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Spatial Ecology of the Coachwhip, *Masticophis flagellum* (Squamata: Colubridae), in Eastern Texas

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Abstract - We radio-tracked nine *Masticophis flagellum* (Coachwhips) to determine home range, habitat use, and movements in eastern Texas from April to October 2000. Home ranges of Coachwhips contained more oak savanna macrohabitat than early-successional pine plantation or forested seep, based on the availability of these three macrohabitats in the study area. Likewise, within their individual home ranges, Coachwhips used oak savanna more than the other two macrohabitats, based on availability. An analysis of microhabitat use revealed that, relative to random sites within their home range, Coachwhips were found at sites with fewer pine trees and more herbaceous vegetation taller than 30 cm. Results of the two analyses, macrohabitat and microhabitat, were consistent: oak savannas contained relatively few pine trees but much herbaceous vegetation taller than 30 cm. Coachwhips made frequent long-distance moves, which resulted in large home ranges. Core activity areas, however, were small. These core activity areas were always within the oak savanna macrohabitat. Long movements, large home ranges, and small core activity areas likely were a result of the preferred oak savanna macrohabitat being patchily distributed in the landscape.

Introduction

Spatial ecology of snakes has been less studied than that of most other vertebrates, probably because of the secretive nature of snakes (Reinert 1993). *Masticophis flagellum* (Shaw) (Coachwhip) is a widely-distributed and common snake, yet little is known about its spatial ecology. Only one modern study (Secor 1995) has investigated this species' spatial ecology. Moreover, Secor's study site, in the Mojave Desert of California, was near the western limit of the species' distribution. We are unaware of any quantitative studies of home range or habitat use of this species in the southeastern United States.

We studied the Coachwhip in eastern Texas, where it is a relatively common snake. The Coachwhip is a fast, active, diurnal predator, and is considered a thermal specialist, maintaining its body temperature between 30 and 35 °C (Hammerson 1989, Jones and Whitford 1989, Secor 1995). In their popular field guide, Conant and Collins (1991) noted that eastern

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Coachwhips are found in a wide variety of habitats, from dry sandy flatwoods to creek valleys and swamps. The objectives of our study were to describe habitat use, movements, and home range of the Coachwhip in eastern Texas.

Field-site Description

The study site, privately owned by a timber company and known as "Tonkawa Sands," is located in Nacogdoches County, approximately 25 km north of Nacogdoches, TX. Soils at Tonkawa Sands are classified as sand or fine sand (Dolezel 1980) and are part of the east–west trending Carrizo sands that encompass approximately 20 km^2 of the area. Topographic relief is minimal with elevations ranging from 133 to 216 m above sea level.

Three macrohabitat types were identified on the study site. The first, oak savanna, was an open-canopy woodland dominated by *Quercus incana* Bartram (bluejack oak) and *Q. stellata* Wangenhein (post oak) on upland xeric sandy sites with a dense ground layer of grasses, forbs, and woody vines. The second macrohabitat type was early-successional pine plantations, consisting of a mosaic of even-aged stands of *Pinus taeda* Linnaeus (loblolly pine). The stands differed in age and height, but in all stands the trees were closely-spaced, the canopy was nearly closed, a thick layer of pine needles existed on the forest floor, and little ground-layer vegetation was present. The third macrohabitat type was located at lower elevations and consisted of closed-canopy mesic forested seeps dominated by *Acer rubrum* Linnaeus (red maple) and *Magnolia virginiana* Linnaeus (sweetbay magnolia), with sphagnum moss and various fern species as ground-layer vegetation.

The study site experienced drought conditions during the year of our study. The previous ten-year (1989–1999) average rainfall from July to October was 10.4 cm, almost 3.5 times more than during 2000 (3.0 cm; Stephen F. Austin University Weather Station data).

Methods

Radiotelemetry

Ten adult Coachwhips, seven males and three females, were captured on the study site between 27 March and 21 June 2000 in drift-fence traps that were placed in grids without regard to habitat type. Radiotransmitters (50 x 11 x 5 mm, with a 44-cm whip antenna) were implanted subcutaneously following the procedures described by Reinert and Cundall (1982) and Weatherhead and Anderka (1984). The mass of the transmitters (3.4–6.3 g) was always less than 2% of snake mass (192–1030 g; snout-vent length: 104–152 cm). Snakes were held in the laboratory a minimum of seven days post-surgery for recovery. Snakes were released at the original point of capture and relocated three to four times per week from 18 April through 19 October; this period roughly coincides with the entire active season of Coachwhips at the site (during 4 years of drift-fence sampling at the site, the average first date of capture was 29 March and the average last capture date was 30 September; D.C. Rudolph, unpubl. data).

Each time a snake was relocated, the site coordinates were recorded using a GPS unit (Trimble Geoexplorer II). Data points were differentially post-processed for increased accuracy by correcting against a known location base station (Kennedy 2002). We recorded which of the three macrohabitat types was dominant at the snake's location, and whether the snake was below ground, on the soil surface, or above ground in vegetation. Microhabitat characteristics of basal area (measured with a 1-factor metric prism [m^2/ha]), canopy closure, distance to nearest tree, and foliage density of ground-layer vegetation (measured using a density board; MacArthur and MacArthur 1961) were recorded. Additional characteristics of the microhabitat, recorded in a 1-m radius circle around each snake location, included proportional cover of leaf litter, bare ground, and herbaceous vegetation greater than and less than 30 cm in height; these proportions always summed to 1. Depth of leaf litter (average of four measurements) and the presence or absence of a protective overhang (measured as dense herbaceous vegetation, woody vegetation, or woody debris) available for snake concealment also were recorded

The same data recorded at snake locations were recorded at random locations within each snake's home range to determine if habitat use within the home range was random, or if certain habitats were used in greater or lesser proportion to their availability. One random location was sampled for each snake relocation point. Random points were chosen by using random number tables for selecting direction and distance from snake relocation points.

Data analyses

Following Aebischer et al. (1993), we considered habitat use at two scales: (1) we tested whether habitat within the snakes' home ranges was a random subset of available habitat in the study area, and (2) we tested whether habitat at snake locations was a random subset of available habitat within the snakes' home ranges.

We defined the study area as the portion of the study site enclosed by a single minimum convex polygon (594 ha) bounded by the outermost relocation points of all snakes. This circumscribed an area within which our snakes were moving and potentially using sites from the available habitats. The proportion of the study area and the proportion of each snake's home range composed of each of the three macrohabitat types was calculated using a satellite image of the study area and the GIS program Arc View 3.1 (Environmental Systems Research Institute, Redlands, CA). We analyzed these data with compositional analysis (Aebischer and Robertson 1992, Aebischer et al. 1993) using the software package Resource Selection for Windows ver. 1.0.

To compare habitats at snake locations to available habitats within the snakes' home ranges, we used compositional analysis for macro- and microhabitat variables that were proportionally based wherein the proportions of multiple categories summed to one (i.e., proportions of the three macrohabitat types: oak savanna, pine plantation, forested seep; proportional microhabitat data collected within a 1-m radius of snake and random points: proportion dominated by leaf litter, bare ground, vegetation greater than 30 cm in height, or vegetation less than 30 cm). Unlike traditional methods of analysis (i.e., conventional analysis of variance [ANOVA]/ multiple analysis of variance [MANOVA]), compositional analysis is appropriate for analyzing these types of non-independent proportions (Aebischer et al. 1993).

Other microhabitat data (i.e., canopy closure, density of ground-layer vegetation, basal area of pine and hardwood trees, distance to nearest tree, leaf-litter depth, and presence of a protective overhang) were analyzed using 9 x 2 two-way mixed-model ANOVAs with no replication (one data point per snake to avoid pseudoreplication; Aebischer et al. 1993, Hurlbert 1984), with individual snake being a random factor (nine snakes), snake/random points being a fixed factor, and the average value for the microhabitat characteristic being the dependent variable. Analysis of variance procedures followed Sokal and Rohlf (1995) using the STATISTICA 5.1 software package (Statsoft Inc, Tulsa, OK).

A movement was defined as the location of a snake at a site farther than 5 m from its previous relocation point. Movement frequency was calculated as the number of movements divided by the number of relocations (Charland and Gregory 1995). Because individuals were not relocated every day, average movement rates were calculated by two different methods as described by Charland and Gregory (1995). Overall movement rate (OMR) was calculated by dividing the total distance moved by the total number of days in the analysis period. Actual movement rate (AMR) was calculated by dividing total distance moved by the number of relocations in which a movement was detected. Since AMR excluded days when a snake did not move, the value of AMR was always greater than OMR.

Three different methods were used to analyze Coachwhip home range using the computer program CALHOME (Kie et al. 1996). Because of their widespread use in other studies, the minimum convex polygon (MCP) and the harmonic mean (HM) methods were used as a basis of comparison. We also used the adaptive kernel method (ADK) because Worton (1987, 1995) suggested that this method was superior to the HM method. Since the statistically-based HM and ADK methods allow the computation of core activity areas, we calculated the 50% core activity areas of each snake using both of these methods.

One female snake lost significant mass (47%) during the tracking period. Because animals may not behave normally when sick or when deprived of food and water (Bernheim and Kluger 1976, Dunlap 1995, Kluger 1978), data obtained from this individual were not used in analyses due to possible bias. Of the remaining nine snakes, four were tracked until the end of the study (19 October), four died from unknown causes, presumably predation, and the transmitter signal was lost from one. To determine if the snakes were healthy, we recaptured and briefly examined each of them at least once during the study. Additionally, all remaining snakes were recaptured at the end of the study, and the radiotransmitter was removed from each of them. All nine snakes appeared healthy when checked, and there were no noticeable complications from the surgical implantation of the radiotransmitters. We tracked these nine snakes an average of 106 days each (SD = 32.4, range = 75–184 d), and we recorded a total of 336 locations (range = 24–62 per snake).

All relocation points, from time of release until 19 October, were used in computing home ranges; however, habitat and movement data collected prior to 14 days post-release were omitted from all analyses to decrease the chance of bias due to the effects of surgery or re-acclimatization to the natural environment (Peterson et al. 1993, Rudolph et al. 1998). To avoid biases associated with seasonal differences in movement rates, movement data were analyzed only between 7 July and 10 September, the longest consecutive time period when the greatest number (seven) of snakes were monitored. For the habitat-use data, we analyzed data collected over the entire study period, and then we re-analyzed those data collected between 7 July and 10 September; however, because of the high degree of congruence between these two analyses, we only present details of the analysis of the complete data set.

Results

Habitat use

The study area was composed of 16% forested seep, 34% oak savanna and 50% pine plantation. The average snake MCP home range was composed of 5% (SD = ± 9.7%) forested seep, 57% (± 15.0) oak savanna, and 38% (± 9.7) pine plantation. Compositional analysis revealed that macrohabitat proportions within the snakes' MCP home ranges differed significantly from the macrohabitat proportions available on the study area ($\lambda = 0.209$, $P < 0.001$; Fig. 1). Pairwise comparisons of macrohabitat types indicated that home ranges included significantly more oak savanna than pine plantation ($t = 4.13$, $df = 8$, $P = 0.0033$; see Aebischer et al. [1993] for a justification of using standard significance levels of t-tests for comparisons following a significant λ-value in compositional analysis) and forested seep ($t = 4.13$, $df = 8$, $P = 0.0033$) based on proportions available in the study area (Fig. 1). Furthermore, snake home ranges contained significantly more pine plantation than forested seep macrohabitat ($t = 3.22$, $df = 8$, $P = 0.0123$; Fig. 1).

Because home ranges may contain large portions of unused habitat, further analysis was conducted to determine if snakes were disproportionately using certain macrohabitat types within their home range. Coachwhips were more often located within oak savanna habitats (mean = 91 ± 5.3%; $n = 9$ snakes) than pine plantations (8 ± 5.9%) and forested seeps (1 ± 1.5%). Compositional analysis revealed that snakes used macrohabitats significantly differently than available within their home ranges ($\lambda = 0.243$, $P < 0.05$; Fig. 1). Pairwise comparisons indicated that within their home ranges, Coachwhips used oak savannas disproportionately more than pine plantations (t = 4.70, df = 8, P = 0.0015) and forested seeps (t = 2.36, df = 8, P = 0.0457; Fig. 1). No significant difference was detected between pine plantations and forested seeps (t = 1.13, df = 8, P = 0.29).

To determine if snakes disproportionately used certain microhabitat features, based on availability within their home ranges, random points within each individual's home range were compared to snake locations. Of all microhabitat variables, only pine basal area and the presence of a protective overhang were significant (Table 1). Pine basal area, analyzed using a two-way ANOVA, was significantly lower at snake locations than at random points (P =

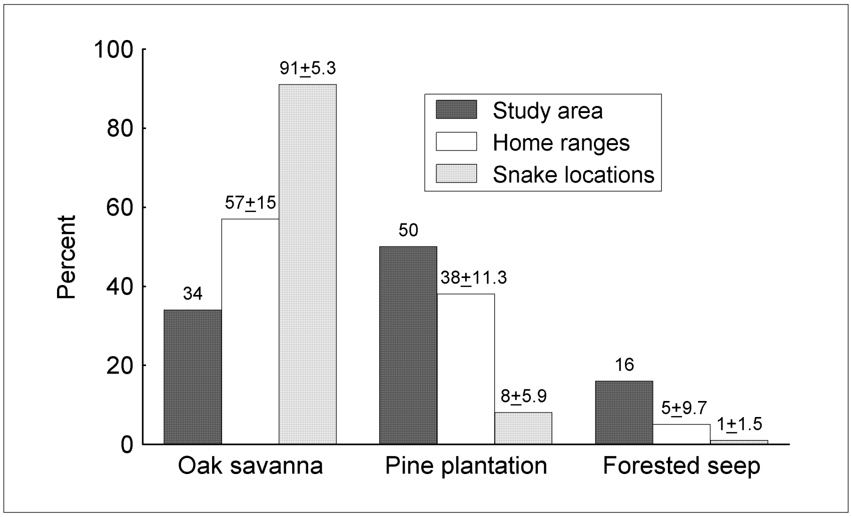

Figure 1. Percentage of the study area, coachwhip MCP home range, and coachwhip location points within each of three macrohabitat types. Above each bar is the mean ± SD. Macrohabitat use at two scales is demonstrated: (1) available habitat in the study area compared to habitat in snake home ranges, and (2) available habitat in snake home ranges compared to snake location points. At both scales, oak savanna was used more than the other two macrohabitats, based on availability.

Table 1. Mean ± standard deviation for microhabitat variables at Coachwhip locations and random points within Coachwhip home ranges. The last column represents the results of two-way mixed-model ANOVAs comparing the snake locations to random points (see Methods: Data analysis). A significant difference was defined as P < 0.05 and is designated by an asterisk.

	Snake locations	Random points	P
Canopy closure (%)	45.6 ± 6.7	43.8 ± 5.9	0.602
Foliage density (m)	11.6 ± 3.5	11.3 ± 1.9	0.857
Basal area pine (m^2/ha)	3.1 ± 1.5	6.2 ± 2.3	0.004*
Basal area hardwood (m^2/ha)	4.5 ± 1.4	4.4 ± 2.6	0.897
Distance to tree (m)	3.7 ± 1.3	4.2 ± 2.1	0.244
Litter depth (cm)	1.5 ± 0.6	2.0 ± 0.7	0.058
Protective overhang (%)	68.8 ± 0.2	21.9 ± 0.2	0.001*

0.004). These results support the findings of the macrohabitat analysis wherein Coachwhips avoided areas of pine plantations. The presence of a protective overhang, variously composed of woody debris, grass, or forbs, was found more often at snake locations than at random points ($P = 0.001$; Table 1).

Proportion of four categories of ground cover (bareground, leaf litter, herbaceous vegetation < 30 cm, herbaceous vegetation > 30 cm) was analyzed using compositional analysis (Table 2). The analysis indicated these microhabitat features were not used in proportion to their availability ($\lambda = 0.253$, $P < 0.05$). Pairwise comparisons indicated that snake locations had significantly more herbaceous vegetation greater than 30 cm in height than both bare ground ($t = 3.41$, df = 8, $P = 0.0093$) and herbaceous vegetation less than 30 cm in height ($t = 2.66$, df = 8, $P = 0.0287$). Snake locations also contained more herbaceous vegetation greater than 30 cm in height than leaf litter, but the difference was not quite statistically significant ($t = 2.21$, df = 8, $P = 0.0578$).

Snakes had returned to previously used refugia, often small mammal burrows, on 19% of telemetry relocations (range of individuals: 0–30%, n = 9). Individuals also used refugia previously used by other individuals, but no two radio-tracked individuals occupied the same refuge at the same time. Individuals were surface active on the ground 28% of the time, arboreal 11% of the time, and in underground refugia 61% of the time.

The results of the macro and microhabitat analyses restricted to the late summer period, 7 July–10 September, were congruent with the analyses of the complete active season with one minor exception: in the microhabitat analysis, herbaceous vegetation greater than 30 cm tall was used significantly more than leaf-litter microhabitats in the late summer ($t = 3.00$, df = 6, $P = 0.024$), but this result was not quite statistically significant in the analysis of the complete active season ($P = 0.0578$; see above).

Movements and home ranges

We detected no significant difference in home-range size between males and females (MCP: $t = 0.87$, df = 7, $P > 0.41$; all data April–Oct included), and we detected no significant intersexual difference in the actual movement rate (AMR) of males and females tracked between 7 July and 10 September

Table 2. Mean ± standard deviation of four categories of ground cover at snake locations and random points within snake home ranges. The columns sum to 100%. Compositional analysis indicated that these microhabitat features were not used in proportion to their availability ($\lambda = 0.253$, $P < 0.05$). A significant difference (as determined by pairwise t-tests) in usage by coachwhips is indicated by cells in the second column not having at least one superscript in common; thus, coachwhip locations contained more herbaceous vegetation greater than 30 cm tall than bare ground or herbaceous vegetation less than 30 cm tall, based on the availability of these microhabitats.

	Snake locations	Random points
Bare ground	$9 \pm 6.3\%^{A}$	14 ± 9.9%
Leaf litter	$39 \pm 13.9\%^{AB}$	43 ± 12.9%
Vegetation < 30 cm tall	$9 \pm 7.0\%^{A}$	14 ± 3.5%
Vegetation > 30 cm tall	$43 \pm 13.3\%^{B}$	29 ± 8.9%

(t = 0.58, df = 5, P > 0.58). One of the two females tracked between 7 July and 10 September oviposited 12 eggs in the laboratory on 22 June, before transmitter implantation. Both of these females were palpated and known to be non-gravid in early July. Consequently, both must have been non-gravid through the end of the study (oviposition dates for Coachwhips are typically in June or early July [Fitch 1970, Wright and Wright 1994]). Therefore, we pooled the data from both sexes for summary statistics.

Coachwhips moved frequently and for long distances (Table 3). They occupied large home ranges but small core areas (50%) of activity (Table 4; Fig. 2). Two snakes with exceptionally large MCP home ranges (142.1 and 268.4 ha) strongly influenced the mean home-range size (MCP = 70.4 ± 83.8 ha). However, mean home range calculated without these two individuals was still large (MCP = 31.9 ha). The 50% core activity area estimates were 2.2 ha (HM) and 13.6 ha (ADK), both less than 11% of the total home range (100%) calculated by those methods. There was broad overlap among the home ranges of different snakes (Fig. 3). Home-range size (MCP) was not significantly correlated with body mass (r = -0.22, n = 7, P = 0.63) or with snout vent length (r = -0.15, n = 7, P = 0.76).

Discussion

During the active season (April–October) at our study site, Coachwhips used oak savanna more frequently than expected based on its availability on the study area and within the snake home ranges (Fig. 4). These oak savannas are found on xeric sandy upland sites and have a dense ground layer of grass and other herbaceous vegetation within an open canopy forest of bluejack oak and post oak. The disproportionate use of this macrohabitat could be due to several factors including thermoregulatio, prey availability, and predator avoidance.

Coachwhips are known to be thermal specialists (Hammerson 1989, Jones and Whitford 1989, Secor 1995) and oak savanna macrohabitat may provide conditions allowing them to effectively thermoregulate. These

Table 3. Mean and range of movements (in meters) for seven Coachwhips tracked from 7 July to 10 September. Movement frequency, minimum (Min), and maximum (Max) movement distance (in meters) also are listed. See Methods for definition of overall movement rate (OMR) and actual movement rate (AMR).

	OMR	AMR	Frequency	Min	Max
Mean	73	93	78%	37	653
Range	53–133	70–177	50–95%	6–96	302–1084

Table 4. Home ranges of nine Coachwhips (in hectares). MCP = minimum convex polygon; HM = harmonic mean; ADK = adaptive kernel. All 336 data points (24–62 per snake) gathered April–October were included in these calculations.

	MCP 100%	HM 100%	ADK 100%	HM 95%	ADK 95%	HM 50%	ADK 50%
Mean	70.4	64.6	133.1	38.3	84.9	2.2	13.6
Range	16.1–268.4	19.4–227.4	35.9–470.4	14.2–142.3	17.0–328.3	0.3–5.7	0.6–68.8

conditions are most likely provided by the absence of a well-developed canopy, which permits sunlight to penetrate to the surface, yielding a mosaic of substrate temperatures (Swaim and McGinnis 1992). Our microhabitat

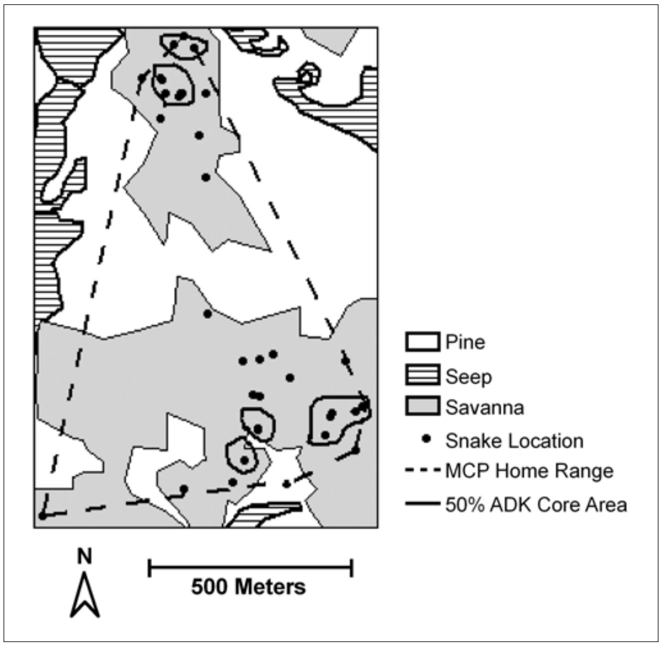

Figure 2. Example of a Coachwhip home range. Although the 100% minimum convex polygon (MCP) home range was large (56.2 ha), the 50% adaptive kernel (ADK) core areas were much smaller (total area = 8.9 ha) and always located in oak savanna habitat. Some snake location points (filled circles) represent multiple telemetry locations for this snake.

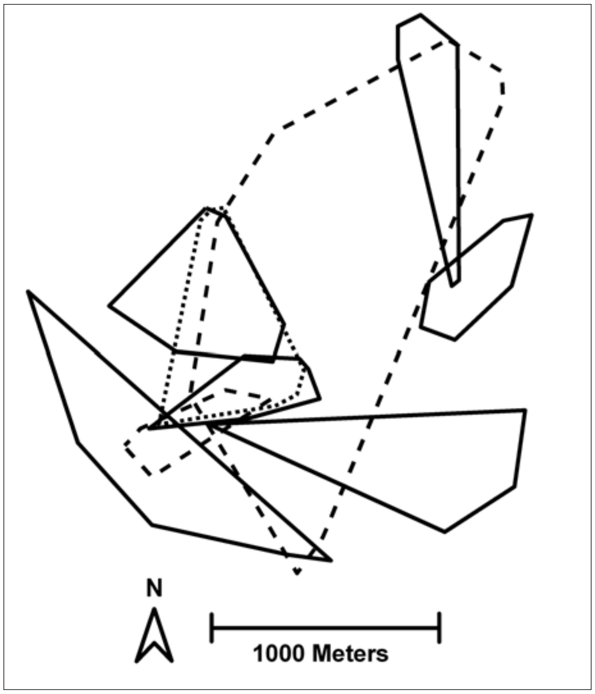

Figure 3. 100% MCP home ranges of nine Coachwhips. The home ranges of the snakes overlapped considerably.

analysis, which indicated that Coachwhips did not disproportionately use open-canopy sites (Table 1), might appear inconsistent with the hypothesis that Coachwhips select sites with open canopies. However, we stress that our microhabitat analyses, unlike our macrohabitat analyses, compared snake locations to random locations within snake home ranges. The home ranges of the Coachwhips, which were dominated by open-canopy oak savanna, were not representative of the study site as a whole.

The oak savanna environment used by Coachwhips in eastern Texas may be important for thermoregulation, but it also likely provides a habitat of high prey density. We observed no feeding by Coachwhips, but scat analysis of Coachwhips trapped from this study site revealed a diet dominated numerically by lizards (*Sceloporus*, *Aspidoscelis*, and scincids), orthopterans and other insects, and small rodents (D.C. Rudolph, unpubl. data); the density of these prey species likely increases with increasing amounts of ground-cover vegetation (Collins et al. 2002, Parajulee et al. 1997, Thill et al. 2004, Windberg 1998). Ground-cover vegetation was most abundant in the oak savanna macrohabitat.

The ground-cover vegetation of oak savannas also may be important for protection from predators. Active species incur higher risks because movement can attract predators (Plummer and Congdon 1994, Plummer and Mills 2000,

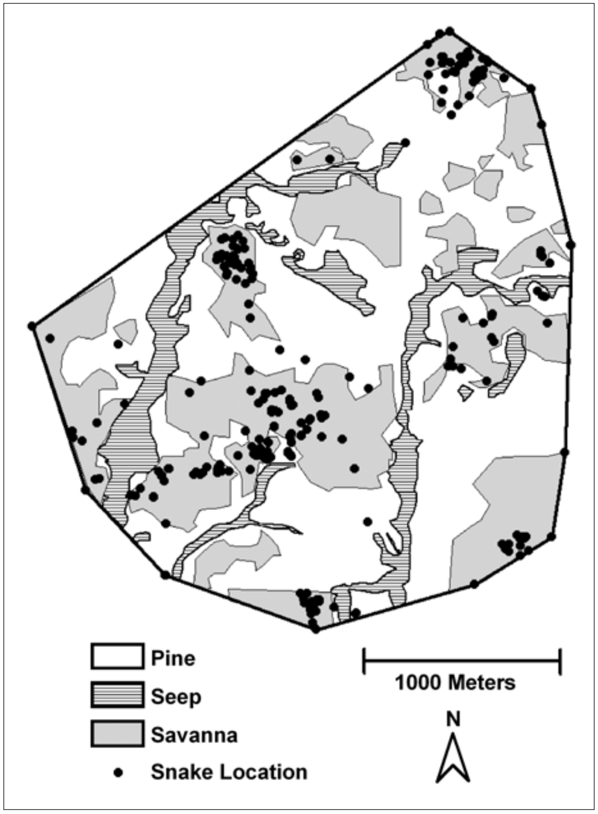

Figure 4. Telemetry locations (denoted by filled circles) of nine Coachwhips (336 relocation points), and available macrohabitats on the study area. Relocations of telemetered snakes were clustered in the oak savanna macrohabitat.

Secor 1995). We observed no direct predation on Coachwhips, but potential predators that were common at the study site included *Buteo jamaicensis* (Gmelin) (Red-tailed Hawks), *Buteo lineatus* (Gmelin) (Red-shouldered Hawks), *Canis latrans* Say (coyotes), and *Procyon lotor* (Linnaeus) (raccoons). Coachwhips in eastern Texas used microhabitats that offered great concealment. In the open-canopy oak savanna, Coachwhips often were found in dense herbaceous vegetation which provided protective overhead concealment; snakes used these microhabitat sites in greater proportion than their availability within their home ranges.

As further evidence of the importance of concealing vegetation for predator avoidance, our experience in relocating these snakes indicated that when sensing our presence they would climb trees, descend mammal burrows, or hide beneath other concealing objects. In retreating to these refugia, the snakes did not take the most direct route, rather they took routes through ground cover that offered the greatest concealment.

Coachwhips in eastern Texas exhibited a pattern of frequent, long-distance moves, sometimes exceeding a straight-line distance of 1 km in a 24-hour period. Secor (1995) found that Coachwhips in the Mojave Desert did not move in a straight line, but rather moved in a meandering fashion that resulted in a total distance moved of 1.4 times the straight-line distance. Thus, for comparison, the AMR of eastern Texas Coachwhips was recalculated using Secor's meander ratio of 1.4. Using the meander ratio, our estimate of the movement rate of eastern Texas Coachwhips approached those observed in the Mojave Desert (eastern Texas: 134 m/day; Mojave Desert: 186 m/day).

Mating presumably occurs primarily in May at our study area. We base this presumption on the peak in multiple Coachwhip captures, generally consisting of an adult female and one or more adult males, in funnel traps during this period (D.C. Rudolph, unpubl. data). A mating season in April or May would be generally consistent with observations of mating and oviposition reported by others (Fitch 1970, Werler and Dixon 2000, Wright and Wright 1994). Since most of our data were collected after May, we do not believe that the frequent long-distance moves exhibited by Coachwhips were a result of reproductive behavior. Thus, the abundance and distribution of prey may have been the primary factor governing movement of snakes in our study. If prey is frequently encountered in the habitat, movements may be short, but if prey is widely dispersed and patchily distributed, frequent and/or long-distance movements between prey patches may be necessary (Gregory et al. 1987, King and Duvall 1990, Macartney et al. 1988, Shine and Fitzgerald 1996, Whitaker and Shine 2003).

The high degree of movement activity resulted in a very large average home range, one of the largest home ranges of any snake that has been studied (Macartney et al. 1988, Secor 1995). However, comparisons of home-range size across studies/species are complicated by differing methodologies, quality of data, and by habitat variability (Gregory et al. 1987, Macartney et al. 1988). Additionally, so few snake species have been studied that attempts to form general conclusions concerning the home-range size of particular taxonomic or ecological groups are further complicated.

Despite dissimilar habitats, Coachwhips in eastern Texas and in the Mojave Desert had similar home ranges; the observed 100% MCP was somewhat larger in eastern Texas (70.4 ha in eastern Texas versus 57.9 ha in the Mojave Desert [Secor 1995]), but the observed 95% HM was somewhat smaller in eastern Texas. (38.3 ha versus 53.4 ha).

Home-range size was large for eastern Texas Coachwhips using three different estimators (Table 4). However, these home ranges contained large areas of unused or underused habitat (Fig. 2). Within their home ranges, Coachwhips used the patchily-distributed oak savanna macrohabitat more than expected based on its availability; hence, they underused early-successional pine plantations and forested seeps. The Coachwhips' high degree of movement activity, wherein individuals returned to previously occupied patches of oak savanna and repeatedly returned to previously used refugia (mean = 19%), indicates a high degree of familiarity with their environment.

Frequent repeated use of the same oak savanna patches resulted in relatively small 50% core activity areas (Table 4). These core activity areas were, in all cases, areas of preferred oak savanna macrohabitat that were patchily distributed within the snakes' home ranges. These areas must have provided resources essential to the Coachwhips, which may explain the high degree of overlap among different snakes' home ranges; individuals often were found in close proximity to one another and at times used the same refugia (but not simultaneously). The essential resources at these sites were most likely an abundance of prey, which is required for this species to support its high energetic needs (Ruben 1977, Secor and Nagy 1994), and open habitat necessary for optimal thermoregulation. The patchy availability of resources (suitable macrohabitat, optimal refugia, prey) may best explain the frequent long-distance movements, large 100% home ranges with small 50% core activity areas, and repeated use of underground refugia within the home ranges.

In summary, at the landscape level, Coachwhips were found in dry sandy uplands. At the macrohabitat level, they were found in oak savannas, and at the microhabitat level, they were found in tall herbaceous vegetation, frequently under protective overhangs or in burrows. Although Coachwhips moved frequently and had large home ranges, they consistently used the same patchily distributed oak savanna habitats. Future studies should investigate whether structurally similar but taxonomically different habitats, such as *Pinus palustris* Miller (longleaf pine) savanna, also are used disproportionately by Coachwhips in the southeastern United States.

Acknowledgments

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