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Authors: Waldron, Jayme L., Lanham, Joseph D., and Bennett, Stephen H.

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USING BEHAVIORALLY-BASED SEASONS TO INVESTIGATE CANEBRAKE RATTLESNAKE (*CROTALUS HORRIDUS*) MOVEMENT PATTERNS AND HABITAT SELECTION

JAYME L. WALDRON^{1,3,4}, JOSEPH D. LANHAM¹, AND STEPHEN H. BENNETT²

¹Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA

²South Carolina Department of Natural Resources, Columbia, SC 29201, USA

ABSTRACT: Both abiotic factors and behavioral patterns may influence snake activity. However, other than reproductive activities, behavioral patterns have rarely been incorporated into studies of snake habitat selection. We investigated seasonal differences in canebrake rattlesnake (*Crotalus horridus*) movement patterns and habitat selection. We modeled habitat selection in two ways, with and without regard to behaviorally-based seasons, and compared the two models to determine which yielded the most informative results. Behaviorally-based seasons (foraging, breeding, and hibernation) were determined from field observations of study animals. Habitat selection was modeled as habitat use versus availability using a case control sampling design for males and non gravid females using logistic regression. Males had significantly larger home ranges, moved more often, and traveled greater distances between successive locations during the breeding season as compared to non gravid females. The male no-season habitat model lacked significance, and the non gravid female no-season model revealed a positive association with pine savannas. When behaviorally-based seasons were included in the models, both sexes showed distinct seasonal variation in habitat selection, with males and non gravid females using similar habitat for breeding and hibernation, but partitioning habitat during the foraging season. Our results indicate that behaviorally-based seasons provide important details about intraspecific canebrake rattlesnake habitat selection and movement patterns, and that future research should benefit from the inclusion of snake behavior in habitat studies.

Key words: *Crotalus horridus*; Habitat partitioning; Habitat selection; Movement; Rattlesnake; Snake behavior

HABITAT structure and resource availability each may have an important influence on animal movement patterns (Garton et al., 2001; Gregory et al., 1987). For snakes in particular, both gender and reproductive condition may also influence movement patterns (Gregory et al., 1987; Madsen, 1984; Prestt, 1971; Reinert and Zappalorti, 1988; Timmerman, 1995). For example, male snakes tend to increase movement activity during the breeding season as compared to females (Gregory et al., 1987; Madsen, 1984; Prestt, 1971; Timmerman, 1995), perhaps because increased activity promotes opportunities for males to encounter reproductively receptive females. Furthermore, gravid females often have small home ranges and move shorter distances than both non gravid females and males (Reinert, 1984; Reinert and Zappalorti, 1988).

The effects of abiotic, environmentally-defined seasons (e.g., dry versus wet) on snake movement patterns have been described in several previous studies (Gibbons and Semlitsch, 2001; Godley, 1980; Reinert and Zappalorti, 1988; Shine and Lambeck, 1985; Timmerman, 1995), in which snakes responded to changes in environmental conditions by either increasing or decreasing their activity. Although it is widely accepted that both abiotic factors and behavioral patterns may influence snake activity, these variables are rarely incorporated into studies of snake habitat selection. Previous studies have reported shifts in resource use due to the effects of sex, reproductive status, and ontogenetic variation (Burger and Zappalorti, 1989; Reinert, 1984, 2001; Reinert and Zappalorti, 1988; Shine, 1986), but seasonal variation in intraspecific resource use has not been examined.

The purpose of this study was to investigate intraspecific differences in both movement and habitat selection patterns of canebrake rattlesnakes (*Crotalus horridus*) in the South

³ PRESENT ADDRESS: Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, SC 29802, USA.

⁴ CORRESPONDENCE: e-mail, waldron@srel.edu

Carolina Coastal Plain. Specifically, we addressed two questions pertaining to movement patterns and habitat selection: (1) Are there intraspecific differences (i.e., between males and nongravid females) in seasonal movement patterns (i.e., home-range size, number of movements, and movement distances between successive locations)?, (2) Does modeling habitat selection with regard to behaviorally-based seasons give different results than no-season habitat models, and if so, which model gives the most informative results?

Crotalus horridus is a declining species that is listed as vulnerable, critically imperiled, or imperiled in 20 of the 30 states in which it still occurs, and has been extirpated from Maine, Rhode Island, and Ontario, CA (Brown, 1993). Coastal Plain populations of *C. horridus* have no listing in South Carolina, and it is generally accepted that the species is common and apparently secure in the South Carolina Coastal Plain (Tennant and Bartlett, 2000). The results of this study will provide important information on habitat associations of a southeastern Coastal Plain *C. horridus* population, where little is known about the habitat requirements and general ecology of the species. This study will provide important baseline ecological information on canebrake rattlesnakes from which management guidelines can be developed and implemented for more imperiled populations.

MATERIALS AND METHODS

Study Area

This study was conducted on 4900 ha of state-owned property in Hampton County, South Carolina, consisting of upland longleaf pine (*Pinus palustris*) savanna, cultivated fields, mixed pine hardwood forests, planted pine forests, and hardwood bottoms. We used a minimum convex polygon that encompassed all recorded snake radio relocations to delineate our 2800 ha study area. The South Carolina Department of Natural Resources has managed the property since 1941, focusing primarily on game species, including bobwhite quail (*Colinus virginianus*) and white tailed deer (*Odocoileus virginianus*). Fields and wildlife openings within the study

area were maintained with annual plowing and planting, and new fields were occasionally created. Slashpiles of pulled trees and stumps from maintenance bordered most fields. Managers used controlled burns every one to four years between January and April to maintain pine savannas.

Radio Telemetry

We used radio telemetry to measure home-range size and model within-home range habitat selection by canebrake rattlesnakes during three field seasons from 2002 to 2004. Radio transmitters (SI-2, 11–13 g, Holohil Systems, Carp. ON) were surgically implanted into adult canebrake rattlesnakes (nongravid females, $n = 9$; gravid females, $n = 1$; males, $n = 8$). We anesthetized snakes with isoflurane, which was administered using an anesthesia machine equipped with an isoflurane vaporizer. Following surgery, snakes were monitored for 3 d and then released at their capture locations. Handling and surgeries were conducted under Clemson University Animal Use Protocol #20032 and #50062.

Each rattlesnake was monitored using radio telemetry for up to one year. Three canebrake rattlesnakes (males, $n = 1$; females, $n = 2$) were monitored only between four and nine months due to predation, road mortality, or transmitter failure. Study animals were located approximately 5 d each week during spring, summer, and fall using a radio receiver (Telonics, TR-2, Mesa, AZ) and a directional antenna. Winter (inactive season) radio relocations ranged from biweekly to monthly between December and March. Each snake location was recorded using a Global Positioning System (GPS; Trimble Pro XR, Sunnyvale, CA) with real-time differential correction and an estimated spatial accuracy of less than 5 m.

Home Range Estimation and Movement Patterns

We measured distance moved (m) between successive radio locations, the number of snake movements, and home-range size by season. Analysis of movement and home-range size was based on GPS positions of radio locations. We calculated home-range size and measured distance between succes-

TABLE 1.—Telemetered canebrake rattlesnakes (*Crotalus horridus*) observed breeding (B), foraging (F), and hibernating (H) during seasons that were classified according to snake behavior at a South Carolina study site, U.S.A. An “R” corresponds to observations of the gravid female (female #10) at her birthing area. Missing data correspond to individuals that were lost due to mortality or transmitter failure.

| | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar |
|---------|------------|-----|-----|-----|------------|-----|-----|---------------|-----|-----|-----|-----|
| | (Foraging) | | | | (Breeding) | | | (Hibernation) | | | | |
| Males | | | | | | | | | | | | |
| 1 | F | F | F | F | B/F | B/F | B/F | H/B | H | H | H | H |
| 2 | F | F | F | F | F | B/F | F | H/B | H | H | H | H |
| 3 | F | F | F | F | B/F | B/F | F | H | H | H | H | H |
| 4 | F | F | F | F | B | B/F | F | F/H | H | H | H | H/F |
| 5 | F | F | F | F | B/F | B/F | F | H | H | H | H | H |
| 6 | F | F | F | F | B/F | B/F | F | H | H | H | H | H |
| 7 | F | F | F | F | B/F | B | B/F | F/H | H | H | H | H |
| 8 | F | F | F | F | . | . | . | . | . | . | . | . |
| Females | | | | | | | | | | | | |
| 1 | F | F | F | F | B/F | B/F | F | F/H | H | H | H | H |
| 2 | F | F | F | F | B/F | F | F | H | H | H | H | H/F |
| 3 | F | F | F | F | F | F | F | F/H | H | H | H | H |
| 4 | F | F | F | F | F | F | F | H | H | H | H | H |
| 5 | F | F | F | F | F | F | F | H | H | H | H | H |
| 6 | F | F | F | F | . | . | . | . | . | . | . | . |
| 7 | F | F | F | F | F | F | F | F/H | H | . | . | . |
| 8 | F | F | F | F | F | F | F | F/H | H | H | H | H |
| 9 | F | F | F | F/B | F/B | F/B | F/B | H | H | H | H | H |
| 10 | F/R | R | R | R | R/F | F | F | H | H | H | H | H |

sive radio locations using ArcView GIS version 3.3 (ESRI, Redlands, CA) and Spatial Analyst with the Animal Movement Extension (Hooge and Eichenlaub, 1997). We calculated home range using fixed Kernel Analysis (95% activity core), which gives a nonparametric estimate of home-range size (Worton, 1987, 1989), instead of other estimators because it does not have distributional assumptions and the home range boundaries are calculated based on the complete distribution of radio locations, rather than using only the outermost locations (Kernohan et al., 2001). ArcView calculated the smoothing parameter, *h*, used in home range estimation.

Rattlesnake locations were grouped into behaviorally-based seasons that were determined from field observations of study animals (Table 1). The foraging season began in April, when the telemetered rattlesnakes moved from their hibernacula and began foraging, and ended in July just prior to the onset of breeding. During the foraging season, snakes were commonly observed in ambush posture (Reinert et al., 1984) and rarely went underground. Breeding season (Aug–Oct) classification was based on observations of males and reproductively receptive females. Breeding behavior included male and female pairing (e.g., one or more males gathering around a single female), copulation, courting, and scent trailing (i.e., males tongue flicking and moving fixedly rather than sitting in ambush posture). The hibernation season (Nov–Mar) began with the cessation of activity at hibernacula, and ended with spring emergence (i.e., snakes emerging from hibernacula and basking until first shed). There was some overlap between seasons (e.g., scent trailing in late July and breeding at hibernacula; Table 1), and snakes occasionally foraged during the breeding season. However, we classified the behaviorally-based seasons so that each season adequately represented the time at which the behaviors were observed (Table 1).

Habitat Data Collection

To characterize habitats within the study area, we combined aerial photographs with National Wetlands Inventory (NWI) classifications (Cowardin et al., 1979; Table 2). Upland pine habitat was divided into two categories based on canopy cover. Open-canopy upland pine, including longleaf, lob-

TABLE 2.—Habitat types used by canebrake rattlesnakes (*Crotalus horridus*) in southeastern South Carolina, USA (Waldron et al., 2006).¹

| NWI classification | Habitat type | Description |
|---------------------|-----------------|---|
| Upland Planted Pine | Pine Savanna | Upland mature pine savanna/wiregrass community with open canopy; dominant tree species include longleaf pine (<i>Pinus palustris</i>), slash pine (<i>P. elliottii</i>), loblolly pine (<i>P. taeda</i>), post oak (<i>Quercus stellata</i>), blackjack oak (<i>Q. marilandica</i>) and hickory species (<i>Carya</i> spp.). |
| Upland Planted Pine | Planted Pine | Upland planted pine; dominated by closed canopy, unthinned loblolly, slash, or longleaf pine. |
| Palustrine Pine | Pine Hardwood | Forested wetland; holds water seasonally; overstory dominated by loblolly pine and hardwood species, including sweet gum (<i>Liquidambar styraciflua</i>), willow oak (<i>Q. phellos</i>), and southern red oak (<i>Q. falcata</i>). |
| Palustrine Hardwood | Hardwood Bottom | Forested wetland; holds water seasonally; overstory dominated by hardwoods; Dominant species include overcup oak (<i>Q. lyrata</i>), willow oak, red maple (<i>Acer rubrum</i>), sweet gum, southern red oak, black gum (<i>Nyssa sylvatica</i>), and bald cypress (<i>Taxodium distichum</i>). |
| Crops | Fields | Fields and wildlife openings maintained for game management; seasonally plowed and planted; edges consist mostly of slashpiles resulting from field construction and maintenance. |

¹ Habitats within the study area were characterized by combining aerial photos with National Wetlands Inventory (NWI) classification.

lolly (*P. taeda*), and slash (*P. elliottii*) pine, was classified as pine savanna. Closed canopy, planted loblolly, slash, and longleaf pine stands were classified as planted pine. This classification was verified by systematic field visits to the various habitats.

Data Analysis

We used SAS 9.1 (SAS Institute 2002) for statistical analyses. Home-range estimates were log10 transformed to meet assumptions of normality. Movement and home range data were analyzed using repeated measures ANOVA, with individual snakes as the repeated factor, sex and season as independent variables, and multiple comparisons across seasons by sex using least squares means. We excluded the single gravid female from movement analyses and only compared home ranges between foraging and breeding seasons due to low sample sizes during the hibernation season. Assumptions of normality were tested using Shapiro-Wilk tests ($\alpha = 0.05$), and homogeneity of variance was tested using Levene’s tests ($\alpha = 0.05$).

We modeled within-home range habitat selection for males and nongravid females using logistic regression with use as the binary dependent variable and habitat type (Table 2) as the categorical independent variable. We used a case control sampling design (Hosmer and Lemeshow, 2000) by randomly selecting from the samples of used and available (i.e.,

random observations within home ranges) locations to ensure that an adequate and proportional number of used locations were included in the final sample to compare with random locations. Habitat selection was modeled separately for males and nongravid female canebrake rattlesnakes. Maximum likelihood estimates and odds ratios were used to compare habitat selection across habitat types. To ensure that individual males and females could be pooled by sex for analysis, we investigated the influence of individual snakes in the models. The effect of individual snake was not significant for males ($\chi^2 = 3.2$, df = 7, $P > 0.05$) or nongravid females ($\chi^2 = 2.0$, df = 8, $P > 0.05$). Habitat selection was modeled in two ways. First, habitat selection was modeled without regard to behaviorally-based seasons (no-season model). Second, habitat selection was modeled by season, such that there was a separate model for each season (i.e., foraging, breeding, and hibernation). Models were compared and discussed based on their ability to significantly predict habitat selection.

RESULTS

Analysis of home-range size revealed no effect of season (df = 1, 14; $F = 3.96$; $P > 0.05$), a significant effect of sex (df = 1, 15; $F = 5.77$; $P < 0.05$), and a significant season by sex interaction (df = 1, 14; $F = 12.74$; $P < 0.05$). Multiple comparisons revealed no

seasonal difference ($df = 14$; $t = -1.19$; $P > 0.05$) between nongravid female home ranges (foraging, $\bar{x} = 39.73$; $SD = 64.47$; $Range = 7.7\text{--}207.4$; breeding, $\bar{x} = 23.71$; $SD = 26.42$; $Range = 3.4\text{--}89.8$). Male home ranges were smaller ($df = 14$; $t = 3.72$; $P < 0.05$) during the foraging season ($\bar{x} = 32.83$; $SD = 17.95$; $Range = 12.9\text{--}57.9$) than during the breeding season ($\bar{x} = 80.24$; $SD = 54.11$; $Range = 23.2\text{--}180.0$), and males had significantly larger home ranges than nongravid females during the breeding season ($df = 14.9$; $t = -3.65$; $P < 0.05$). Males expanded their foraging season home ranges during the breeding season, such that most of the foraging season home ranges were included within the respective breeding season home range (Fig. 1).

Analysis of variance of distance moved between successive locations revealed a significant effect of season ($df = 2, 12$; $F = 4.59$; $P < 0.05$), no significant effect of sex ($df = 1, 13$; $F = 0.09$; $P > 0.05$), and a slight interaction between season and sex ($df = 2, 12$; $F = 3.06$; $P = 0.08$). Males moved greater distances during the breeding season ($\bar{x} = 155.65$; $SD = 45.29$) than during the foraging ($\bar{x} = 95.05$; $SD = 34.22$) and hibernation ($\bar{x} = 4.26$; $SD = 9.58$) seasons ($df = 2, 12$; $F = 5.57$; $P < 0.05$), but nongravid females did not vary in distance moved by season ($df = 2, 11$; $F = 0.75$; $P > 0.05$; Fig. 2). On average, nongravid females moved 86.81, 91.42, and 7.47 m during the foraging, breeding, and hibernation seasons, respectively. Analysis of variance of number of movements revealed an effect of sex ($df = 1, 13$; $F = 6.96$; $P < 0.05$) and season ($df = 2, 13$; $F = 41.51$; $P < 0.001$), but no interaction between sex and season ($df = 2, 13$; $F = 1.49$; $P > 0.05$; Fig. 2). Multiple comparisons indicated that males ($df = 2, 13$; $F = 21.70$; $P < 0.0001$) and nongravid females ($df = 2, 13$; $F = 21.28$; $P < 0.0001$) moved less often during the hibernation season as compared to the foraging and breeding seasons (Fig. 2). On average, nongravid females moved 28.62 times during the foraging season and 3.62 times during the hibernation season. Similarly, males moved 30.43 times during the foraging season and 7.85 times during the hibernation season. The only season in which males and nongravid females differed in their movement patterns was the

breeding season (Fig. 2). Males moved farther distances between successive locations ($df = 10$; $t = -3.48$; $P < 0.01$) and more often ($\bar{x} = 32.28$; $SD = 6.21$; $df = 13$; $t = -3.08$; $P < 0.01$) than nongravid females (\bar{x} number of movements = 23.25; $SD = 5.17$).

The no-season habitat selection model indicated no significant habitat associations ($df = 4$; $\chi^2 = 7.58$; $P > 0.05$) for males, whereas this model was significant for nongravid females ($df = 4$; $\chi^2 = 19.55$; $P < 0.001$), showing a positive association with pine savannas and a negative association with hardwood bottoms (Table 3). Seasonal habitat selection varied in both sexes (Table 4), and the results of the seasonally-based models for nongravid females differed markedly from the no-season model (Table 3).

During the foraging season, males showed a positive association with hardwood bottoms (Table 4), and were 2.4 and 1.6 times more likely to select hardwood bottoms than fields and pine hardwood forests, respectively. Nongravid females showed their strongest positive association with pine hardwood forests during the foraging season (Table 4), and were ≥ 3.0 times more likely to select pine hardwood forests than hardwood bottoms or fields. Males and nongravid females were associated with similar habitat during the breeding season. Although nongravid females showed no significant habitat associations during the breeding season (Table 4), they were 3.6 times more likely to select fields or pine savannas than pine hardwood forests. Similarly, males had a strong positive association with fields (Table 4), and were ≥ 3.3 times more likely to select fields than hardwood bottoms or pine hardwood forests. Both sexes were more likely to hibernate in pine hardwood forests than other habitat types (Table 4). Specifically, males were 143 and 14 times more likely to select pine hardwood forests for hibernation than hardwood bottoms and pine savannas, respectively. Females were > 20 times more likely to select pine hardwood forests for hibernation than planted pine and hardwood bottoms.

DISCUSSION

Because we observed seasonal variation in both movement patterns and habitat selection,

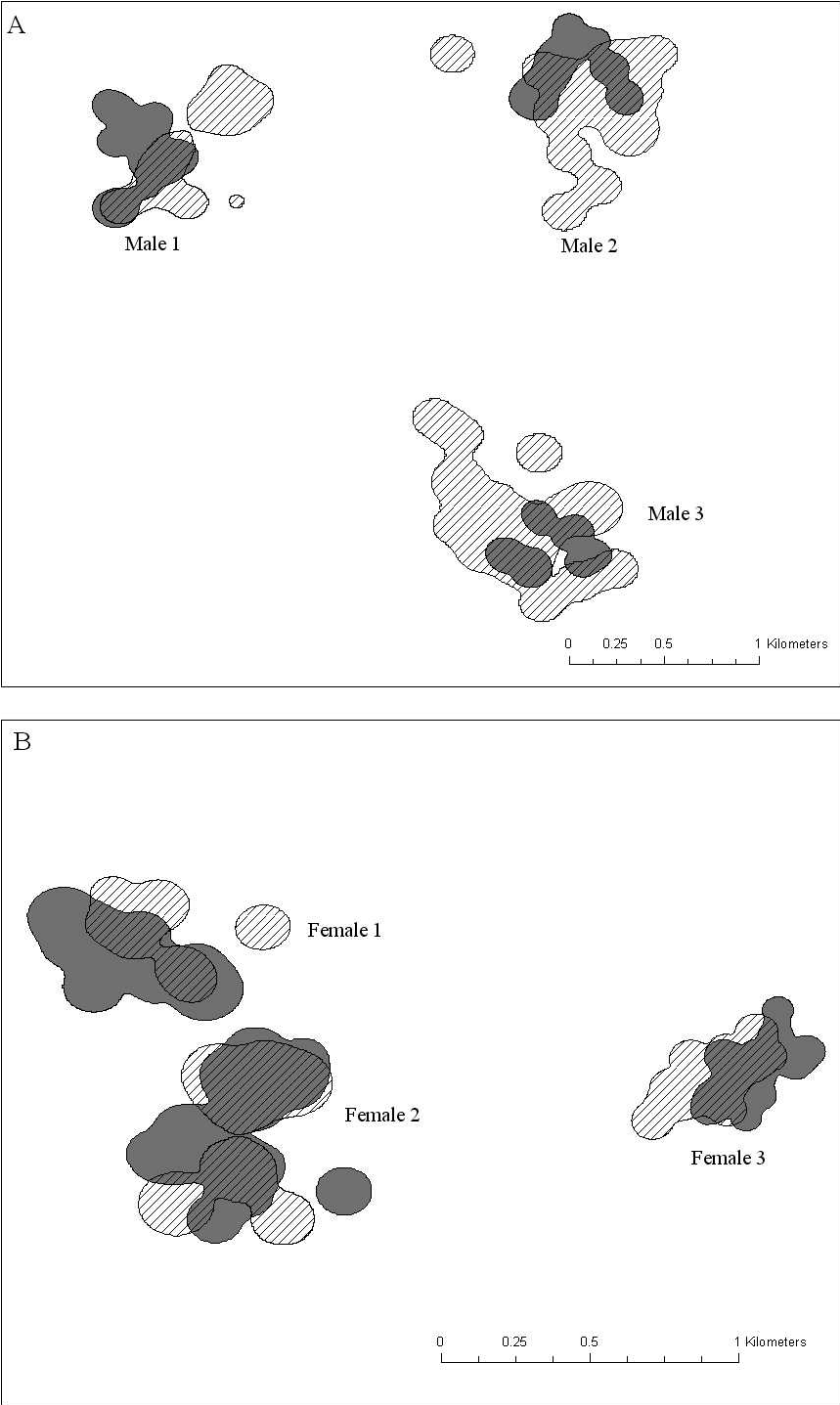


FIG. 1.—Examples of seasonal variation (i.e., breeding and foraging seasons) in home-range size by male (A) and female (B) canebrake rattlesnakes (*Crotalus horridus*) at a southeastern South Carolina study site, USA. Striped polygons represent breeding season home ranges and shaded polygons represent foraging season home ranges.

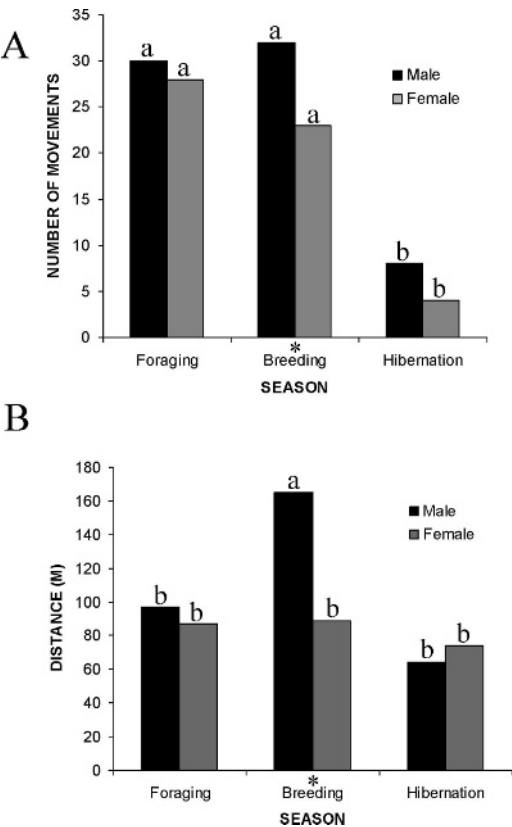


FIG. 2.—Seasonal variation in average number of movements between successive radio locations (A) and average distance moved (B) by male ($n = 8$) and nongravid female ($n = 9$) canebrake rattlesnakes (*Crotalus horridus*) at a southeastern South Carolina study site, USA. Different letters indicate statistical difference among seasons within sex. Asterisks indicate statistical differences between males and females within season.

the results of this study suggest that analyses including behaviorally-based seasons may elucidate patterns of intraspecific habitat partitioning. Without the inclusion of seasons in the habitat models, important shifts in habitat selection by male and nongravid female canebrake rattlesnakes would have been overlooked in this study.

Without regard to season, male canebrake rattlesnakes had larger home ranges than nongravid females within the study area (Waldron et al., 2006). The seasonal variation in home-range size observed in this study suggests that male movement during the breeding season is largely responsible for their larger home ranges. A coastal Virginia population of canebrake rattlesnakes had similar home ranges (A. Savitzky and C. Petersen, personal communication) to those in our study site (see Waldron et al., 2006). However, Reinert and Zappalorti (1988) reported home ranges from a coastal New Jersey population that were nearly double the values observed within our study area. Geographic variation in home-range size can reflect differences in local habitat quality, prey availability, and body size (Gregory et al., 1987; Harestad and Bunnell, 1979; McNab, 1963). Because of differences in methodology and sampling effort, which can hamper efforts to compare movement patterns across populations (Gregory et al., 1987), we were unable to compare our analysis of number of movements and distance moved between successive locations to other studies.

Both sexes were associated with different habitats during the foraging season, with

TABLE 3.—Maximum likelihood estimates from no-season logistic regression models of habitat selection by male ($n = 8$) and nongravid female ($n = 9$) canebrake rattlesnakes (*Crotalus horridus*) from a southeastern South Carolina study site, U.S.A.

| Sex | Variables ¹ | Estimate \pm SE | df | χ^2 | P |
|-------------------|------------------------|----------------------|----|----------|--------|
| Males | HWB | -0.2766 ± 0.1070 | 1 | 6.68 | 0.0098 |
| | PHWD | 0.2812 ± 0.1915 | 1 | 2.16 | 0.1419 |
| | PP | 0.0496 ± 0.0929 | 1 | 0.29 | 0.5933 |
| | PSAV | -0.0039 ± 0.0941 | 1 | 0.00 | 0.9672 |
| | FD | -0.0504 ± 0.1186 | 1 | 0.18 | 0.6707 |
| Nongravid females | HWB | -0.3468 ± 0.1387 | 1 | 6.26 | 0.0124 |
| | PHWD | 0.2309 ± 0.2232 | 1 | 1.07 | 0.3008 |
| | PP | -0.1380 ± 0.1006 | 1 | 1.88 | 0.1700 |
| | PSAV | 0.2394 ± 0.0863 | 1 | 7.70 | 0.0055 |
| | FD | 0.0145 ± 0.1051 | 1 | 0.02 | 0.8906 |

¹ HWB = hardwood bottom, PHWD = pine hardwood forest, PP = planted pine forest, PSAV = pine savanna, and FD = field.

TABLE 4.—Maximum likelihood estimates from logistic regression model of male ($n = 8$) and nongravid female ($n = 9$) canebrake rattlesnake (*C. horridus*) habitat selection during the breeding, foraging, and hibernation seasons in a southeastern South Carolina study site, U.S.A.

| Parameters ¹ | Estimate ± SE | df | χ ² | P |
|-------------------------|------------------|----|----------------|---------|
| Males | | | | |
| Breeding | | 4 | 24.13 | <0.0001 |
| HWB | −0.6362 ± 0.2047 | 1 | 9.66 | 0.0019 |
| PHWD | −0.4931 ± 0.3750 | 1 | 1.72 | 0.1885 |
| PP | 0.2576 ± 0.1597 | 1 | 2.60 | 0.1067 |
| PSAV | 0.1709 ± 0.1576 | 1 | 1.17 | 0.2782 |
| FD | 0.7008 ± 0.1857 | 1 | 14.24 | 0.0002 |
| Foraging | | 4 | 12.48 | 0.0141 |
| HWB | 0.3189 ± 0.1498 | 1 | 4.53 | 0.0332 |
| PHWD | −0.1211 ± 0.3386 | 1 | 0.13 | 0.7205 |
| PP | 0.2482 ± 0.1437 | 1 | 2.98 | 0.0843 |
| PSAV | 0.1036 ± 0.1503 | 1 | 0.50 | 0.4792 |
| FD | −0.5523 ± 0.2025 | 1 | 7.44 | 0.0064 |
| Hibernation | | 4 | 23.16 | 0.0001 |
| HWB | −2.2617 ± 0.6106 | 1 | 13.72 | 0.0002 |
| PHWD | 2.6507 ± 0.6241 | 1 | 18.04 | <0.0001 |
| PP | −0.2778 ± 0.2985 | 1 | 0.87 | 0.3520 |
| PSAV | 0.0200 ± 0.2940 | 1 | 0.01 | 0.9457 |
| FD | −0.1312 ± 0.3831 | 1 | 0.12 | 0.7311 |
| Nongravid Females | | | | |
| Breeding | | 4 | 2.32 | 0.5053 |
| HWB | 0.2492 ± 0.2575 | 1 | 0.94 | 0.3333 |
| PHWD | −0.9937 ± 0.6116 | 1 | 2.64 | 0.1042 |
| PP | 0.1556 ± 0.2027 | 1 | 0.59 | 0.4426 |
| PSAV | 0.2954 ± 0.1885 | 1 | 2.46 | 0.1171 |
| FD | 0.2935 ± 0.2069 | 1 | 2.01 | 0.1561 |
| Foraging | | 4 | 13.00 | 0.0133 |
| HWB | −0.4257 ± 0.1837 | 1 | 5.37 | 0.0205 |
| PHWD | 0.8059 ± 0.2914 | 1 | 7.65 | 0.0057 |
| PP | −0.1215 ± 0.1367 | 1 | 0.79 | 0.3740 |
| PSAV | 0.0478 ± 0.1207 | 1 | 0.16 | 0.6920 |
| FD | −0.3065 ± 0.1516 | 1 | 4.09 | 0.0432 |
| Hibernation | | 4 | 27.65 | <0.0001 |
| HWB | −1.1208 ± 0.4359 | 1 | 6.61 | 0.0101 |
| PHWD | 1.9719 ± 0.5368 | 1 | 13.01 | 0.0003 |
| PP | −1.2735 ± 0.3041 | 1 | 17.54 | <0.0001 |
| PSAV | 0.1315 ± 0.1425 | 1 | 0.85 | 0.3562 |
| FD | 0.2910 ± 0.2678 | 1 | 1.18 | 0.2773 |

¹ HWB = hardwood bottom; PHWD = pine hardwood forest; PP = planted pine forest; PSAV = pine savanna; and FD = field.

males preferring hardwood bottoms and nongravid females preferring pine hardwood forests. Presumably, inter-sexual competition for food was avoided through habitat partitioning. Cotton rats (*Sigmodon hispidus*) and gray squirrels (*Sciurus carolinensis*), which are common prey items for canebrake rattlesnakes (see Clark, 2002; Klauber, 1956), were abundant in the study area (J. L. Waldron, personal observation). Gray squirrels are associated with hardwood bottoms in

the southeastern Coastal Plain (Webster et al., 1985), and cotton rats are old field/edge specialists (Pagels et al., 1992). Whether the observed habitat partitioning reflects differences in prey preference or foraging strategy is uncertain. In the most extensive study of *C. horridus* diet, Clark (2002) detailed geographical and ontogenetic trends in dietary preference. Although prey mass was positively correlated with body size, Clark (2002) did not indicate dietary differences in males and females. *Crotalus horridus* diet includes larger prey items as they grow (Clark, 2002), and telemetered males (\bar{x} = 115.68 cm SVL; SD = 13.34) tended to be larger than females (\bar{x} = 106.75 cm SVL; SD = 3.69) at our study site and thus, may have been selecting gray squirrels for prey. Reinert et al. (1984) described a foraging behavior in this species in which snakes assume an ambush posture adjacent to logs. We commonly observed females (i.e., 31% of female foraging observations) using ambush tactics near logs at our study site. By contrast, we often observed males (i.e., 23% of male foraging observations) using ambush foraging posture at the base of hardwood trees, sometimes facing up the trunk, whereas we only observed nongravid females using this ambush posture on one occasion. These observations support the hypothesis that differences in habitat selection during the foraging season reflect dietary partitioning between the sexes.

Logistic regression analysis revealed a shift in habitat selection between the foraging and breeding seasons by both sexes. Males shifted from an association with hardwood bottoms during the foraging season to an association with fields during the breeding season. Similarly, nongravid females shifted from pine hardwood forests to fields. Although nongravid females lacked significant habitat associations during the breeding season, odds ratios indicated that they were three times more likely to use fields than other habitat types. Why fields were selected rather than other habitat types is unclear. Males likely selected habitat that would increase their chances of encountering females; thus, both sexes shifted to a common habitat type (i.e., fields) during the breeding season. Savitzky and Petersen (A. Savitzky and C. Petersen, personal communi-

cation) have observed male canebrake rattlesnakes courting females in pre-shedding condition in southeastern Virginia. We believe that males in this study were courting receptive females in pre-shedding condition that were using field edges for optimal basking opportunities.

Both sexes strongly selected pine hardwood forests for hibernation. Similar to northern and montane *C. horridus* populations, some southeastern Coastal Plain populations hibernate communally (M. Martin, S. Hoss, and L. Smith, personal communication). The reason for the absence of communal hibernation in our study area is not clear. The abundance of suitable hibernacula, e.g., rotten pine stumps, hardwood stumps, hurricane "tip-ups," and armadillo burrows, might make communal hibernation unnecessary. Furthermore, hibernacula in our study area may lack size and depth as compared to the rock outcrops used for communal hibernation in other regions within the range of the species. However, there were two occasions in this study in which more than one snake used the same hibernaculum. An adult female and a juvenile canebrake rattlesnake hibernated together in a stump hole, while another adult female hibernated with an adult cottonmouth (*Agkistrodon piscivorus*).

The seasonal shifts in habitat selection observed in this study illustrate the importance of incorporating behavior in habitat selection models. When models did not include behaviorally-based seasons, males showed no significant habitat association. This finding is misleading because it suggests that males have little habitat specificity, when in reality, both sexes exhibit habitat specificity that shifts in response to seasonal changes in behavior. Furthermore, this study provides a unique framework for conservation and management of *C. horridus* populations with potential range-wide application. Radio telemetry data revealed that male and nongravid female canebrake rattlesnakes use a variety of habitats, including those resulting from management activities (e.g., fields), those maintained by fire (e.g., pine savanna), and "unaltered" habitats (e.g., hardwood bottoms). Future research efforts should incorporate multiple-year radio telemetry studies to de-

termine whether canebrake rattlesnakes show long-term site fidelity to particular habitats.

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