

SUMMER RESTING AND DEN SITE SELECTION BY EASTERN SPOTTED SKUNKS (*SPILOGALE PUTORIUS*) IN ARKANSAS

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Denning and resting site use by radiocollared eastern spotted skunks (*Spilogale putorius*) in the Ouachita Mountains of western Arkansas was investigated from May through August 2005 and 2006. We identified and characterized microhabitat and landscape characteristics of 127 resting and den sites. Sites were located in burrows excavated by other mammal species (48%), in decayed or burned root systems (22%), in rocky outcrops (14%), in eastern woodrat (*Neotoma floridana*) nests (9%), or in ground-level tree or log cavities (7%). Reuse of sites by the same individual was common (32.3%), but use of the same site by different individuals was rare, as was communal use of sites (<1.0% each). Contrasting used and putatively available dens and resting sites, we found that sites were selected based primarily on increased vegetative cover, which supports hypotheses that thermal regulation and predator avoidance may underlie den and resting site selection. Higher rock and vine densities, younger pine forest stands, older hardwood stands, steeper slope, and smaller site entrance also positively influenced resting and den site selection. These findings suggest that eastern spotted skunks select structurally complex sites, likely to enhance protection from predators. Eastern spotted skunks may thus be vulnerable to habitat alterations that reduce this structural complexity.

Key words: carnivore, den site, eastern spotted skunk, habitat selection, Ouachita Mountains, resting site, *Spilogale putorius*

Sites used for denning and resting are important features of carnivore home ranges, and site availability can potentially limit the distribution and abundance of populations (Doncaster and Woodroffe 1993; Larivière and Messier 1998). Although den sites used for parturition and care of dependent offspring are occupied for extended periods, and rest sites are used for a brief interval, both den and rest site selection may be among the most important choices made by small forest carnivores (Zielinski et al. 2004). These sites must provide thermoregulatory benefits and protection from weather, as well as protection from predators (Endres and Smith 1993; Frafjord 2003).

Research on carnivores has long sought to understand the mechanisms that influence resource selection and several hypotheses have been proposed. Depending on their size and habitat requirements, carnivores can be either positively or negatively affected by habitat edges (Crooks 2002; Revilla

et al. 2001; Woodroffe and Ginsberg 1998). Competition between carnivores can reduce the population size and distribution of the smaller of the interacting species. Thus, predation risk for many carnivore species is believed to pressure individuals to select habitat that reduces their susceptibility to larger predators (Buskirk and Powell 1994; Caro and Stoner 2003; Creel et al. 2001). Additionally, the availability and density of prey species influences carnivore populations and behavior (Fuller and Sievert 2001; Litvaitis et al. 1986). Finally, the amount and type of thermal cover available can influence resource selection by carnivores (King and Powell 2007; Zielinski et al. 2004).

We examined the microhabitat characteristics of resting and den sites selected by radiocollared eastern spotted skunks (*Spilogale putorius*) in the Ouachita Mountains in western Arkansas in relation to the hypotheses identified above. Although currently localized in distribution, the eastern spotted skunk was once abundant throughout the central and southeastern United States (Gompper and Hackett 2005; Kinlaw 1995). Precipitous population declines have occurred beginning in the 1940s, and the eastern spotted skunk is now recognized as a species of conservation concern throughout much of its

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geographic range, including Arkansas (Gompper and Hackett 2005; Sasse and Gompper 2006). Although habitat alteration is one possible explanation for the range-wide decline of the species (Choate et al. 1974; Gompper and Hackett 2005; McCullough 1983), a paucity of studies have been conducted to elucidate habitat requirements of the eastern spotted skunk.

Resting and denning ecology of the eastern spotted skunk is virtually unknown. Crabb (1948) simply identified the need for the exclusion of light, protection against weather, and protection against predators. Polder (1968) reported extensive use of Franklin's ground squirrel (*Spermophilus franklinii*) and plains pocket gopher (*Geomys bursarius*) burrows as resting sites. McCullough and Fritzell (1984) reported hollow logs and rocky outcroppings as primary resting sites. However, none of these studies quantitatively addressed selection of resting or den sites. Studies of western spotted skunk (*S. gracilis*) denning ecology suggest selection for ground sites with vegetative cover (Carroll 2000; Crooks 1994; Doty and Dowler 2006), but it is unknown if eastern spotted skunks select similar sites. To compare support for edge effect, predator avoidance, prey availability, and thermal regulation hypotheses that could underlie den and rest site selection, we identified used resting and den sites and contrasted these to nearby unused but putatively available sites.

MATERIALS AND METHODS

Study site.—This study was conducted in the 96,755-ha Poteau Ranger District, which is part of the 690,000-ha Ouachita National Forest in Scott County, Arkansas, United States (34°48'N, 94°21'W). The Ouachita Mountain physiographic region is located in west-central Arkansas and southeastern Oklahoma. Mountain ridges were formed from sedimentary rock formations compressed into great folds. Linear ridges reach maximum elevations of about 790 m and trend east–west. The climate is characterized by warm winters (average 13°C), hot, dry summers (average 32°C), and average annual precipitation of 105 cm. Southern and western aspects and dry sandstone ridges are covered with as much as 40% shortleaf pine (*Pinus echinata*) and 73% of the study site is managed as shortleaf pine stands. Hardwoods (*Quercus* and *Carya*) dominate the rich alluvial soil bottomlands of the valleys and northern aspects of the mountains (Bailey 1980).

The study site has been intensively managed to meet a shortleaf pine–bluestem (*Andropogon* and *Schizachyrium*) restoration objective (United States Department of Agriculture 1996). To provide habitat for a recovered population of federally endangered red-cockaded woodpeckers (*Picoides borealis*), this management program creates an open canopy and herbaceous vegetation in the understory (Bukenhofer and Hedrick 1997; Lochmiller et al. 1994; Masters et al. 1998). Forest restoration and maintenance is accomplished by reducing tree basal areas through commercial and noncommercial thinning of shortleaf pine stands and increasing the use of prescribed fire (Bukenhofer et al. 1994; Bukenhofer and Hedrick 1997). Additionally, the increased shortleaf pine stand rotation age increases the number of shortleaf pine trees infected with

fungal heart rot (*Phellinus pinii*) available for cavity construction by red-cockaded woodpeckers (Bukenhofer and Hedrick 1997; United States Department of Agriculture 1996). Forest management in the Poteau Ranger District also aims to retain streamside management zones within the intensively managed shortleaf pine stand mosaic. Streamside management zones are managed natural hardwood forest stands retained along intermittent and perennial streams (Miller et al. 2004) and account for 87% of the hardwood management stands in the study site.

Capture and handling.—We conducted a telemetry-based study from March 2005 through January 2007. Detailed capture and handling methodology is given in Lesmeister (2007). We captured most eastern spotted skunks between late autumn and early spring when the species is more easily trapped (Hackett et al. 2007), and fitted each individual with a 12-g radiotransmitter before release at the capture site. We followed animal care procedures outlined in University of Missouri Animal Care and Use Protocol 4039 and carried out fieldwork under Arkansas Game and Fish Commission permit 111520042. Procedures met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Radiotelemetry and site characterization.—From May through August 2005 and 2006, we tracked radiocollared eastern spotted skunks to their den or resting sites approximately 3 times per week in daytime hours. We used a handheld receiver and 3-element Yagi antenna for tracking. For each individual, approximately 1 den or resting site per week was selected for microhabitat characterization. Repeated site use and localized movement of females indicated that a maternal den had been located. We attempted to identify equal numbers of used sites for each individual by not characterizing a 2nd used site for an individual until sites used by all study animals being tracked during the study period had already been characterized. For each used site, a nearby, available, but unused and putatively appropriate site also was located and paired with the used site for comparison. We selected the available unused site by searching, ≥ 50 and ≤ 300 m from the used site, along a randomly selected azimuth for a burrow, hollow log, hollow tree, rocky outcrop, or woodrat nest that could possibly be used as a den or resting site by eastern spotted skunks. A site was judged as reasonable by having an entrance size of at least 10×10 cm, a cavity large enough for spotted skunks, and meeting the 3 criteria described by Crabb (1948). Upon location of a putatively available site, we measured habitat characteristics as for the used site.

Within 1 week of the den or resting site being vacated, we used a combination of variable radius plot and transect methods to collect microhabitat data. For each used and available site, we established a 25×25 -m true-north grid with 9 nodes. We centered the grid at the site entrance and established four 25-m node-to-node transects. In cardinal directions from the entrance, we centered 2 transects, and 2 others extended between the outer eastern and western nodes. Using the 9 nodes, we identified 4 quadrants. We classified the substrate for each site (Burrows = animal-dug sites in soil substrates; Root system = burned or decayed root systems; Rocky outcrop = cavities among rocky outcrops; Hollow log/tree = cavity of

TABLE 1.—Codes and descriptions of measured parameters used in models comparing used eastern spotted skunk (*Spilogale putorius*) den and resting sites to nearby unused and putatively available sites in the Ouachita National Forest, Arkansas, 2005–2006.

Variable	Description
Age	Stand age in years based on United States Forest Service records
BA	Basal area measured in square feet (ft ²) from site entrance
Vine	Estimated number of vines in randomly selected quadrant
Ground	Mean percentage of ground cover estimated at each node of characterized site
Ent	Site entrance size measured in square centimeters (cm ²)
Rock	Number of rocks ≥ 10 cm diameter counted in randomly selected quadrant
Mgt_##	Management type of stand taken from United States Forest Service records (reference is management type mgt_slp (Shortleaf Pine); other types for comparison: mgt_other (all other types), mgt_hw (Hardwood))
Rgh_##	Classification of the number of growing seasons between fire and use taken from United States Forest Service records (reference is rgh_3 (rough year of 3 or less); other rough year classifications for comparison: rgh_3_6 (rough year greater than 3 and less than 7), rgh_7_10 (rough year greater than 6 and less than 11), and rgh_11 (rough year greater than 10))
CWD	Number of coarse woody debris ≥ 10 cm diameter counted in the 4 transects of site
Snag	Number of snags counted in randomly selected quadrant
Road	Distance in meters to nearest road calculated in ArcGIS
Edge	Distance in meters to nearest stand edge calculated in ArcGIS
Size	Size of stand in hectares calculated in ArcGIS
Canopy	Mean percent canopy cover for all 9 nodes
Slope	Degree (°) slope measured at characterized site
Sine	Sine of the orientation of the site entrance, using an orientation of 45° as the reference point
Water	Distance in meters to nearest water calculated in ArcGIS
Age_other	Interaction term between stand age and all other management types
Age_hw	Interaction term between stand age and hardwood management stands

hollow logs or trees; Woodrat nest = eastern woodrat [*Neotoma floridana*] nests). We documented entrance orientation, entrance size, basal area, and slope within the site transect grid. At each node we used a densiometer to calculate percent canopy cover and estimated percent ground cover for a 1-m² plot. We averaged canopy and ground cover for the site. Coarse woody debris (≥ 10 cm diameter) was counted along transects. One of the 4 quadrants was randomly selected and the following data collected: rocks (≥ 10 cm) were counted and documented, snags (≥ 1.5 m tall) were quantified, and the numbers of vines and briars were estimated.

We collected additional landscape-scale data using United States Forest Service records and geographic information system analysis. From United States Forest Service records, we identified the size of the stand for each site, ages of the stands since last timber harvest, time since the last burn, and the silviculture management for the stand (shortleaf pine, hardwood, and “other”), in which the site was located. Stands categorized as “other” were loblolly pine stands and private property. We used the ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California) near feature to determine distance to the nearest road, stand edge, and water.

A priori model development.—We used an information-theoretic approach to develop a priori hypotheses regarding the den and resting site selection by eastern spotted skunks (Burnham and Anderson 2002). Based on the carnivore ecology literature and preliminary field observations, we formulated 4 hypotheses that may explain eastern spotted skunk den and resting site selection: edge effects, predator avoidance, prey availability, and thermal regulation. Using the empirical data collected for each site (Table 1), we developed a set of a priori models for each hypothesis (Table 2).

Incorporating the covariates distance to road, stand edge, and stand size, we developed 4 a priori models that represent our edge effects hypothesis. We proposed 5 a priori models associated with the predator avoidance hypothesis and selected vine numbers and tree basal area, stand age, entrance size, and percent ground cover as our surrogate variables representing the hypothesis. To determine support for the prey availability hypothesis, we developed 5 a priori models, using stand management, rough year, and number of rocks, woody debris, and snags. Last, we developed 5 a priori models representing the thermal regulation hypothesis. The covariates in these models included percent canopy cover, slope, distance to water, and orientation of site entrance (Table 2).

Statistical analyses.—We compared differences between resting site reuse by males and females and individual resource variables using the PROC MIXED procedure in SAS 9.1 (SAS Institute Inc., Cary, North Carolina), by treating individual eastern spotted skunks as random effects. Additionally, we used PROC MIXED to compare characteristics and the amount of reuse between dens and resting sites. We used the REPEATED statement to accommodate the repeated measures from the same individual and modeled 3 covariance structures, including autoregressive, compound symmetry, and unstructured (Littell et al. 1998). Using Akaike’s information criterion adjusted for small sample sizes (AIC_c) values, we selected the best model for covariance structure, which was the autoregressive covariance structure for each comparison.

We used discrete choice analysis to fit site selection models because of the paired used/available design (Cooper and Millspaugh 1999, 2001). The main benefit of discrete choice analysis is that the researcher can define resource availability separately for each site (Cooper and Millspaugh 1999), which

TABLE 2.—Description and expected direction of a priori models used to evaluate microhabitat effects on eastern spotted skunk (*Spilogale putorius*) den and resting site selection in the Ouachita Mountains, Arkansas. See Table 1 for measured parameter codes and descriptions.

Hypothesis	Model	Model structure	Expected result
Predator avoidance (Pred)			
1. Positive effects of vine numbers	Pred _{vine}	$\beta_0 + \beta_1(\text{vine})$	$\beta_1 > 0$
2. Negative effects of increased stand age and low basal area	Pred _{age + BA}	$\beta_0 + \beta_1(\text{age}) + \beta_2(\text{BA})$	$\beta_1 < 0, \beta_2 > 0$
3. Positive effects of vine numbers and negative effects of increased stand age	Pred _{vine + age}	$\beta_0 + \beta_1(\text{vine}) + \beta_2(\text{age})$	$\beta_1 > 0, \beta_2 < 0$
4. Positive effects of increased vine numbers and basal area and negative effects of stand age	Pred _{vine + BA + age}	$\beta_0 + \beta_1(\text{vine}) + \beta_2(\text{BA}) + \beta_3(\text{age})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 < 0$
5. Positive effects of vine numbers, basal area and ground cover, combined with negative effects of stand age and entrance size	Pred _{vine + BA + ground + ground² + age + ent}	$\beta_0 + \beta_1(\text{vine}) + \beta_2(\text{BA}) + \beta_3(\text{ground}) + \beta_4(\text{ground})^2 + \beta_5(\text{age}) + \beta_6(\text{ent})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0, \beta_4 < 0, \beta_5 < 0, \beta_6 < 0$
Prey availability (Prey)			
6. Positive effects of rock number	Prey _{rock}	$\beta_0 + \beta_1(\text{rock})$	$\beta_1 > 0$
7. Positive effects of rock and course woody debris number	Prey _{rock + CWD}	$\beta_0 + \beta_1(\text{rock}) + \beta_2(\text{CWD})$	$\beta_1 > 0, \beta_2 > 0$
8. Positive effects of rock and course woody debris number, combined with negative effects of rough year	Prey _{rock + CWD + rgh_3_6 + rgh_7_10 + rgh_11}	$\beta_0 + \beta_1(\text{rock}) + \beta_2(\text{CWD}) + \beta_3(\text{rgh}_3_6) + \beta_4(\text{rgh}_7_10) + \beta_5(\text{rgh}_11)$	$\beta_1 > 0, \beta_2 > 0, \beta_3 < 0, \beta_4 < 0, \beta_5 < 0$
9. Negative effects of management type and rough year	Prey _{mgt_other + mgt_hw + rgh_3_6 + rgh_7_10 + rgh_11}	$\beta_0 + \beta_1(\text{mgt_other}) + \beta_2(\text{mgt_hw}) + \beta_3(\text{rgh}_3_6) + \beta_4(\text{rgh}_7_10) + \beta_5(\text{rgh}_11)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0, \beta_4 < 0, \beta_5 < 0$
10. Negative effects of management type and rough year class, combined with positive effects of rock, course woody debris, and snag number	Prey _{mgt_other + mgt_hw + rgh_3_6 + rgh_7_10 + rgh_11 + rock + CWD + snag}	$\beta_0 + \beta_1(\text{mgt_other}) + \beta_2(\text{mgt_hw}) + \beta_3(\text{rgh}_3_6) + \beta_4(\text{rgh}_7_10) + \beta_5(\text{rgh}_11) + \beta_6(\text{rock}) + \beta_7(\text{CWD}) + \beta_8(\text{snag})$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0, \beta_4 < 0, \beta_5 < 0, \beta_6 > 0, \beta_7 > 0, \beta_8 > 0$
Edge effects (Edge)			
11. Positive effects of stand size	Edge _{size}	$\beta_0 + \beta_1(\text{size})$	$\beta_1 > 0$
12. Positive effects of stand size and distance to stand edge	Edge _{size + edge}	$\beta_0 + \beta_1(\text{size}) + \beta_2(\text{edge})$	$\beta_1 > 0, \beta_2 > 0$
13. Positive effects of distance to road and stand edge	Edge _{road + edge}	$\beta_0 + \beta_1(\text{road}) + \beta_2(\text{edge})$	$\beta_1 > 0, \beta_2 > 0$
14. Positive effects of stand size, distance to road, and distance to stand edge	Edge _{size + road + edge}	$\beta_0 + \beta_1(\text{size}) + \beta_2(\text{road}) + \beta_3(\text{edge})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0$
Thermal regulation (Ther)			
15. Negative effects of distance from water	Ther _{water}	$\beta_0 + \beta_1(\text{water})$	$\beta_1 < 0$
16. Positive effects of slope	Ther _{slope}	$\beta_0 + \beta_1(\text{slope})$	$\beta_1 > 0$
17. Positive effects of canopy cover and negative effects of distance from water	Ther _{canopy + water}	$\beta_0 + \beta_1(\text{canopy}) + \beta_2(\text{water})$	$\beta_1 > 0, \beta_2 < 0$
18. Positive effects of slope, combined with negative effects of the sine of the site entrance	Ther _{slope + sine}	$\beta_0 + \beta_1(\text{slope}) + \beta_2(\text{sine})$	$\beta_1 > 0, \beta_2 < 0$
19. Positive effects of canopy cover and slope, combined with negative effects of distance from water and sine of site entrance	Ther _{canopy + slope + water + sine}	$\beta_0 + \beta_1(\text{canopy}) + \beta_2(\text{slope}) + \beta_3(\text{water}) + \beta_4(\text{sine})$	$\beta_1 > 0, \beta_2 > 0, \beta_3 < 0, \beta_4 < 0$

matches our study design. Discrete choice models have the general form:

$$P_J(A) = \frac{\exp(\mathbf{B}'\mathbf{X}_{AJ})}{\sum \exp(\mathbf{B}'\mathbf{X}_{iJ})}$$

where $P_J(A)$ is the probability of individual J choosing resource A rather than any other of the i resources available, \mathbf{X}_{iJ} is

a vector of the attributes of resource i as perceived by individual J , and \mathbf{B} is a vector of estimable parameters that determine each attribute's contribution to utility. We fit discrete choice models using the PROC MDC procedure in SAS 9.1. We used AIC_c values and Akaike weights (w_i) to predict the most-parsimonious model (Burnham and Anderson 2002). The w_i for each model represents the probability of a model being the best approximating model of those evaluated.

We estimated the relative importance of covariates from averaged models by summing the w_i s across all models in the 90% confidence set where the covariate occurred (Burnham and Anderson 2002). We calculated odds ratios and associated confidence interval for all parameter estimates in the 90% confidence set (Hosmer and Lemeshow 2000). The odds ratio is the probability increase of a site being selected for resting or denning for every unit increase in the predictor variable at one site compared to another. We also compared relative support for the various groupings of predator avoidance, prey availability, thermal regulation, and edge effects models.

Because some variables could potentially influence site selection within the context of several hypotheses and to develop a single best model, we also conducted a 2nd-stage analysis to create an AIC_c minimized model for eastern spotted skunk den and resting site selection. We began with a full main-effects model that included all covariates used in stage 1 modeling and 3 interaction terms (stand age \times vine, stand age \times management type, and basal area \times vine). We tested the influence of each covariate by individually removing them and recording changes to AIC_c . Using changes in AIC_c , we removed the least-supported variable (e.g., the one that reduced AIC_c the most when it was removed). We removed covariates until the AIC_c value was minimized. We retained in the final model any main effect involved in a significant interaction regardless of its individual significance (McCullagh and Nelder 1989).

RESULTS

Between March 2005 and March 2006 we captured and radiocollared 23 eastern spotted skunks (11 males and 12 females), of which 13 (7 males and 6 females) survived for a period long enough to be tracked and have sites characterized. We identified and characterized 127 ($n = 68$ male, $n = 59$ female; $n = 115$ resting sites, $n = 12$ dens) inhabited sites and an additional 127 paired unused but putatively available sites. We recorded 174 resting and 195 denning events at characterized sites. The mean number of sites characterized per individual tracked during the summer was 9.69 (± 1.53 SE) with 7.92 (± 0.78 SE) days between site locations. Most used sites ($n = 61$; 48%) were located in burrows. Twenty-eight sites (22%) were located in burned or decayed root systems and 18 (14%) occurred in rocky outcrops. Eleven sites (9%) were located inside eastern woodrat nests and 9 (7%) occurred in the cavity of hollow logs or trees at ground level.

We characterized 68 resting sites used by male eastern spotted skunks and 47 used by females, and observed study animals reusing 25% of resting sites. Males and females did not differ in the amount of resting site reuse ($F = 1.06$, $d.f. = 1, 10$, $P = 0.3274$). Four percent of characterized resting sites were reused by an eastern spotted skunk after the animal used a resting site elsewhere. A larger percentage of the resting sites of males (34%) were located in hardwood stands compared to resting sites of females (15%). Resting sites of males were located in managed stands 20 years older than the stands where the resting sites of females were found (Table 3). Communal

TABLE 3.—Mean (\bar{X}), standard error (SE), autoregressive covariance structure in PROC MIXED F -value, and significance probability for used eastern spotted skunk (*Spilogale putorius*) resting site (male, $n = 68$ versus female, $n = 47$) variable parameters in the Ouachita Mountains, Arkansas. See Table 1 for measured parameter codes and descriptions.

Variable	Male		Female		F -value	Pr > F
	\bar{X}	SE	\bar{X}	SE		
Age (years)	54.25	3.68	34.40	4.34	5.30	0.0419
BA (ft ²)	107.21	5.87	104.47	6.03	0.08	0.7804
Vine	131.03	32.12	83.70	17.84	0.25	0.6302
Ground (%)	46.96	2.26	47.17	3.27	0.16	0.6972
Ent (cm ²)	175.94	16.38	130.74	15.70	0.02	0.8851
Rock	50.50	9.25	45.66	7.71	0.43	0.5275
CWD	6.31	0.73	4.68	0.60	0.30	0.5921
Snag	2.26	0.38	4.38	1.03	1.27	0.2840
Road (m)	417.76	41.82	376.72	36.20	0.81	0.3864
Edge (m)	40.01	5.14	39.09	5.89	0.00	0.9697
Size (ha)	63.28	10.17	31.55	2.17	1.19	0.2985
Canopy (%)	84.26	1.21	79.64	1.74	1.59	0.2335
Slope (°)	5.97	0.69	7.57	0.70	0.15	0.7024
Sine (°)	1.08	0.09	1.08	0.10	0.14	0.7145
Water (m)	142.50	16.64	217.55	20.42	1.67	0.2226

resting was only observed on 1 occasion when an adult male and female were observed together in April 2006 during the breeding period. Additionally, use of the same resting site by different animals on separate occasions also was rare. We observed only 1 such event, where a resting site used in mid-June 2006 by an adult male was used by another adult male in late July 2006.

Of the 127 sites characterized, 12 were den sites used by 5 females. One female was monitored for 2 seasons with 2 maternal den sites per season. The other 4 females each had 2 dens identified and characterized. We observed denning only in burrows, and no communal denning. Den sites were used for a mean of 16.25 (± 2.48 SE) consecutive days, which is greater than the reuse of resting sites ($F = 888.16$, $d.f. = 1, 15$, $P < 0.0001$). No variable differed between dens and resting sites ($F = 0.00$ – 1.17 , $d.f. = 1, 15$, $P > 0.05$ for all tests). Therefore, dens and resting sites were combined for subsequent analyses.

Eastern spotted skunks selected sites in managed stands of shortleaf pine 69% of the time ($n = 88$), which is similar to the 73% availability of this habitat. However, study animals used sites in hardwood stands to a greater extent (28%) than their proportional availability (16%). Used sites were found in areas where the mean growing seasons since last burn was 4.4 (± 0.3 SE) years. Used sites were located in younger stands, and had >2 times as many vines than nearby available sites (Table 4). Compared to available sites, used sites also had greater percent canopy cover, more rocks, and smaller entrances (Table 4).

Discrete choice analyses supported the thermal regulation and predator avoidance hypotheses (Table 5). The most-supported model was the thermal regulation subglobal model Ther_{canopy + slope + water + sine} (Table 5). Model uncertainty existed, however, with 2 other models falling into the 90% confidence set. The next competing models were the predator

TABLE 4.—Mean (\bar{X}) and standard error (SE) for used ($n = 127$) versus available site ($n = 127$) continuous variable parameters used in discrete choice analysis of eastern spotted skunk (*Spilogale putorius*) den and resting site selection in the Ouachita Mountains, Arkansas. See Table 1 for measured parameter codes and descriptions.

Variable	Used		Available	
	\bar{X}	SE	\bar{X}	SE
Age (years)	45.66	2.81	58.35	2.81
BA (ft ²)	106.30	3.92	108.11	4.68
Vine	113.61	18.85	51.65	10.07
Ground (%)	47.38	1.80	48.35	1.87
Ent (cm ²)	163.11	12.29	222.11	13.14
Rock	47.67	5.85	31.53	8.41
CWD	5.61	0.51	6.00	0.50
Snag	3.23	0.51	3.42	0.79
Road (m)	389.63	26.56	362.43	24.51
Edge (m)	39.65	3.62	46.30	4.89
Size (ha)	48.69	5.71	42.22	5.71
Canopy (%)	82.74	0.98	76.34	1.31
Slope (°)	6.53	0.48	5.76	0.35
Sine (°)	1.11	0.06	1.10	0.06
Water (m)	171.10	12.48	195.35	11.61

avoidance subglobal model $Pred_{vine + BA + ground + ground^2 + age + ent}$, and the thermal regulation candidate model $Ther_{canopy + water}$ (Table 5). The edge effects and prey availability models received no support. Based on importance values, the most influential covariates in top a priori models were percent canopy cover, slope, distance to water, estimated number of vines, stand age, and entrance size.

The 2nd stage analysis resulted in a more-supported model than a priori models ($AIC_c = 108.74$ versus 151.44 for a priori models; Table 5). The 8 parameters in the AIC-minimized model were rock, entrance size, slope, canopy cover, vine, stand age, management type, and the interaction between stand age and management type (Table 6). Although 5 of these variables (canopy cover, entrance size, vine, slope, and stand age) were contained in the a priori models, additional parameters, such as an interaction between stand age and management type, management type, and rock were included in the AIC-minimized model. This result indicates that a combination of features associated with different a priori hypotheses was related to den and resting site selection. Thus, although the a priori model fitting allowed us to investigate the relative support among hypotheses, the AIC-minimized

analysis suggests that covariates from multiple hypotheses were important. Increases in the parameters rock, slope, canopy, and vine positively influenced the likelihood of a site being selected (Table 6). Used sites were in younger stands and were more often in shortleaf pine managed stands than other stands. However, an interaction between stand age and management type occurred; radiocollared animals selected hardwood and other stands over shortleaf pine stands as stand age increases. The odds of selecting a hardwood stand over a shortleaf pine stand increased by 1.038 times for each year increase in stand age (Table 6).

DISCUSSION

Eastern spotted skunks appear to be opportunistic in their resting site selection, using multiple available sites within their home ranges and a variety of substrate types. This flexibility in site selection is further supported by the variability in resting site use reported elsewhere (Crabb 1948; McCullough and Fritzell 1984; Polder 1968), and is similar to the variability reported for site selection by western spotted skunks (Carroll 2000; Crooks 1994; Doty and Dowler 2006). Although all den and resting sites provided exclusion of light, shelter from weather, and protection from predators, we observed, as did Polder (1968), greater use of burrows for resting than did other researchers (Crabb 1948; McCullough and Fritzell 1984). Additionally, we observed burrows used only for denning, which may indicate more restricted requirements for denning sites than resting sites. We observed less use of hollow logs than did McCullough and Fritzell (1984) and no use of man-made structures as reported by Crabb (1948), because man-made structures are rare in our study site. Crooks (1994) reported that island spotted skunks (*S. g. amphiala*) excavated all burrows used as dens and resting sites; however, eastern spotted skunks in the Ouachita Mountains occupied burrows excavated by other species. Given large entrance sizes and lack of fresh diggings, we found no evidence of eastern spotted skunks excavating burrows.

Examination of our data on resting and den site use by eastern spotted skunks supports the hypothesis that the species is a solitary carnivore in western Arkansas (see also Lesmeister 2007). Communal resting was rare and communal denning and cooperative young-rearing behavior were not observed. Only 1 observation was made of multiple occupancy of a single site by our study animals, which is in agreement with observations of

TABLE 5.—Ranking of a priori hypothesized models in the 90% confidence set relating habitat covariates to eastern spotted skunk (*Spilogale putorius*) den and resting site selection in the Ouachita Mountains, Arkansas. Columns include the number of variables (K), Akaike's information criterion adjusted for small sample sizes (AIC_c), distance from lowest AIC_c (ΔAIC_c), and Akaike model weight (w_i). See Table 1 for measured parameter codes and descriptions.

Hypothesis	Model	K	AIC_c	ΔAIC_c	w_i
15. Thermal ^a	$Ther_{canopy + slope + water + sine}$	5	151.446	0	0.464
4. Predator avoidance ^a	$Pred_{vine + BA + ground + ground^2 + age + ent}$	7	152.695	1.248	0.248
16. Thermal	$Ther_{canopy + water}$	3	152.777	1.331	0.238

^a Subglobal model.

low home-range overlap (Lesmeister 2007). We also observed moderate reuse of individual resting sites by either sex, which is similar to that reported for other mephitids and mustelids (Larivière and Messier 1997; Norbury et al. 1998; Zielinski et al. 2004). The number of different sites used by individuals may indicate that eastern spotted skunks do not restrict use to a few central locations, but instead opportunistically use multiple resting structures distributed throughout their home ranges. Additionally, the lack of communal resting suggests that resting and den sites are not limiting distribution or abundance of eastern spotted skunks in the Ouachita Mountains. Similar conclusions also were reported for western spotted skunks in Texas and California (Carroll 2000; Crooks 1994; Doty and Dowler 2006).

As reported for other forest carnivores, our models of resting and den site selection indicate that combinations of vegetation and topographic features contribute to resting and den site selection (King and Powell 2007; Zielinski et al. 2004). Canopy closure, slope, number of vines, stand age, and entrance size were influential parameters in both the hypothesis testing models and the 2nd-stage best-fit model. We also found an important interaction between stand age and management type, where shortleaf pine stands were selected if the stand was young and hardwood stands were selected if the stands were old. The significance of this interaction is likely due to the importance of forest structure that provides protection from predators, a finding also reported at a larger scale based on home-range structure (Lesmeister 2007).

Forest structure appears to be important to eastern spotted skunk ecology, and populations may be limited to areas with dense cover. The factor with the strongest influence on eastern spotted skunk den and rest site selection appears to be the amount of vegetative cover, which also was reported for western spotted skunks (Carroll 2000; Doty and Dowler 2006). No den or resting sites were found in open areas in those studies or this study. Areas selected for resting and denning have greater canopy closure than nearby sites. Relative to other measured parameters, canopy closure was the most influential main effect on resting site and den selection by eastern spotted skunks, and likely enhances predator avoidance in addition to thermal regulation. The importance of canopy closure underlies why mature stands that are used for denning and resting are hardwood stands, which have more canopy closure than mature shortleaf pine stands. Further, management type had negative impact on model performance when not part of an interaction term with stand age; however, when interacting with one another, they were the most influential predictor of site selection.

Increased vine densities and the availability of young shortleaf pine stands contribute to the vegetative cover and likely serve a similar predator avoidance function as shrubs and prickly pear cactus do for western spotted skunks (Carroll 2000; Doty and Dowler 2006). Radiocollared animals selected den and rest sites with more than double the number of vines (Table 4) and selected young shortleaf pine stands for home-range use (Lesmeister 2007). Given their agility, body size, and shape, eastern spotted skunks can easily maneuver through

TABLE 6.—Parameter estimates, unconditional standard errors (*SEs*), odds ratios, and odds ratio 95% confidence intervals (*CI*s) for eastern spotted skunk (*Spilogale putorius*) den and resting site selection Akaike's information criterion–minimized model in the Ouachita Mountains, Arkansas. See Table 1 for descriptions of variable codes.

Parameter	Estimate	SE	Odds ratio	Lower CI	Upper CI
Rock	0.004	0.003	1.004	1.003	1.005
Ent	-0.003	0.002	0.997	0.992	1.003
Slope	0.145	0.085	1.156	1.131	1.182
Canopy	0.063	0.026	1.065	1.052	1.077
Vine	0.009	0.002	1.009	1.004	1.013
Age	-0.047	0.014	0.954	0.879	1.029
Age_other	0.171	1.562	1.010	0.888	1.132
Age_hw	0.095	0.102	1.038	1.019	1.056
Mgt_other	-8.761				
Mgt_hw	-4.093	8.171			

patches of vines and the dense vegetation of young forest, while those stands provide enhanced protection from predators. Primary predators such as coyotes (*Canis latrans*), bobcat (*Lynx rufus*), and great horned owls (*Bubo virginianus*—Kinlaw 1995) prefer more open habitats over forest with dense vegetation (Chamberlain et al. 2003; Ganey et al. 1997; Litvaitis and Shaw 1980; Smith et al. 1999). Thus, the open canopy and herbaceous understory conditions of mature shortleaf pine–bluestem habitat may be favorable to predators of eastern spotted skunks and thereby detrimental to eastern spotted skunks. Great horned owls were the primary predator of our study animals (D. B. Lesmeister, pers. obs.), and 11 of the 12 avian predation events occurred in the mature, fully restored pine–bluestem habitat that is characterized by a more open canopy and herbaceous understory. If predation limits use of more open habitats by eastern spotted skunks and plays a role in den and rest site selection, the association of eastern spotted skunks with areas of dense forest cover would appear to make the species highly susceptible to changes in forest ecosystems that reduce protective habitat.

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LITERATURE CITED

- BAILEY, R. G. 1980. Descriptions of the ecoregions of the United States. United States Department of Agriculture Miscellaneous Publications 1391:1–77.
- BUKENHOFER, G. A., AND L. D. HEDRICK. 1997. Shortleaf pine/bluestem grass ecosystem renewal in the Ouachita Mountains. Pp. 509–515 in Transactions of the 62nd North American Wildlife and Natural Resources Conference (K. G. Wadsworth, ed.). North American Wildlife and Natural Resources Conference, Washington, D.C.

- BUKENHOFER, G. A., J. C. NEAL, AND W. G. MONTAGUE. 1994. Renewal and recovery: shortleaf pine/bluestem grass ecosystem and red-cockaded woodpeckers. *Proceedings of the Arkansas Academy of Science* 48:243–245.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- BUSKIRK, S. W., AND R. A. POWELL. 1994. Habitat ecology of fishers and American martens. Pp. 283–296 in Martins, sables, and fishers: biology and conservation (S. W. Buskirk, A. S. Harestad, and M. G. Raphael, eds.). Cornell University Press, Ithaca, New York.
- CARO, T. M., AND C. J. STONER. 2003. The potential for interspecific competition among African carnivores. *Biological Conservation* 110:67–75.
- CARROLL, K. N. 2000. Macro and microhabitat characteristics of the western spotted skunk, *Spilogale gracilis*, in the Sierra Nevada of northern California. M.S. thesis, California State University, Sacramento.
- CHAMBERLAIN, M. J., B. D. LEOPOLD, AND L. M. CONNER. 2003. Space use, movements and habitat selection of adult bobcats (*Lynx rufus*) in central Mississippi. *American Midland Naturalist* 149:395–405.
- CHOATE, J. R., E. D. FLEHARTY, AND R. J. LITTLE. 1974. Status of the spotted skunk, *Spilogale putorius*, in Kansas. *Transactions of the Kansas Academy of Science* 76:226–233.
- COOPER, A. B., AND J. J. MILLSPAUGH. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566–575.
- COOPER, A. B., AND J. J. MILLSPAUGH. 2001. Accounting for variation in resource availability and animal behavior in resource selection studies. Pp. 243–273 in *Radio tracking and animal populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego, California.
- CRABB, W. D. 1948. The ecology and management of the prairie spotted skunk in Iowa. *Ecological Monographs* 18:201–232.
- CREEL, S., G. SPRONG, AND N. CREEL. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pp. 35–60 in *Carnivore conservation* (J. L. Gittleman, S. M. Funk, D. Macdonald, and R. Wayne, eds.). Cambridge University Press, Cambridge, United Kingdom.
- CROOKS, K. R. 1994. Den-site selection in the island spotted skunk of Santa Cruz Island, California. *Southwestern Naturalist* 39:354–357.
- CROOKS, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16:488–502.
- DONCASTER, C. P., AND R. WOODROFFE. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* 66:88–93.
- DOTY, J. B., AND R. C. DOWLER. 2006. Denning ecology in sympatric populations of skunks (*Spilogale gracilis* and *Mephitis mephitis*) in west-central Texas. *Journal of Mammalogy* 87:131–138.
- ENDRES, K. M., AND W. P. SMITH. 1993. Influence of age, sex, season and availability on den selection by raccoons within the central basin of Tennessee. *American Midland Naturalist* 129:116–131.
- FRAFIJORD, K. 2003. Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition overtaken by interspecific competition? *Biological Conservation* 111:445–453.
- FULLER, T. K., AND P. R. SIEVERT. 2001. Carnivore demography and the consequences of changes in prey availability. Pp. 161–178 in *Carnivore conservation* (J. L. Gittleman, S. M. Funk, D. Macdonald, and R. Wayne, eds.). Cambridge University Press, Cambridge, United Kingdom.
- GANEY, J. L., W. M. BLOCK, J. S. JENNESS, AND R. A. WILSON. 1997. Comparative habitat use of sympatric Mexican spotted and great horned owls. *Journal of Wildlife Research* 2:115–123.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GOMPPER, M. E., AND H. M. HACKETT. 2005. The long-term, range-wide decline of a once common carnivore: the eastern spotted skunk (*Spilogale putorius*). *Animal Conservation* 8:195–201.
- HACKETT, H. M., D. B. LESMEISTER, J. DESANTY-COMBES, W. G. MONTAGUE, J. J. MILLSPAUGH, AND M. E. GOMPPER. 2007. Detection rates of eastern spotted skunks (*Spilogale putorius*) in Missouri and Arkansas using live-capture and non-invasive techniques. *American Midland Naturalist* 158:123–131.
- HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd ed. John Wiley & Sons, Inc., New York.
- KING, C. M., AND R. A. POWELL. 2007. The natural history of weasels and stoats: ecology, behavior, and management. Oxford University Press, New York.
- KINLAW, A. 1995. *Spilogale putorius*. *Mammalian Species*. 511:1–7.
- LARIVIÈRE, S., AND F. MESSIER. 1997. Seasonal and daily activity patterns of striped skunks (*Mephitis mephitis*) in the Canadian prairies. *Journal of Zoology (London)* 243:255–262.
- LARIVIÈRE, S., AND F. MESSIER. 1998. Denning ecology of the striped skunk in the Canadian prairies: implications for waterfowl nest predation. *Journal of Applied Ecology* 35:207–213.
- LESMEISTER, D. B. 2007. Space use and resource selection by eastern spotted skunks in the Ouachita Mountains, Arkansas. M.S. thesis, University of Missouri, Columbia.
- LITTELL, R. C., P. R. HENRY, AND C. B. AMMERMAN. 1998. Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science* 76:1216–1231.
- LITVAITIS, J. A., AND J. H. SHAW. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. *Journal of Wildlife Management* 44:62–68.
- LITVAITIS, J. A., J. A. SHERBURNE, AND J. A. BISSONETTE. 1986. Bobcat habitat use and home range size in relation to prey density. *Journal of Wildlife Management* 50:110–117.
- LOCHMILLER, R. L., R. E. MASTERS, AND S. T. MCMURRY. 1994. Wildlife stand improvement in the Ouachita National Forest: effects of midstory vegetation removal and fire on small mammal communities. Final report. United States Department of Agriculture Forest Service, Hot Springs, Arkansas.
- MASTERS, R. E., R. L. LOCHMILLER, S. T. MCMURRY, AND G. A. BUKENHOFER. 1998. Small mammal response to pine-grassland restoration for red-cockaded woodpeckers. *Wildlife Society Bulletin* 26:148–158.
- MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. 2nd ed. Monographs on statistics and applied probability number 37. Chapman & Hall, London, United Kingdom.
- MCCULLOUGH, C. R. 1983. Population status and habitat requirements of the eastern spotted skunk on the Ozark Plateau. M.S. thesis, University of Missouri, Columbia.
- MCCULLOUGH, C. R., AND E. K. FRITZELL. 1984. Ecological observations of eastern spotted skunks on the Ozark Plateau. *Transactions of the Missouri Academy of Science* 18:25–32.
- MILLER, D. A., R. E. THILL, M. A. MELCHORS, T. B. WIGLEY, AND P. A. TAPPE. 2004. Small mammal communities of streamside management zones in intensively managed pine forests of Arkansas. *Forest Ecology and Management* 203:381–393.

- NORBURY, G. L., D. C. NORBURY, AND R. P. HEYWARD. 1998. Space use and denning behavior of wild ferrets (*Mustela furo*) and cats (*Felis catus*). *New Zealand Journal of Ecology* 22:149–159.
- POLDER, E. 1968. Spotted skunk and weasel populations den and cover usage by northeast Iowa. *Iowa Academy of Science* 75:142–146.
- REVILLA, E., F. PALOMARES, AND M. DELIBES. 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. *Conservation Biology* 15:148–158.
- SASSE, D. B., AND M. E. GOMPPER. 2006. Geographic distribution and harvest dynamics of the eastern spotted skunk in Arkansas. *Journal of the Arkansas Academy of Science* 60:119–124.
- SMITH, D. G., T. BOSAKOWSKI, AND A. DEVINE. 1999. Nest site selection by urban and rural great horned owls in the northeast. *Journal of Field Ornithology* 70:535–542.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1996. Environmental impact statement for the renewal of the shortleaf pine/bluestem grass ecosystem and recovery of the red-cockaded woodpecker. United States Department of Agriculture Forest Service, Hot Springs, Arkansas.
- WOODROFFE, R., AND J. R. GINSBERG. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- ZIELINSKI, W. J., R. L. TRUEX, G. A. SCHMIDT, F. V. SCHLEXER, K. N. SCHMIDT, AND R. H. BARRETT. 2004. Resting habitat selection by fishers in California. *Journal of Wildlife Management* 68:475–492.

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