantly different (H = 21.1, P < .005; Kruskal-Wallis test) due to depressed perch heights on the lowest vegetation (Non-parametric multiple comparisons by STP, Sokal and Rohlf, 1969). Because of the equal sample sizes required by these tests, 28 data in each of the lower 3 categories were randomly chosen to complement the 28 total cases in the \geq 7.1 category.

Height of vegetation (m)*	Mean perch height (m)	Range	n	Maximum non-significant subsets
≤ 3.0	1.4	.6–2.6	28	I
3.1-5.0	1.9	.7-4.5	28	Ŧ
5.1-7.0	2.5	.7–5.5	28	
≥ 7.1	4.0	.8-8.5	28	<u> </u>

*estimated

TABLE 4. Diet of *O. aestivus* based on the analysis of 443 prey items from 148 stomachs.

Prey Category	n	Frequency in stomachs	% total number of items	% total volume of items
Caterpillars	180	66.2	40.6	46.1
Spiders	109	50.0	24.6	16.8
Grasshoppers				
& crickets	50	25.7	11.3	15.6
Odonates	40	20.9	9.0	11.0
Moths	16	7.4	3.6	4.7
Mantids	12	8.1	2.7	1.3
Phalangids	11	6.1	2.5	1.4
Snails	9	6.1	2.0	1.2
Flies	8	1.4	1.8	.6
Crayfish	2	1.4	.5	.1
Leafhoppers	1	.7	.2	.2
Ants	3	.7	.7	< .1
Roaches	1	.7	.2	< .1
Mayflies	1	.7	.2	< .1
Plants		2.7		.3
Unidentified				.6

ing spiders (of which 59% were salticids), whereas 46% were web-spinners (of which 52% was *Tetragnatha* sp.). Of the grasshoppers and crickets, 54% were tettigonids, 8% were acridids, and 38% were gryllids. The four major food item categories were most abundant near the shoreline and, except for caterpillars, were more abundant at lower heights (Table 5). All prey categories except caterpillars reached maximum abundance in the emergent vegetation. Relative proportions of prey in stomachs did not correspond to abundances in habitats (Table 5).

Movements.—Eight of 171 recaptures (4.7%) of males and 6 of 225 recaptures (2.7%) of females involved movement from the forest on one side of the channel to the forest on the other side. One male and one female which crossed the channel returned to the original side at a later date. Although mean distance between recaptures for males appears greater than that for females (Table 6) the difference is not significant (P > .05, t-test). Mean vertical movement of all snakes

TABLE 5. Distribution and abundance of potential prey items for *O. aestivus* compared to abundance in diet. All distribution values are percent of total items in a particular prey category. Samples were taken at heights of 1–3 m unless otherwise noted. Items were included only if they were large enough to be taken by *O. aestivus* (minimum ca 10 mm). Relative abundance is the percent of the total prey sample at 0–3 m from the shoreline. Weighted abundance is the summation of the percent diurnal utilization of habitat 0–3 m from the shoreline at heights of 0–1, 1–3 and > 4 m (perch heights from Table 2) times the percent relative abundance of prey items at the 3 respective heights.

		Distance from shoreline (m)						
Prey category	(n)	0–3 ¹	0–3	0–32	≥10	Relative abundance	Weighted abundance	% of diet ³
Caterpillars	(41)	2.4	39.0	36.6	22.0	21.1	21.0	40.6
Spiders	(121)	42.1	36.4	9.3	12.4	69.7	56.2	24.6
Grasshoppers	(12)	75.0	16.7	0	8.3	7.2	3.9	11.3
Odonates	(3)	100.0	0	0	0	2.0	1.0	9.0
Combined	(177)	39.0	33.3	14.1	13.6	100.0	82.1	85.5

¹Emergent vegetation .5-.75 m in height

²Sampled at a height of 4-7 m

3From Table 4

TABLE 6. Opheodrys aestivus: Statistics of horizontal distances (m) between recaptures and time (days) between recaptures within a season. The 1-day recapture category includes snakes which were recaptured the day following a previous capture.

Category	Males	Females	Males & Females
Total recaptures			
Mean	28.0	24.5	25.8
S.E.	2.88	2.06	1.68
Range	0–230	0–200	0–230
N	128	195	323
1-day recaptures			
Mean	18.0	6.9	11.1
S.E.	8.69	1.92	3.57
Range	360	1-22	160
N	6	10	16
Time between recaptures			
Mean	32.6	22.9	26.7
S.E.	2.79	1.82	1.57
Range	1155	1–146	1-155
N	128	195	323

between 99 total recaptures was 1.4 \pm .11 m (range 0–5.5). For 14 1-day recaptures (*sensu* Table 6) mean vertical movement was .9 \pm .23 m (range 0–3.1). No sexual difference in vertical movement was noted. The time between intraseasonal recaptures is significantly greater for males than for females (Table 6; t = 2.91, P < .01).

Snakes restricted their movements within a particular area (activity range) especially within a season. Because most movement was parallel to the shoreline at the vegetation edge, activity range sizes may be expressed as lengths. For 38 snakes captured \geq 4 times within a season the average activity range length was 62 ± 7.2 m (range 15–247). Range size of 17 males (56 ± 6.5 m, range 15–102) was not significantly different (P > .40, t-test) from that of 21 females (68 ± 12.0 m, range 21–247). Although the correlation between time and distance between intraseasonal recaptures is significant (r = .167, P < .01, n = 323), time explains little variation in distance between recaptures (r² = 2.8%). No. 175, a young adult male,

was captured 8 times from 13 July 1978 to 4 June 1979 along a 30 m shoreline stretch. For 75 snakes which were captured \geq 2 times in each of \geq 2 seasons, interseasonal shifts in activity range location averged 45 \pm 7.2 m (range .5–420).

DISCUSSION

The physical structure of the habitat serves as a key stimulus for habitat selection in several reptiles (Heatwole, 1977). The nocturnal and diurnal perches used by O. aestivus appear to be narrowly selected with regard to distance from shoreline, perch height, perch diameter, position on perch and perch angle. Alternatively, the samples may reflect availability of certain perch types. This is unlikely, however, as a large variety of perch sizes, heights and angles were extremely abundant. The narrow selection of perches may reflect functional correlations between locomotory ability of O. aestivus and certain perch characteristics. Intuitively, perch spacing, diameter and angle should affect locomotion more than perch height, distance from edge, or position on branch. Perch spacing increases above the brushy 1-3 m stratum or away from the forest edge. Likewise, perch spacing and perch diameter increase toward the proximal parts of the branches. The reduction of perch selection factors to diameter, angle, and spacing could be tested experimentally. The broader structural niche in the daytime reflects foraging movements of snakes in which a wider variety of perch types are encountered and temporarily used. Diurnal movement may take snakes further back into the vegetation which accounts in part for the greater difficulty in finding them at this time. There seem to be little intraspecific class differences in microhabitat selection. However, the significantly greater time between recaptures of males compared to females may be due to the greater tendency of males to move farther into the vegetation. The trends, although nonsignificant, of greater perch heights, greater vagility, and fewer odonates in the diet support this contention.

Although snakes statistically did not prefer any particular plant taxon, willow and ironwood tended to have numbers which deviated more from the expected than other forms (Table 1). Willows most often towered over the lower strata and had a canopy that was accessible only by a

single, thick trunk thus accounting for the less than expected numbers. Ironwood, with greater than expected numbers, had a finely-branched, small-leaved growth pattern which provided abundant preferred structure for *O. aestivus*. Although certain other perch characteristics (e.g., exposure, color, texture) were not measured, my impression is that these mattered little.

Several authors (McCauley, 1945; Clark, 1949; Duellman, 1949; Richmond, 1952; Smith, 1961; Anderson, 1965; Webb, 1970; Mount, 1975; Martof, et al., 1980) commented on the proclivity of *O. aestivus* for lake, pond, and stream margins. At the forest margin of Bald Knob Lake a large population does exist. However, large populations also exist in forest edge habitat along roads in the vicinity (4.5 snakes/man-hour).

Selection of perches by *O. aestivus* also may be influenced by distribution of prey. At Bald Knob Lake the horizontal and vertical distribution of potential prey items approximates the distribution of *O. aestivus*. The major exception is the abundance of prey in the emergent *Justicia*. The growth pattern of *Justicia* is a central vertical stem with short leaf petioles arising from it at near vertical angles. This does not provide preferred structure for *O. aestivus* as only about 3% of snakes were captured in it. The sub-optimal structure of *Justicia* may discourage snakes from utilizing it despite the abundance of prey contained within. Possible predation by fish (Clark, 1949) may also influence avoidance of *Justicia*. The data in Table 5 suggest that prey are not eaten in proportion to their abundance in different habitats relative to differential habitat use by the snakes. Caterpillars were eaten about twice as frequently as might be expected whereas spider consumption was about one half the expected. Possibly the greater activity and mobility of spiders renders them less susceptible to predation than caterpillars. My methods probably were inadequate for sampling flying grasshoppers and odonates so that statements regarding abundances of these items relative to diet should not be made.

The diet of *O. aestivus* shows little qualitative geographic variation (see Conant, 1938; McCauley, 1945; Clark, 1949; Smith, 1956; Smith, 1961; Anderson, 1965; Mount, 1975; Martof, et al., 1980). At Bald Knob Lake caterpillars appear to constitute a larger proportion of the diet than in any of these studies, judging from the authors' subjective remarks. Odonates probably would not be important in the diet of populations distant from aquatic habitats.

Activity range areas may be calculated for *O. aestivus* on the basis that movement is restricted to approximately 3 m within the edge (Table 2). Using the convex polygon method mean activity range area is about 1.9 ares. Mean distance between recaptures for *O. aestivus* is about 26 m (Table 6). Thus, contrary to what might be expected, *O. aestivus*, a smaller active forager, is more restricted in these two measures of movement than is the arboreal *Oxybelis aeneus* (4.4 ares and about 42 m, respectively), a larger sit-and-wait predator (Henderson, 1974). *Oxybelis aeneus*, the only other slender-bodied arboreal snake that has been studied to any extent in the field, is more restricted in its movement than many non-arboreal snakes (Henderson, 1974). Rather than feeding infrequently on large prey, *O. aestivus* is probably atypical for many snakes in that it feeds frequently on small arthropods. Therefore, the diel time budget of *O. aestivus* probably would include a large amount of foraging time. If prey density is great then movements might be expected to be restricted.

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