

## Does Prey Availability Determine Seasonal Patterns of Habitat Selection in Texas Ratsnakes?

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**ABSTRACT.**—An animal's requirements (e.g., food vs. shelter) from its environment are likely to vary seasonally and, therefore, so too should habitat selection. Here, we test the hypothesis that Texas Ratsnakes (*Elaphe obsoleta*) choose habitats based on prey availability during their active season and on cover during winter. We examined snake habitat selection at three spatial scales and compared that to abundance of small mammals and nesting birds, which we confirmed by diet analysis to be the snakes' principal prey. Small mammal trapping and avian point counts showed that overall prey abundance was higher on mesas and slopes compared to savannahs. Compared to availability of habitats within the entire study area, snakes selected home ranges with a high proportion of slope habitat. Within home ranges, however, selection for slopes was exhibited only during winter when foraging is at a minimum and snakes are relatively inactive. Snakes did not use habitat within home ranges selectively during the active season or during the avian breeding season. The latter result suggests that ratsnakes are effective avian nest predators despite preying on birds opportunistically. However, it is also possible that some individual ratsnakes specialize on birds, whereas the majority preys on mammals. Microhabitat analysis comparing winter and active season sites showed that snakes preferentially used areas of high canopy cover and rock ground cover during winter. Collectively these results provide limited support for the hypothesis that ratsnakes use habitats based on prey availability but do indicate that ratsnakes select winter habitat based on cover availability.

An animal's habitat must provide multiple ecological services, each of which can potentially affect how habitats are selected. For predators, prey availability should be an important basis for habitat selection because habitats with more prey can promote increased growth and reproduction of the predator (e.g., Ward and Lubin, 1993; Pearce-Higgins and Yalden, 2004). For ectothermic predators such as snakes, however, the availability of appropriate thermal resources could be the most important basis for habitat selection (Huey, 1991; Reinert, 1993). The relative importance of various factors affecting habitat selection is likely to vary both among populations (e.g., latitudinally) and within populations (e.g., seasonally). Here, we examine seasonal variation in habitat selection within a population of Texas Ratsnakes (*Elaphe obsoleta*). We consider habitat selection at multiple spatial scales and relative to the abundance of small mammals and nesting birds, the snakes' two principal types of prey. Scale is important in ecology (Levin, 1992; Schneider, 2001), and in the case of habitat selection, examining patterns at multiple spatial scales can improve our understanding of both what habitat is selected and how selection occurs

(Harvey and Weatherhead, 2006a; Row and Blouin-Demers, 2006a).

The possibility that snakes use the abundance of breeding birds to select habitat is of particular interest to ornithologists. Many recent studies have identified snakes as important avian nest predators (Thompson et al., 1999; Morrison and Bolger, 2002; Renfrew and Ribic, 2003; Thompson and Burhans, 2003), including studies of Texas Ratsnakes (Stake and Cimprich, 2003; Stake et al., 2004). By identifying the factors that bring snakes into contact with birds, we will improve our understanding of avian nest predation (Weatherhead and Blouin-Demers, 2004). There are two general reasons that snakes could be successful finding and preying on birds' nests. First, snakes that prey extensively on birds' nests might select habitat based on nest abundance. Second, snakes might choose habitats for reasons unrelated to nest abundance and coincidentally prey on nests while in that habitat (Blouin-Demers and Weatherhead, 2001a; Weatherhead and Blouin-Demers, 2004). In this second scenario, snakes might still be selecting habitat based on prey abundance, but based on alternative prey such as small mammals rather than birds, or they might be attracted to the same habitat as birds for reasons other than prey abundance, such as thermoregulation (Blouin-Demers and Weatherhead, 2001b; Weatherhead and Blouin-Demers, 2004).

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Ratsnakes are primarily predators of small mammals, with avian prey becoming important (although still not surpassing mammals) during the bird-nesting season (Fitch, 1963; Weatherhead et al., 2003; Carfagno et al., 2006). If ratsnakes use habitats based on prey abundance, then habitats with more prey would be used more by snakes than habitats with fewer prey. In addition, if ratsnakes are actively seeking and attracted to bird nests, a seasonal shift to bird nesting habitat would be expected when the birds are breeding, unless bird and small mammal abundance coincide. Studies in Ontario and Illinois found that ratsnakes preferentially used forest edges, but that the preference was not because small mammals were more abundant in edges (Blouin-Demers and Weatherhead, 2001a; Carfagno et al., 2006). Ratsnakes in both Ontario and Illinois displayed seasonal variation in habitat use, but because nesting bird populations were not surveyed, neither study was able to test the prediction that snakes selected habitats based on avian nest abundance.

In addition to seasonal habitat shifts in response to prey availability, habitat selection has been shown to shift seasonally because of other aspects of life history such as hibernation or breeding requirements (Waldron et al., 2006). For snakes in northern climates, availability of winter hibernation sites is a critical aspect of habitat selection (Prior and Weatherhead, 1996; Harvey and Weatherhead, 2006b). In fact, even during the snakes' active season, thermoregulation has a strong influence on habitat selection by ratsnakes in the northern part of their range (Blouin-Demers and Weatherhead, 2001a,b, 2002). Texas Ratsnakes are at the southern end of the range of the *E. obsoleta* complex. Relative to ratsnakes at higher latitudes, we expect that thermoregulation should be less important in habitat selection, thus increasing the potential importance of prey abundance. However, even though Texas Ratsnakes do not exhibit hibernation typical of more northern ratsnakes, they do become inactive in winter (JHS, unpubl. data), at which time their habitat requirements are likely to change. Therefore, we predict that during the winter the snakes should choose habitats based on features such as thermoregulatory properties (e.g., greater availability of edges; Blouin-Demers and Weatherhead, 2001a,b) or more cover that would provide protection from weather and predators.

To test the hypothesis that snakes are choosing habitats based on prey availability, we examined snake habitat selection at three spatial scales and compared that to relative prey abundance. Determining habitat selection at a single spatial scale can lead to erroneous

conclusions of selection patterns and mechanisms (Orians and Wittenberger, 1991). For example, snakes may choose landscape level habitats and use microhabitats within each habitat in proportion to availability (e.g., Weatherhead and Charland, 1985). Conversely, snakes may choose microhabitat features and use landscape level habitats in proportion to the amount of microhabitat features contained within (e.g., Harvey and Weatherhead, 2006a). Although several recent studies have examined snake habitat selection at multiple spatial scales (Shine and Fitzgerald, 1996; Johnson et al., 2007; Row and Blouin-Demers, 2006a; Wund et al., 2007), multiscale habitat studies that consider prey availability are rare (Heard et al., 2004).

#### MATERIALS AND METHODS

We conducted this study from 2004–2007 at Fort Hood, an 87,890-ha military installation in central Texas (30°10'N, 97°45'W). The habitat of Fort Hood is predominantly oak-juniper (*Juniperus ashei* and *Quercus* spp.) woodlands and oak savannahs. The topography of Fort Hood is characterized by flat-top mesas and oak savannahs. Our study took place on and around one large (approximately 1,850-ha) mesa. Because of past disturbance regimes (grazing, military activity, fire), habitat on the mesa tops is comprised primarily of patchy, often early successional woody vegetation. Vegetation on steep mesa slopes, which prohibit military activity and grazing, consists primarily of dense, oak-juniper woods. The habitat off the mesas consists primarily of open oak savannah and grasslands.

*Prey Availability.*—We measured the relative abundance of small mammals and birds at two study areas located at opposite ends of the mesa and that encompassed approximately equal proportions of mesa, slope, and savannah habitats. We trapped small mammals over three-week periods in early spring and again in late fall in 2005 through 2007. Trapping was restricted to these times to avoid biases in abundance or mortality that can be caused by red fire ants (*Solenopsis invicta*; Masser and Grant, 1986; Gettinger, 1990). These ants are extremely abundant at Fort Hood and are inactive only during cooler weather. We created trapping grids that consisted of transects 15 m apart along which traps were placed every 15 m, for a total of 504 traps. Grids included an approximately equal number of traps on mesa, slope, and savannah sites. We used Sherman live traps (H. P. Sherman Co., Tallahassee, Florida) baited with black oil sunflower seeds. Traps were baited at sunset and then checked at sunrise the following morning. Traps were open

for three consecutive nights for a total of 1,512 trap nights each trapping session. All small mammals were identified to species, and new captures were marked by clipping a small area of fur from the dorsal surface near the tail, which allowed us to differentiate new captures from previously captured individuals. Fur samples from each species were retained as a reference collection used for identification of small mammal hairs in fecal samples.

To determine the species of mammals snakes were eating and the proportion of bird and mammalian prey in the snakes' diet during the bird-breeding season, we collected fecal samples from snakes that defecated while in captivity (primarily when transmitters were implanted; see below). Samples were first classified as containing mammalian, avian, or reptilian prey based on evidence of fur, egg shells, feathers, or bone fragments, using methods similar to Weatherhead et al. (2003). We then used hair impressions on polyvinyl acetate to identify species of mammalian prey (Williamson, 1951).

We conducted avian point counts from April through July to correspond with the bird nesting season. Points were placed every 100–150 m with approximately equal numbers in each of the three habitat types for a total of 65 points. Bird species, mode of detection (song, call, visual, or fly over), estimated distance, and direction were recorded for all detections. Only detections less than 50 m from the point were used in analysis. Point counts are a commonly used technique for estimating bird abundance, although many biases have been acknowledged (Ralph et al., 1995; Rosenstock et al., 2002). Because we were primarily interested in relative abundance among habitat types, we attempted to minimize biases by covering a similar number of points in each habitat daily and by using the same observer across all habitats. We assume here that number of bird detections would provide an index of the number of active nests (DeSante, 1986; Jones et al., 2000).

*Snake Habitat Use.*—Snakes were caught opportunistically by hand throughout the field season. Snakes for which transmitters weighed <3% total body mass had a radio transmitter surgically implanted and were then released at their capture locations. Transmitters were implanted using Blouin-Demers and Weatherhead's (2001a) modification of Reinert and Cundall's (1982) method. Transmitters weighed 9 g or 13 g with batteries lasting 12 months and 24 months, respectively (Model SI-2T, Holohil Systems Incorporated, Ontario). Snakes were relocated approximately every 48 h, and date, location (UTM coordinates), and behavior (basking/resting, traveling, or concealed) were

recorded. Snakes that were traveling were not included in the microhabitat analysis because these locations may not represent preferred habitats.

We used color infrared aerial photos (0.35 m accuracy) from February 2004 to quantify habitat at the study area and home-range scale. Home ranges were determined using minimum convex polygon and 95% kernel analysis in Hawth's analysis tools (Beyer, 2004). As suggested by Row and Blouin-Demers (2006b), we manipulated the kernel smoothing factor until the 95% kernel area approximately equaled the minimum convex polygon area. We defined our study site as the minimum convex polygon that encompassed all snake locations. We digitized habitat boundaries to determine the proportion of each habitat type within the study site and within each snake's kernel home range.

To determine microhabitat selection, we measured a variety of features at every other snake location. Previous work examining snake-selected and random sites with this ratsnake population has found that snakes prefer sites with bigger trees, closer to cover objects, more leaf litter, less bare ground, less grass cover, and closer to edges (Sperry et al., 2009). Here, we are interested only in how patterns of habitat use vary seasonally; hence, our analyses are restricted to seasonal comparisons of snake-selected sites. The microhabitat variables (Table 1) were chosen because they are important for ratsnakes in other parts of their range (Blouin-Demers and Weatherhead, 2001; Carfagno and Weatherhead, 2006). Ground cover and canopy height were estimated using a sighting tube with a crosswire at one end, similar to Winkworth and Goodall's (1962) apparatus. For ground cover, we aimed the sighting tube at 50 random locations within a 2-m radius and recorded the type of substrate in the crosshairs. These values were multiplied by 2 to estimate percent cover of each substrate type. Canopy cover was similarly estimated as the number of canopy "hits" recorded out of 20 random sightings at an angle >45° from horizontal. Canopy and nest height were estimated using a clinometer. Canopy included any tree vegetation layer >2 m in height. If a snake was within woody vegetation, distance to edge was measured as the distance to the nearest canopy break >3 m in diameter. If the location was in grassland, distance to edge was measured as the distance to the nearest clump of woody vegetation.

*Statistical Analysis.*—We compared small mammal capture rates and avian point counts among habitats using ANOVA. Small mammal capture rates were determined as the number of new captures per 100 trap nights per study plot.

TABLE 1. Habitat variables used to compare active season and winter snake-selected sites at Fort Hood, Texas, 2004–2007.

Variable	Variable description
HCAN	Height (m) of canopy
CANCLO	Canopy closure (%)
DCOVER	Distance (m) to nearest rock ( $\geq 20$ -cm length) or log ( $\geq 7.5$ -cm diameter) in 30-m radius
DOVER	Distance (m) to nearest overstory tree ( $\geq 7.5$ -cm dbh) in 30-m radius
DBHOVER	Dbh (cm) of nearest overstory tree
DUNDER	Distance (m) to nearest understory tree ( $\leq 7.5$ -cm dbh, $\geq 2$ m height) in 30-m radius
DBHUNDER	Dbh (cm) of nearest understory tree
TREES	Number of trees ( $\geq 7.5$ -cm dbh) in 10-m radius
SNAGS	Number of snags ( $\geq 7.5$ -cm dbh) in 10-m radius
NUNDER	Number of understory trees ( $\leq 7.5$ -cm dbh) in 5-m radius
LITTER	Litter depth (cm) at 4 directions in 1-m radius
%GRASS	Coverage (%) of grass in 2-m radius
%BARE	Coverage (%) of bare ground in 2-m radius
%WOOD	Coverage (%) of woody debris in 2-m radius
%ROCK	Coverage (%) of rock in 2-m radius
DEDGE	Distance (m) to nearest edge

Avian abundance was determined as the average number of detections per point per study plot.

We examined snake habitat selection at three spatial scales. First, we determined whether the habitat composition within each snake's home range differed from habitat composition within the total study area. Next, we determined whether snake locations within their home ranges were distributed among the habitat types in proportion to the amount of each habitat in their home range. Finally, we determined whether snakes exhibited seasonal shifts in selection of features within habitats by comparing microhabitat variables between winter and active season snake-selected sites. We used compositional analysis (Johnson, 1980; Aebischer et al., 1993) and the resource selection program (F. Leban, Resource Selection for Windows, vers. 1.00, 1999, University of Idaho, Moscow, Idaho) to examine habitat selection at the study area and home-range scale. We examined habitat selection separately by sex and by season, with the latter divided into the bird-breeding season (April to July), the snake active season (April to November), and winter (December to March). We used MANOVA to analyze snake-selected microhabitat variables between the active snake season and winter season. We then used ANOVA to determine individual variables that differed between active and winter season sites. For the microhabitat analysis with all habitats combined, we analyzed data with all snake locations pooled and also ran a separate analysis using mean values for individual snakes. The pooled analysis allows inclusion of individual variation, whereas the analysis using individual means allows us to assess patterns without pseudo-

replication that could potentially affect the pooled analysis. For the pooled analysis, no individual snake accounted for more than 10% of total locations. All means are expressed  $\pm 1$  SE.

## RESULTS

*Prey Availability.*—We caught a total of 416 small mammals during our spring trapping and 105 during fall trapping. Over 88% (460 of 521) of captures were *Peromyscus* spp. (either *Peromyscus attwateri* or *Peromyscus pectoralis*). Of the remaining captures, 4% were northern pygmy mice (*Baiomys taylori*), 4% eastern wood rat (*Neotoma floridana*), 2% fulvous harvest mouse (*Reithrodontomys fulvescens*), and 2% hispid cotton rats (*Sigmodon hispidus*). In all years, spring capture rates were lowest on the savannahs, followed by mesas, with the most captures on slopes, although not all were statistically significant (2005,  $F_{2,3} = 6.91$ ,  $P = 0.08$ ; 2006,  $F_{2,3} = 12.02$ ,  $P = 0.02$ ; 2007,  $F_{2,3} = 4.55$ ,  $P = 0.09$ ; Fig. 1). Pairwise Tukey-Kramer analyses indicate that only 2006 savannah differed significantly from other habitats for any year with savannahs having fewer captures than mesas or slopes. Capture rates were greatly reduced during fall trapping sessions, and although not statistically significant, trends were similar with capture rates lowest in savannahs, followed by mesas and then slopes ( $1.33 \pm 0.37$ ,  $2.44 \pm 0.73$ ,  $3.49 \pm 0.83$ , respectively;  $F_{2,15} = 2.61$ ,  $P = 0.11$ ).

By individual species, *Peromyscus* spp. showed trends similar to the overall analysis with 4% of captures in savannahs, 49% on slopes, and 47% on mesas. Northern pygmy mice and hispid cotton rats were captured more

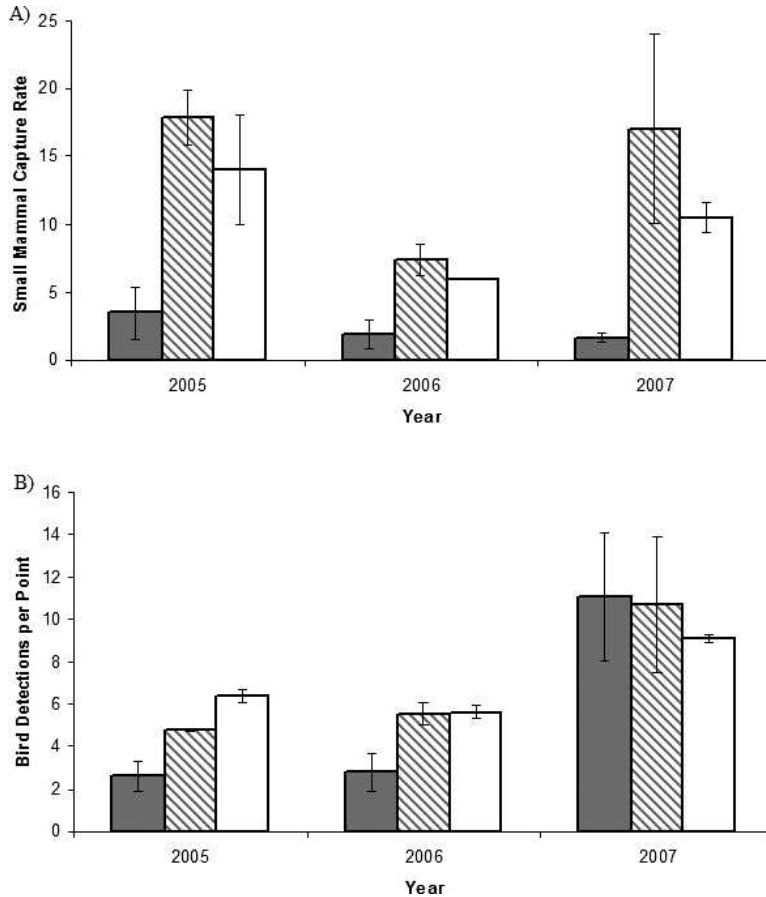


FIG. 1. (A) Small mammal capture rates (per 100 trap nights) by habitat type and year at Fort Hood, Texas, in spring 2005–2007. (B) Number of birds detected per point count location by habitat type and year at Fort Hood, Texas, 2005–2007. Grey bars indicate savannah, dashed bars indicate slopes and white bars indicate mesa. Error bars represent  $\pm 1$  SE.

often in savannahs (65% and 70% of captures, respectively), followed by slopes (20% and 20%) and mesas (15% and 10%). Eastern wood rats were captured most frequently on the slopes (61% of captures) with similar capture frequency in savannahs (22%) and mesas (17%). Fulvous harvest mice were captured in similar numbers across savannahs, slopes, and mesas (25%, 38%, and 38% of captures, respectively).

In the point counts we detected a total of 42 bird species in 2005, 38 in 2006, and 46 in 2007. The most common bird species detected in all years were northern cardinals (*Cardinalis cardinalis*), white-eyed vireos (*Vireo griseus*), blue-grey gnatcatchers (*Poliophtila caerulea*), and painted buntings (*Passerina ciris*). We detected fewer birds in savannahs in 2005 and 2006 ( $F_{2,3} = 17.77$ ,  $P = 0.02$  and  $F_{2,3} = 6.98$ ,  $P = 0.07$ , respectively; Fig. 1), but similar numbers across habitats in 2007 ( $F_{2,3} = 0.17$ ,  $P = 0.85$ ). Tukey-Kramer tests indicate that savannahs and mesas

differed significantly in number of detections only in 2005. In addition to having the highest overall abundance of birds, mesas also had the greatest species richness compared to the slopes and savannahs in 2005 and 2006 (2005 = 33, 24, and 17 species, respectively; 2006 = 30, 28, and 16 species, respectively). In 2007, there were similar numbers of species across all habitats (31, 28, and 34 species, respectively). Average number of detections per point did not differ by month ( $F_{3,8} = 0.68$ ,  $P = 0.59$ ).

We analyzed 21 fecal samples for determination of snake prey items. One was from 2004, two from 2005, two from 2006, and 16 from 2007. Most samples (15 of 21) were from May, with the rest from April, June, and August. Although most samples were collected during the peak bird-breeding season, only five (24%) contained evidence of avian prey. Most (67%) of the samples contained mammalian prey and two contained evidence of reptilian prey in-



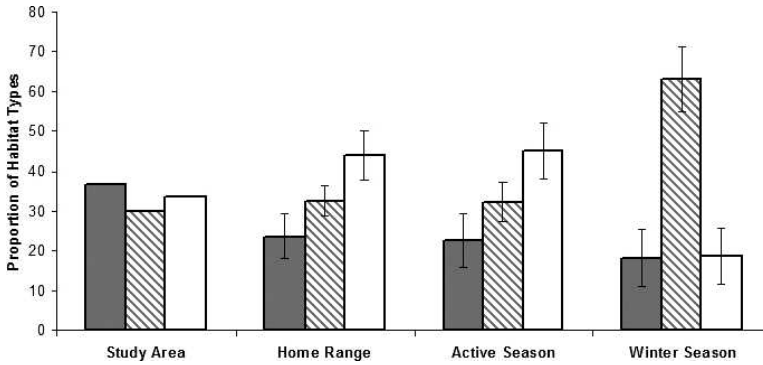


FIG. 2. Proportion of habitat types available within the entire study area, mean ( $\pm$  SE) proportion within Texas Ratsnake kernel home ranges, mean ( $\pm$  SE) proportion within home ranges used by ratsnakes during the active season (April to November), and during winter on Fort Hood, Texas, 2004–2007. Grey bars indicate savannah, dashed bars indicate slopes, and white bars indicate mesa.

cluding one partially digested lizard skeleton. Of the 14 samples with mammalian prey, two were identified as northern pygmy mice, three as hispid cotton rats, four as eastern wood rats, and five as *Peromyscus* spp. Combining these results with the trapping data, slopes and mesas had the highest abundance of the mammal species most commonly found in the snakes' diet.

**Snake Habitat Use.**—We tracked 27 snakes between 2004 and 2007, resulting in 4,100 snake relocations. The range of locations per individual varied from 19–351 with a mean of 151.9. Home-range size based on locations throughout the year and determined by kernel analysis, varied from 1.69–179.91 ha with a mean of 35.12 ha. Habitat composition of home ranges differed from the habitat in the overall study area ( $\chi^2 = 21.12$ ,  $P \leq 0.001$ ; Fig. 2), with slopes most preferred and savannahs least preferred. Snakes preferred slope habitat over both savannah ( $t = 3.75$ ,  $P \leq 0.001$ ) and mesa ( $t = 2.01$ ,  $P = 0.05$ ) habitats. Preference for mesa habitats over savannah habitats was not significant ( $t = 0.98$ ,  $P = 0.33$ ). Preference was similar when males

and female snakes were analyzed separately ( $N = 16$ ,  $\chi^2 = 8.09$ ,  $P < 0.05$  and  $N = 11$ ,  $\chi^2 = 16.16$ ,  $P < 0.001$ , respectively). The rank order selection presented here differs slightly from the pattern shown in Figure 2 because the figure represents the mean habitat use of all snakes and does not reflect individual habitat use. Four individuals had very high proportions (>76%) of mesa habitat in their home range which skewed the overall mean.

Given that prey (mammals and birds) were most abundant on slopes and mesas, we predicted that snakes would preferentially use these habitats within their home ranges during the time of year the snakes were active. However, snakes used habitats in proportion to their availability within their home ranges from April through November ( $\chi^2 = 0.74$ ,  $P = 0.69$ , Fig. 2). This was true for both male ( $\chi^2 = 2.69$ ,  $P = 0.26$ ) and female snakes ( $\chi^2 = 4.26$ ,  $P = 0.12$ ). Similarly, during the avian breeding season (April through July) and following the avian breeding season (July through November) the snakes used habitat within their home ranges in proportion to its availability ( $\chi^2 =$

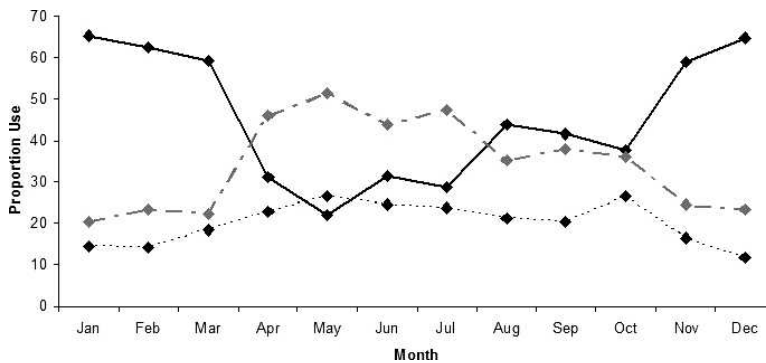


FIG. 3. Mean monthly proportion of habitat types used by Texas Ratsnakes at Fort Hood, Texas, 2004–2007. Dotted line indicates savannah; solid line indicates slopes; dashed line indicates mesa.

1.59,  $P = 0.45$  and  $\chi^2 = 2.58$ ,  $P = 0.28$ , respectively; Fig. 2), suggesting that snakes did not shift habitats to target bird nests. Male ( $\chi^2 = 1.83$ ,  $P = 0.40$ ) and female snakes ( $\chi^2 = 4.57$ ,  $P = 0.10$ ) showed similar results to the overall analysis. Not apparent from these collective results is the extensive variation in habitat use that occurred among individual ratsnakes. Individual snake use of savannah habitat varied from 0–100% of locations, with 18% of snakes using savannah habitat predominantly (>50% of locations). Use of slope habitat also varied from 0–100% of locations, with 30% of snakes using slope habitat predominantly. Use of mesa habitat varied from 0–98% of locations, with 52% of snakes using mesa habitat predominantly. Thirty-three percent of snakes were never found in savannah habitat, and 26% were never found in mesa habitat, but only one snake (4%) did not use slope habitat.

Only 20 snakes were included in the winter analysis because four snakes died during the active season. During the winter the snakes did use habitat within their home ranges nonrandomly, with a preference for slopes and avoidance of savannahs ( $\chi^2 = 6.99$ ,  $P = 0.05$ , Figs. 2 and 3). This result was caused by the strong preference of slope over savannah habitat ( $t = 2.81$ ,  $P = 0.01$ ). Slope was also preferred over mesa habitat ( $t = 1.30$ ,  $P = 0.21$ ) and mesa habitat over savannah habitat ( $t = 0.21$ ,  $P = 0.24$ ), although these preferences were not significant. Preference for slopes during winter was displayed by both males ( $N = 14$ ,  $\chi^2 = 9.23$ ,  $P \leq 0.05$ ) and females ( $N = 6$ ,  $\chi^2 = 5.21$ ,  $P = 0.07$ ).

The shift in habitat preference between the active season and winter could reflect a shift in microhabitat preference. We predicted that during winter the snakes should prefer locations that facilitate thermoregulation (i.e., near edges) or that provide greater protection (i.e., more cover). Because the snakes move relatively little during the winter we had data for only 60 winter locations (compared to 379 active-season locations). Therefore, we limited our analysis of active season versus winter microhabitat to locations in all three macrohabitats combined. Winter sites differed from active season sites (Wilk's  $\lambda = 0.93$ ,  $F_{16,422} = 2.04$ ,  $P = 0.01$ ), with winter sites in areas with higher canopy ( $7.45 \pm 0.33$  and  $6.49 \pm 0.14$ , respectively;  $F_{1,437} = 6.23$ ,  $P = 0.01$ ), closer to understory trees ( $2.29 \pm 0.46$  and  $1.57 \pm 0.14$ , respectively;  $F_{1,437} = 10.98$ ,  $P \leq 0.01$ ), and with more rock ground cover ( $17.12 \pm 2.71$  and  $10.62 \pm 0.81$ , respectively;  $F_{1,437} = 6.70$ ,  $P = 0.01$ ). Analysis using individual snake means shows a similar, although not statistically significant, trend (Wilk's  $\lambda = 0.38$ ,  $F_{16,16} = 1.63$ ,  $P = 0.17$ ), with winter sites in areas

with more rock ground cover ( $21.34 \pm 4.84$  and  $10.43 \pm 1.52$ , respectively;  $F_{1,31} = 5.87$ ,  $P = 0.02$ ) and smaller diameter of nearest over story tree ( $17.22 \pm 1.75$  and  $22.17 \pm 1.20$ , respectively;  $F_{1,31} = 5.54$ ,  $P = 0.03$ ) compared to active season sites, consistent with what would be expected in slope habitats with high density of smaller trees and rock cover. We found no difference in proximity to edges between winter and the active season with all habitats combined ( $12.63 \pm 1.82$  and  $10.16 \pm 0.75$ , respectively;  $F_{1,437} = 1.36$ ,  $P = 0.24$ ), indicating that the shift in microhabitat use does not appear to be related to thermoregulation.

#### DISCUSSION

Texas Ratsnakes exhibited habitat selection at three spatial scales. At the landscape scale, ratsnakes selected home ranges that included more area of wooded slope and less savannah than expected based on availability within the study area. Within home ranges, snakes used habitats in proportion to their availability during the active season but exhibited preference for slope habitat in winter months when snakes were inactive. At the smallest spatial scale, snakes showed a seasonal shift, preferring sites with more cover in winter and more open sites during the active season.

We found limited support for the hypothesis that snakes select habitat on the basis of prey availability. Overall prey abundance (small mammals and birds combined) was highest on slopes and mesas, and these habitats were included disproportionately in snakes' home ranges. Within their home ranges, however, the snakes did not use slope and mesa habitat selectively during the active season (i.e., when the snakes were feeding). These results could be interpreted as indicating that snakes are only selective at the landscape scale and not within their home ranges. However, during the winter the snakes did use their home-range habitat selectively, suggesting that they could have been selective during the active season had it been advantageous for them to do so.

There are several possible explanations for the snakes not selectively using the habitats with the most prey within their home ranges. First because these snakes are generalist predators, they may be able to find prey in all the habitats. Second, we measured prey abundance rather than availability. It is possible that snakes use savannahs, despite their lower prey abundance, because prey are more predictably located in the small clumps of wooded vegetation, which might effectively make prey more available than simple abundance measures indicate. Third, our focus on means may be

inappropriate. It is possible that, although ratsnakes are collectively habitat and prey generalists, individually they might specialize on a particular habitat, prey type or prey species. Individual diet specialization has been shown in a wide variety of taxa (review in Bolnick et al., 2003) and could result in variation in habitat use. Texas Ratsnakes varied widely in habitat use during the active season with 18% of snakes using predominantly savannah habitat, 30% of snakes predominantly slope habitats and 52% of snakes predominantly mesa habitat. Each habitat had a unique suite of prey that may lead to individual foraging behavior and diet specialization within habitat types (Bolnick et al., 2003). Determining whether there is individual diet specialization in ratsnakes would require collecting a series of diet samples from the same individuals.

We did not find evidence for seasonal shifts in snake habitat use during the avian breeding season. When birds were breeding, the snakes used their habitat in proportion to availability, just as they did during the rest of the active season. Results of our diet analysis were consistent with previous studies (Fitch, 1963; Weatherhead et al., 2003; Carfagno et al., 2006) in showing that even when birds were nesting, mammals still comprised the majority of ratsnakes' diets. Combined with the lack of habitat selectivity by the snakes when birds were nesting, it seems that overall ratsnake predation on bird nests is largely opportunistic. If so, it is impressive that ratsnakes can be such effective nest predators, accounting for 27–44% of videotaped predation of two endangered species at our study location (Stake and Cimprich, 2003; Stake et al., 2004). As discussed above, however, a plausible alternative is that some individual ratsnakes specialize on birds, but because the majority of ratsnakes prey on mammals, the collective pattern gives the appearance of opportunistic avian nest predation.

Ratsnakes' preference for slopes in the inactive season is probably a response to the increased canopy and rocky structures on slopes compared to mesa and savannah habitats. Studies of other snake species have found that, compared to active season, snakes overwinter in more heavily forested areas (Brito, 2003; Harvey and Weatherhead, 2006a), most likely because of the availability of suitable retreat sites and possibly because of moderated temperatures. Active snakes are known to prefer certain rocks as retreat sites based on the thermal characteristics of the rocks (Huey et al., 1989; Webb and Shine, 1998). In our study area, slopes provide snakes with a wide variety of rock sizes to use as winter retreat sites. Because the snakes used sites that were associ-

ated with closed canopy trees rather than forest edges, it seems likely that these sites were chosen more for their protective than their thermal value. Anecdotal evidence suggests that suitable winter retreat sites may be limited in availability or distribution. For example, three snakes that had only minor home-range overlap during the active season (one spent the majority of the active season in savannah habitat and the other two in mesa habitat) all used winter retreat sites in the same small area of slope that had extensive rock outcroppings. Winter habitat may not be as critical for ratsnakes in Texas as it is likely to be for ratsnakes at higher latitudes. Nonetheless, based on when Texas Ratsnakes were most selective, it appears that even at this latitude winter habitat is important.

Understanding habitat selection is necessary for determining priorities for habitat conservation, particularly because habitat loss is thought to be responsible for population declines of many species (e.g., Alford and Richards, 1999; Gibbons et al., 2000; Schmiegelow and Monkonen, 2002; Becker et al., 2007). Habitat conservation efforts depend on identifying critical habitats for species and most snake research to date has focused on only one spatial scale and only during the active season. Our results demonstrate that habitat preference can vary across both spatial and seasonal scales. Had we limited our analyses to only one spatial scale and just to the active season, we would have obtained a less complete picture of habitat selection. For example, when assessing the role of prey availability, results at the landscape scale suggest prey availability may be important in habitat selection, whereas patterns of habitat use within home ranges suggest the opposite. Microhabitat selection appears to be common in snakes (Row and Blouin-Demers, 2006a; Carfagno and Weatherhead, 2006; Harvey and Weatherhead, 2006a), most likely because of thermoregulatory requirements (Huey 1991). However, the basis for macrohabitat preference appears to be species-specific, with mechanisms including thermoregulation (Row and Blouin-Demers, 2006a), prey abundance (Madsen and Shine, 1996; Heard et al., 2004), and water proximity (Brito, 2003). Differences among species in habitat use likely depend on the species' ecology, available habitat types and prey availability. Determining general patterns of multiscale habitat use, and the mechanisms behind habitat preference, require similar studies of other species in a range of locations.

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