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Eastern Spotted Skunk Occupancy and Rest Site Selection in Hardwood Forests of the Southern Appalachians

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EASTERN SPOTTED SKUNK OCCUPANCY AND REST SITE SELECTION IN HARDWOOD FORESTS OF THE SOUTHERN APPALACHIANS

A Thesis
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the Graduate School of
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In Partial Fulfillment
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Master of Science
Wildlife and Fisheries Biology

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by
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ABSTRACT

Eastern spotted skunks are a poorly understood mesocarnivore species that suffered a dramatic range-wide decline in the mid-1900s. Little is known about their current distribution or habitat needs, and in the southern Appalachians, where the Carolinas and Georgia converge spotted skunks have never been studied. We investigated eastern spotted skunk habitat selection to develop an understanding of their habitat and conservation needs in this region.

We used remote-camera surveys and occupancy modelling to evaluate factors hypothesized to influence the probability of eastern spotted skunk detection and occurrence at the landscape scale. We detected spotted skunks at 55.6% of our sites and on 18.5% of sampling occasions. Our detection models supported predation risk, camera setup, and scent-based attractants as influential to detection probability but had poor predictive ability overall. Our top occupancy model had moderate predictive power and showed a negative relationship between elevation and occupancy probability. These results suggest spotted skunks in the southern Appalachians may be more widely distributed than previously thought but are also highly cryptic and in need of further investigation. In particular, there is a strong need for researchers to identify thresholds of habitat suitability for this species.

To evaluate fine-scale selection of rest site habitat by eastern spotted skunks we used VHF telemetry and discrete choice modelling. Over two summers we tracked 15 spotted skunks and collected habitat data for 233 rest sites and 233 random available sites. Our top model supported positive effects of understory cover and coarse woody debris (CWD), and a negative effect of distance to nearest drainage channel on rest site selection. Previous studies have identified understory cover as important for protection from avian predators, however ours is the first to identify CWD and drainage channels as important to spotted skunk habitat selection. These attributes were hypothesized to be selected based on prey availability, however direct studies of spotted skunk diet and foraging strategies are needed. We also recommend further investigation regarding the importance of drainage networks to eastern spotted skunks. Finally, we suggest that preservation of understory vegetation and CWD may benefit eastern spotted skunk conservation in the southern Appalachians.

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CHAPTER ONE

EVALUATING DETECTION AND OCCUPANCY PROBABILITIES OF EASTERN SPOTTED SKUNKS IN THE SOUTHERN APPALACHIANS

INTRODUCTION

Eastern spotted skunks (*Spilogale putorius*) are a poorly understood species that have been generally overlooked by wildlife biologists, to the extent that we do not have an accurate estimation of their current distribution despite reported wide-scale declines. Although they were once an important furbearer that ranged from southwestern PA, south to Florida and west to the eastern foothills of the rocky mountains, the species underwent a dramatic range-wide decline in the mid-1900s, which was only identified in 2005 (Gompper and Hackett 2005). The legacy of this population crash has not been thoroughly investigated, and despite their recent upgrading to “vulnerable” by the IUCN (Gompper and Jachowski 2016), the current abundance, demographic trends, and distribution of eastern spotted skunks remain largely unknown. To conserve this species, a better understanding of their habitat needs and how to effectively monitor for eastern spotted skunks is imperative.

Understanding landscape-level habitat associations can provide important information about spotted skunk distribution, habitat needs, and where to focus future studies or management efforts. The large historic range of eastern spotted skunks suggests that they may be largely opportunistic in the array of habitats they can occupy (Kinlaw 1995). However, directed investigations of landscape scale habitat selection by eastern spotted skunks are generally sparse, and strong predictors of occurrence have yet to be identified. Still, one recently completed study from the central Appalachian mountains of Virginia suggests that eastern spotted skunk occurrence is influenced by a combination of forest stand age and elevation (Thorne et al. 2017). Specifically, within occupied landscapes, eastern spotted skunks appear to prefer younger pine forests or mature deciduous forests, presumably because of the increased understory complexity these forest types offer at the respective stages of growth (Lesmeister et al. 2009, Thorne et al. 2017). Forests patches characterized by dense understories are typically distributed sporadically throughout a landscape, and can be determined by a variety of characteristics such as topography, stand age, and management history, making this a difficult habitat attribute to manage (DeGraaf et al. 1992, Lesmeister et al. 2013). Furthermore, although historically eastern spotted skunks were common on homestead farms throughout the Midwest (DeSanty 2001), modern reports of this species in suburban or developed areas are sparse throughout most of their Appalachian and mid-western range. Nonetheless, recent direct investigations of eastern spotted skunk distribution and habitat selection have only been performed in protected areas that are sparsely distributed throughout their large range.

An additional inhibitor to our understanding of eastern spotted skunks is a lack of knowledge regarding the specific methods that may be most effective for studying this species. Historically, the majority of reports of eastern spotted skunks were the product of incidental detections and trapping records (Gompper and Hackett 2005, Diggins et al. 2015, Jachowski et al. 2015). More recently, studies have been successfully completed using remote-camera surveys and dedicated trapping efforts, however reported detection and capture rates are typically low (Lesmeister et al. 2008, Thorne et al. 2017, Sprayberry and Edelman 2018). It remains unclear if these low detection rates are the product of truly low species abundance, or simply the cryptic nature of this species (Wilson et al. 2016). A variety of temporal and site-specific factors are likely to influence the detectability of skunks. For example, Thorne et al. (2017) reported that moon illumination had a significant negative effect on detection rates of eastern spotted skunks, and suggested that spotted skunks could be less active due to increased susceptibility to predation on nights when moonlight was high. Additionally, eastern spotted skunk detection rates were found to be higher during the colder winter months (Hackett et al. 2007), a trend that may be related to food availability or behavioral changes during the mating season (Hackett et al. 2007, Lesmeister et al. 2009). Conversely, more recent efforts to study eastern spotted skunks have reported successful trapping of the species throughout the summer in Alabama (A. Edelman, University of West Georgia, Personal communication), further illuminating the general lack of concrete knowledge about eastern spotted skunk detectability.

We performed an occupancy study in the southern Appalachians of North and South Carolina, with two primary objectives. First, we sought to identify ways in which we might improve our ability to monitor this species by assessing which factors impact the detection probability of eastern spotted skunks. Second, we evaluated landscape scale topographic and habitat attributes that we predicted would influence eastern spotted skunk occupancy probability in this southern Appalachian region. By comparing our results with findings elsewhere throughout their historic range, we can glean insights about the generality of this species' habitat requirements throughout a large portion of their distribution and identify future research that will enhance our understanding of the ecology and conservation needs of eastern spotted skunks.

METHODS

Study Area

We performed this study on an approximately 1,500 km^2 area at the tri-state convergence of North Carolina, South Carolina and Georgia (Figure 1). The surveyed area included parts of three national forest ranger districts and one state management area: the Andrew Pickens Ranger District of Sumter National Forest and Jocassee Gorges State Management Area in northwestern South Carolina, and the Nantahala and Pisgah Ranger Districts of Nantahala and Pisgah National Forests in southwestern North Carolina. This area ranges from 200 to 1600 m in elevation and is characterized by four primary forest compositions: cove hardwoods, mixed deciduous, northern hardwoods, and xeric oak-pine forests (Elliott et al. 1999, Turner et al. 2003). Forests are primarily dominated by deciduous trees, however patches of evergreen coniferous trees are also present on the landscape. Understory cover is dominated by dense stands of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maxima*), particularly in riparian areas and north-facing slopes (South Carolina Department of Natural Resources 2005, Warren 2008).

Field methods

We surveyed 45 baited remote-camera sites (18 in 2016, 27 in 2017) for three months between January and April to monitor spotted skunk occurrence in southern

Appalachian hardwood forests. To capture potential differences in topographic or vegetative conditions associated with elevation and because recent detections of spotted skunks in the Appalachian have been primarily limited to higher elevation sites (Diggins et al. 2015, Wilson et al. 2016, Thorne et al. 2017), we selected sites that were stratified by elevation. We then created random points within our five elevational strata such that sampling points were at least 1.5 km from each other (an area slightly larger than the reported winter home range of male eastern spotted skunks) to meet the assumption of closure within a season of sampling (Lesmeister et al. 2009, Wilson et al. 2016). We then used a generalized random tessellation stratified (GRTS) sampling approach (Gitzen et al. 2012) to identify coordinates for 20 potential sites within each elevational strata of potential sampling points. We navigated to selected sites and identified a suitable site to setup our monitoring station within 50 m of the randomly selected coordinates. If conditions were unsafe or unable to be traversed by foot, we set sites within 250 m of the original coordinates in a direction that would not violate the 1.5 km minimum distance between sites. At each site, monitoring stations consisted of a “bait tree” and a “camera tree” located 1.2 – 4 m apart. We used Bushnell Trophy Cams (model 119736) set to operate continuously and capture one photo every three seconds when triggered. For bait, we used a can of sardines in oil, and one of three scent lure treatments: Caven’s Gusto™ to represent the musky odor of other species, cherry oil to represent a sweet food source, or a control treatment with no additional lure. We rotated scent lure treatment every fourth week and randomly selected the starting lure for each site to avoid confounding the effects of season and scent lure treatment. We revisited monitoring stations every two weeks for three months, for a total of six sampling occasions per site, each approximately 14 days in length (Average 12.6; Median 14; Range 1-31). During every revisit we replaced the bait and SD card, either refreshed or changed the scent lure, and checked that the camera batteries were at least 50% full.

We used a combination of field and remote sensing methods to collect detection and site covariate data for each monitoring site (Table 1). In the field, we estimated understory density by assessing visibility to 30 m in four cardinal directions from the camera site. We evaluated coarse woody debris (CWD) abundance within a 30m radius using an index of 1-10, with 1 representing no CWD greater than 10 cm in diameter, and 10 indicating the area was mostly covered by fallen trees and large woody debris. We used the package ‘suncalc’ (Agafonkin, 2018) in program R version 3.4.2 (R Core Team, 2017) to calculate moon illumination and the number of minutes the moon was above the horizon each night. We multiplied these values to obtain a single measure of moonlight for each sampling occasion of each site. We used ArcGIS 10.5 (ESRI 2017) and data from a 1/3 arc-second digital elevation model (DEM; USGS 2013) and the National Land Cover Dataset (NLCD 2011) to identify the aspect, elevation, and forest canopy type for each sampling site. We calculated the average slope and elevation, the proportion of area covered by evergreen forests, the proportion of area with southwest facing slopes (157.5-292.5 degrees) and the amount and intensity of impervious landcover (as a proxy for human development) within a 750 m radius circle around the site, which equates to an area slightly over 1.75 km^2, or the average winter home range of a male eastern spotted skunk (Lesmeister et al. 2009). Finally, we calculated the distance of each site to the nearest drainage channel, as well as the total length of drainage channels within our 750 m buffer (Montgomery and Foufoula-Georgiou 1993) (Table 1).

Analyses

We used a single season occupancy modeling framework to estimate detection and occupancy probability of eastern spotted skunks in southern Appalachian hardwood forests. By repeatedly sampling a site, occupancy modelling allows for evaluation of species occurrence while also accounting for imperfect detection rates inherent in field monitoring studies (MacKenzie et al. 2006). Because of overall low detection rates, we defined a sampling occasion as the full length of time between visits to a site (approximately two weeks). Owing to the relatively large number of detection and occupancy covariates we evaluated, we carried out our analyses in two stages to prevent the development of a massive and unwieldy candidate set of *a priori* models (MacKenzie et al. 2006, Richmond et al. 2010). We first evaluated support for four hypotheses regarding factors predicted to influence spotted skunk detection probability while holding occupancy probability constant. Then, using the covariates from our top detection models, we evaluated support for three hypotheses regarding factors we predicted to influence eastern spotted skunk occupancy probability. For both stages of analyses, we evaluated *a priori* hypotheses, and ranked models using Akaike's Information Criterion for small samples sizes (AIC_c) with a model retention threshold of two ΔAIC_c units. All quantitative detection and site covariates were scaled to have a mean of zero and a standard deviation of one. Within each set of detection or site covariates, we checked for multicollinearity, but found no variables with a correlation coefficient greater than 0.4

and therefore retained all variables. We used the program R package ‘unmarked’ (Fiske and Chandler 2011) to perform our analyses.

We evaluated support for 13 *a priori* models plus a null and global model representing four primary hypotheses we expected to influence detection probability (Table 2). First, we hypothesized that predation risk influenced detection probability (Lesmeister et al. 2013, Thorne et al. 2017). Specifically, we predicted less moonlight would reduce predation risk and increase chances of eastern spotted skunk detection. We also predicted that increased coarse woody debris (CWD), increased understory cover, and close proximity to a stream or drainage ravine would improve immediate structural cover and refugia from predators, thereby increasing detection probability (Chapter 2). Second, we hypothesized that seasonal prey availability would influence spotted skunk detection (Hackett et al. 2007). We used ordinal date as a proxy for season and predicted that detections would be more frequent during the colder months earlier in the year, when limited food resources may require spotted skunks spend more time actively foraging. Third, we hypothesized that the use of scent-based attractants would influence spotted skunk detection (Schlexer 2008), and we predicted that spotted skunk detections would be highest during sample occasions baited with the cherry scent lure, followed by occasions treated with the Gusto™ lure, while sites baited with the control treatment (sardines alone) would produce the fewest detections. Finally, we hypothesized that camera setup could affect the probability of spotted skunk detection (Kays and Slauson 2008), and we predicted that lower bait height, higher camera height, and greater distance between camera and bait tree would increase our chances of detecting and eastern spotted skunks.

To investigate site occupancy, we evaluated support for 16 *a priori* models plus a null and global model containing six covariates and representing three primary hypotheses that we thought would influence eastern spotted skunk occurrence (Table 3). Our first hypothesis was that spotted skunks would prefer areas that facilitate efficient movement (Fremier et al. 2015), where we predicted areas with more drainage channels, which can facilitate movement through suitable habitat, would improve occupancy probability (Campbell Grant et al. 2007). We also hypothesized skunks would prefer to occupy warmer habitat during the winter to reduce thermoregulatory stress (Lesmeister et al. 2008). We evaluated three covariates in relation to this hypothesis, and predicted that lower elevations, steeper slopes, and southwestern facing slopes would each independently provide warmer temperatures and increase occupancy probability (Fekedulegn et al. 2003, 2004). Finally, our third hypothesis was that eastern spotted skunks would be less likely to occur in areas with increased predation risk. Specifically we predicted that human development (represented by impermeable surfaces for this study) and evergreen forests would both decrease occupancy probability by increasing predation risk from domestic pets (Crabb 1948, Kinlaw 1995) and owls or other native predators (Lesmeister et al. 2010) respectively. In addition to the six single-covariate models described above, we also evaluated more complex *a priori* models that included multiple covariates related to each hypothesis, and sub-global models that represented combinations of these hypotheses.

Model validation

We used k-fold cross validation to assess the predictive ability of our top ranked occupancy models (Boyce et al. 2002). K-fold cross validation allows us to test the accuracy of our top model using only the data we have already collected, by training our top model with only a subset of our data, and then evaluating how well the resulting model can predict the true state of the remaining portion of our data. We validated the detection component and occupancy component of our top occupancy model separately and used all covariates from our candidate models within two ΔAIC_c of our highest ranked occupancy model. We performed 20 iterations of k-fold validation using random divisions of our data into a 90:10 ratio to train and test our top model respectively. We interpreted our validation results using Receiver Operating Characteristics (ROC) and the area under the curve (AUC) value to evaluate how well our models were able to accurately predict if a skunk was detected or a site was occupied, based on the habitat variables contained in our top model (Metz 1978, Cumming 2000). We additionally performed a parametric bootstrap goodness of fit test of our most complex model, using 5000 iterations to assess how well our models fit the collected data (MacKenzie and Bailey 2004).

RESULTS

We detected eastern spotted skunks at 25 of the 45 sites surveyed for this study (55.6% naïve occupancy) and had detections on 47 of our 254 sample occasions (18.5% naïve detection). Sixteen sample occasions were missed owing to logistical constraints and camera malfunctions. On average, latency to first detection was 28.3 days (range: 1-

71, SD: 23.1). Cameras were active for a total of 4689 trap-nights over the course of both years, with an average of 12.6 active trap-nights per sampling occasion (range 0-31, SD 4.6). Of sites known to be occupied, we detected spotted skunks on 14.1% of active trap-nights (129 of 913 trap-nights), however when including sites where spotted skunks were never detected, nightly detection was only 2.8% (129 of 3689 trap-nights).

In step one of our analysis, five of our 13 *a priori* detection models fell within two ΔAIC_c of our top model, and these models supported our hypotheses that predator avoidance, olfactory attractants, and camera station setup affected detection probability. Our top models included seven of our nine detection covariates: scent lure, camera height, bait height, distance to bait, understory cover, coarse woody debris, and distance to nearest drainage channel (Table 2). Distance to bait was our best predictor and showed a strong positive effect on detection probability. Our second-best predictor of detection, CWD, showed a moderately strong effect with its lower confidence limit falling squarely on zero (Figure 2). Understory cover, distance to drainage, and bait height all had moderate effects on detection probability. Our two lure treatments showed moderate and contrasting effects, however, we had relatively high levels of uncertainty regarding these variables (Figure 2). We observed essentially no effect of camera height on detection probability, and average moon illumination and date were not retained in any of our top models (Table 2). Our results indicated that conditional detection probability doubled with every 70 cm increase in distance between camera and bait (Figure 3a), and also doubled with a four-fold increase in CWD (Figure 3b). Based on the seven covariates contained in our three top detection models, our overall conditional point estimate of detection probability was 23.4% based on mean conditions, and average detection probability given the conditions of sample occasions in this study was 28.2%.

We observed support for two of our *a priori* occupancy models in stage two of our analyses, both related to our hypothesis that thermoregulation would influence eastern spotted skunk occupancy probability. Elevation alone comprised our top model, while elevation and slope were both present in our second ranked model (Table 3). Only elevation had a significant relationship with occupancy probability (Figure 2), where the probability of occupancy doubled for every 130 m decrease in elevation (Figure 4). Although retained in our second ranked model, we saw only a moderate effect of slope on occupancy probability, and this covariate had relatively high uncertainty with a confidence interval that overlapped zero (Figure 2). Using model averaged parameter estimates of both slope and elevation, our overall point estimate of eastern spotted skunk occupancy probability given mean conditions was 82.1% in the southern Appalachian hardwood forests where this study took place. Based on conditions at the sites surveyed in our study area, we had an average of 70.4% estimated occupancy probability.

Results of our model validation indicated that our covariates were generally ineffective for accurately predicting eastern spotted skunk detection or occupancy. Validation of our detection covariates returned an AUC value of 0.55, indicating poor predictive ability of our top detection model (Swets 1988, Morelli et al. 2017). The occupancy portion of validation performed slightly better with an AUC value of 0.65, indicating moderately low predictive ability of our top occupancy model. Our data showed slightly less variation than was expected, with the results of our goodness of fit test returning a c-hat value of 0.74.

DISCUSSION

Results from our study suggest that eastern spotted skunks are difficult to detect, but likely more widely distributed in the southern Appalachians than previously thought. We detected eastern spotted skunks at over 50% of our surveyed sites, but observed spotted skunks on <3% of our total trap-nights. Furthermore, latency to initial detection ranged from 1 to 71 days, with first detection occurring on average nearly a month after monitoring began. This suggests that surveys for eastern spotted skunks that monitor sites for less than one month may produce underestimates of true occupancy rates (Wilson et al. 2016). Nonetheless, recent efforts to identify persisting populations of eastern spotted skunks within the core of their historic range have been successful at detecting the general presence of this species overall (Sprayberry and Edelman, 2018; Thorne et al., 2017; Wilson et al., 2016; S. Higdon, University of Missouri, Personal Communication). Therefore, we suggest that more sustained, dedicated survey efforts are needed to evaluate how widely distributed spotted skunks remain throughout their historic range.

Our results also indicate that the species may be extremely cryptic and highlight the need for an improved understanding of monitoring techniques that may increase eastern spotted skunk detection rates. Interestingly, although we had uncertainty in the effects of our scent lure treatments, our results indicate that the cherry lure may work as an attractant while the Gusto™ may act as a deterrent to eastern spotted skunks (Figure 2). Still, when compared with the control treatment (sardines alone), the scent lures did not appear to strongly influence detection rates. Spotted skunks typically did not spend prolonged periods at our baited camera stations, with over one-third of detections consisting of only one photograph, and on average producing less than three photos per detection (range 1-15, median 2). Given that cameras were set to record a photo every three seconds, these results suggest that on average, spotted skunks spent less than nine seconds at our monitoring sites. This prompts the concern that our camera arrays could have missed detections when spotted skunks quickly passed through the camera's triggering frame. Indeed, a greater distance between the camera and bait appeared to increase detection probability in our study, indicating that a larger frame of view may have positive effects on detection rates. That said, when designing camera surveys it should also be considered that increasing the distance between camera and bait too far can also result in decreased camera sensitivity for smaller species (Gompper et al. 2006). Given that a consumable reward can increase the time spent at a monitoring site (Schlexer 2008), we suggest future studies consider using eatable baits, such as deer carcasses (Thorne et al. 2017) or raw chicken (R.Eng, USFS Region 5 Carnivore Monitoring Program, Personal observation) to increase the amount of time a spotted skunk will spend in front of the remote camera (Schlexer 2008).

Elevation was the most important predictor of eastern spotted skunk occurrence in our study, however we found a negative association with elevation that contradicts the findings of previous studies (Diggins et al. 2015, Thorne et al. 2017). These results highlight the lack of understanding we currently possess regarding the biological mechanisms driving eastern spotted skunk occurrence. For instance, in the southern

Appalachians particular forest types (e.g. cove hardwood forests) are associated with low elevation areas (Bolstad et al. 1998, Elliott et al. 1999, Warren 2008), and it may be that these forest types provide preferable habitat for eastern spotted skunks via differences in the vegetative structure and species diversity they support (Turner et al. 2003, South Carolina Department of Natural Resources 2015). Similarly, Thorne et al. (2017) reported eastern spotted skunk occupancy in the central Appalachian was predicted by the interactive effects of elevation and stand age, and they hypothesized that this relationship was due to associated densities of understory cover in the different forest stands. Alternately, low elevation areas in our study may have been preferred because of their proximity to stream beds, where increased herpetofauna and invertebrate forage may be available (Chapter 2; Sprayberry and Edelman, 2016; Thorne and Waggy, 2017). Additional studies evaluating whether eastern spotted skunks discriminate between low elevation sites associated with drainage basins of interior mountains and low elevation sites along the edges of a mountain range could prove extremely valuable. Because this study encompassed a portion of the Blue Ridge Escarpment along the eastern edge of the southern Appalachians, low elevation sites in our study area may not be fully comparable with low elevation sites in other portions of the eastern spotted skunk's range, nor even with other physiographic provinces in the Appalachian mountain range (Simon et al. 2005). In general, identifying which biological factors associated with elevation are most influential to eastern spotted skunk occupancy would enable managers to better predict spotted skunk occurrence and determine priority areas for conservation efforts.

We found a lack of strong relationships between spotted skunk occurrence and many of our site covariates, and suggest that future work should investigate the importance of these and other attributes at multiple spatial and temporal scales. For instance, it is possible that within a heterogenous landscape such as the southern Appalachians, evaluating selection based on attributes averaged across >1.75 km^2 may have captured too much of the variance present in the landscape, and consequently masked our ability to identify the importance of particular attributes. Indeed, results of our goodness of fit test revealed lower than expected variance within the collected data. Additionally, we were unable to evaluate certain attributes that may have been important to predicting occupancy probability in the southern Appalachians. For instance stand age was reported as an important factor in the central Appalachians (Thorne et al. 2017), however we were unable to obtain this data for our study area. Nonetheless, our results indicate that eastern spotted skunks may be highly opportunistic in the range of habitats they can occupy at the landscape scale. Finally, given that we monitored the portion of South Carolina where spotted skunks were predicted to be the most likely to occur (Wilson et al. 2016) and found that over half of our sites were occupied, we suggest future studies additionally sample areas where occupancy may be less likely, such as un-forested habitat, private or heavily managed lands, and sites in the nearby non-mountainous regions. Such studies could help identify elevational thresholds and major habitat features that may constrain the distribution of eastern spotted skunks. Identification of these thresholds for even a small part of the species range will allow for more accurate predictions of the species current distribution.

While our results have contributed to a growing knowledge about the ecology and conservation needs of eastern spotted skunks, the cryptic nature of this species has limited our ability to identify any strong predictors of their occurrence. Furthermore, knowledge of the current abundance and demographic trends of eastern spotted skunks remain virtually unknown. Here, we have provided suggestions for future studies to improve detection rates of eastern spotted skunks and have highlighted particular questions that we think warrant further study. Specifically, we recommend future studies continue working to improve upon our ability to study this species via remote-camera monitoring and other non-invasive techniques. Improvement in camera monitoring methods could produce novel information about spotted skunk abundance and territorial dynamics via identification of individuals by unique spot patterns (M. Ben-David, University of Wyoming and D. Lesmeister, USFS Pacific Northwester Research Station, Personal Communication), while the addition of hair-snares to monitoring stations could allow for genetic evaluations of population health (B. Wuertz, Warren Wilson College, Personal Communication). At the same time, fine-scale studies of eastern spotted skunk survival and reproductive rates are urgently needed to determine the current demographic trend of the species in the southern Appalachians, while evaluation of spotted skunk responses to human development and forest management will be critical for assessing the vulnerability of this species to regional extirpation or extinction.

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TABLES

Table 1 Abbreviations and descriptions of the nine detection covariates and six site covariates included as potential factors influencing eastern spotted skunk detection and occupancy probabilities (respectively) in the southern Appalachian mountains in 2016 and 2017

Variable	Abbrev.	Mean±SE (Range)	Description
<u>*Detection covariates*</u>			
Scent Lure Treatment	Lure	NA	Rotating scent lure added to each monitoring array every check
Cherry			A strong sweet odor representative of a high-sugar food source
Gusto			A strong skunky-musky odor, representative of interspecific information
Control			No added scent lure odor
Bait Height	B.ht	68.19±0.52 (42-100)	Height in cm from the ground to the middle of the can of sardines
Camera Height	C.ht	79.10±1.37 (44-147)	Height in cm from the ground to the middle of the remote camera
Camera to Bait Distance	Dist	2.88±0.04 (1.27-4.10)	Distance in cm between the camera tree and the bait tree
Coarse Woody Debris	CWD	3.46±0.05 (0-8)	Index of coarse woody debris within a 30 m radius of the site
Understory Density	Undst	33.73±1.40 (0.5-91.25)	Average of four estimates of percent visibility to 30 m from the camera tree
Distance to Drainage Channel	Drain	80.69±3.90 (0.20-252.74)	Distance from site coordinates to nearest drainage channel, channels defined by a 250 cell accumulation threshold
Season	Date	63.88±1.43 (18.5-118.25)	Averaged Juliann date for all days included in that sample occasion
Moon Illumination	Moon	267.59±9.75 (9.37-648.20)	Average percent moon illumination * minutes the moon was above the horizon for all days in that sample occasion
<u>*Site covariates*</u>	*Covariates calculated for a 750m radius circle around the site coordinates*		
Slope	Slope	18.69±0.57 (10.0-26.8)	Average slope of the land within the buffered area
Southwestern Aspect	SW	0.42±0.013 (0.22-0.64)	Proportion of slopes facing approximately SW, from 157.5 to 292.5 degrees
Elevation	Elev	810.70±42.06 (340-1298)	Average elevation of the land within the buffered area
Drainage Length	DrainLen	695.6±16.86 (442-901)	Total length of drainage channels, channels defined by a 250 cell accumulation threshold
Evergreen Forests	Everg	0.12±0.017 (0-0.46)	Proportion of land covered by evergreen forest, as determined by the NLCD
Impervious Surfaces	Imperv	0.16±0.046 (0-2.03)	Averaged value of total impervious surfaces, as determined by the NLCD

Table 2 Ranked *a priori* candidate models for evaluating eastern spotted skunk detection probability in the southern Appalachians in 2016 and 2017. Occupancy probability (ψ) was held constant at this stage of analysis. See Table 1 for a description of detection covariates.

Model	df	logLik	AIC_c	ΔAIC_c	w_i
Lure+B.ht+C.ht+Dist+ψ	7	-109.556	236.1	0	0.232
B.ht+C.ht+Dist+ψ	5	-112.569	236.7	0.54	0.178
Lure+ψ	4	-113.919	236.8	0.7	0.164
B.ht+C.ht+Dist+CWD+Drain+Undst+ψ	8	-108.832	237.7	1.52	0.108
Lure+B.ht+C.ht+Dist+CWD+Drain+Undst+ψ	10	-105.7	237.9	1.73	0.098
Lure+CWD+Drain+Undst+ψ	7	-110.933	238.9	2.75	0.059
Null+ψ	2	-117.339	239	2.82	0.057
Moon+ψ	3	-116.962	240.5	4.37	0.026
CWD+Drain+Undst+ψ	5	-114.531	240.6	4.46	0.025
Date+ψ	3	-117.325	241.2	5.1	0.018
Moon+Date+Lure+ψ	6	-113.538	241.3	5.15	0.018
Moon+Date+ψ	4	-116.952	242.9	6.76	0.008
Detection global+ψ	12	-105.303	244.4	8.22	0.004
Moon+Date+Lure+CWD+Drain+Undst+ψ	9	-110.665	244.5	8.33	0.004
Moon+Date+CWD+Drain+Undst+ψ	7	-114.238	245.5	9.36	0.002

Table 3 Ranked *a priori* candidate models for evaluating eastern spotted skunk occupancy probability in the southern Appalachian mountains. The following detection covariates were included in all models (denoted as *p*): bait height, camera height, distance to bait, CWD, distance to nearest drainage channel, understory cover, and scent lure treatment. See Table 1 for all detection and site covariate descriptions.

Model	df	logLik	AIC_c	ΔAIC_c	w_i
p+Elev	11	-102.067	234.1	0	0.385
p+Slope+Elev	12	-100.746	235.2	1.11	0.221
p+Elev+Drain	12	-101.743	237.2	3.1	0.082
p+Elev+Everg	12	-101.82	237.4	3.26	0.076
p+null	10	-105.7	237.9	3.74	0.059
p+Slope	11	-104.003	238	3.87	0.056
p+Slope+SW+Elev	13	-100.536	238.8	4.68	0.037
p+Drain	11	-104.649	239.3	5.16	0.029
p+Imperv	11	-105.252	240.5	6.37	0.016
p+SW	11	-105.627	241.3	7.12	0.011
p+Everg	11	-105.693	241.4	7.25	0.01
p+Slope+SW	12	-103.929	241.6	7.47	0.009
p+Slope+SW+Elev+Drain	14	-100.313	242.6	8.49	0.006
p+Everg+Imperv	12	-105.249	244.2	10.11	0.002
p+Everg+Imperv+Drain	13	-104.492	246.7	12.59	0.001
p+Slope+SW+Elev+Everg+Imperv	15	-100.514	247.6	13.45	0
p+Global	16	-100.174	251.8	17.64	0

Table 4 Model averaged estimates, standard errors, and the cumulative weights of all occupancy (ψ) and detection (p) covariates retained in our top models of eastern spotted skunk occupancy in the southern Appalachians.

Covariate	Estimate	Std. Error	Weight
ψ (Intercept)	1.2767	0.6709	1
ψ (Elev)	-1.2901	0.569	0.36
ψ (Slope)	0.9657	0.679	1
p (Intercept)	-1.1871	0.334	1
p (B.Ht)	-0.4269	0.2833	1
p (C.Ht)	0.1195	0.242	1
p (Dist)	0.751	0.2262	1
p (Lure_Cherry)	0.6688	0.4333	1
p (Lure_Gusto)	-0.4688	0.4957	1
p (Undst)	0.4397	0.2743	1
p (CWD)	0.4476	0.229	1
p (Drain)	-0.2556	0.2057	1

FIGURES

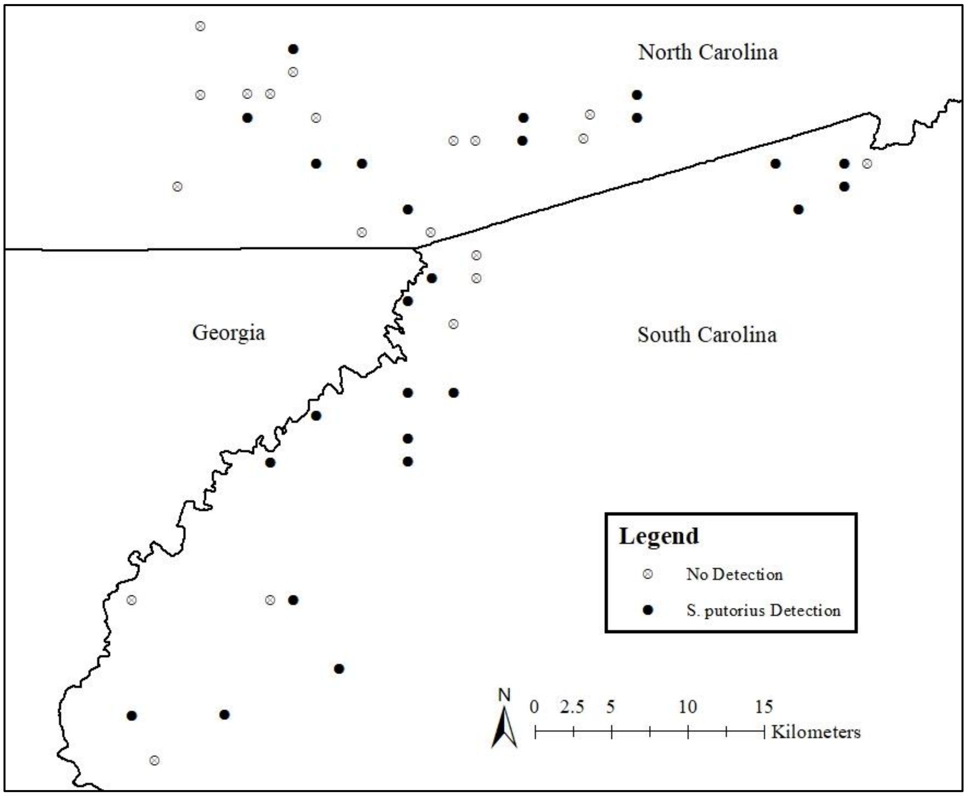

Figure 1 Study area for our evaluation of eastern spotted skunk occupancy in the southern Appalachians; filled points denote sites where eastern spotted skunks were detected, while empty points are indicate surveyed sites where spotted skunks were not detected.

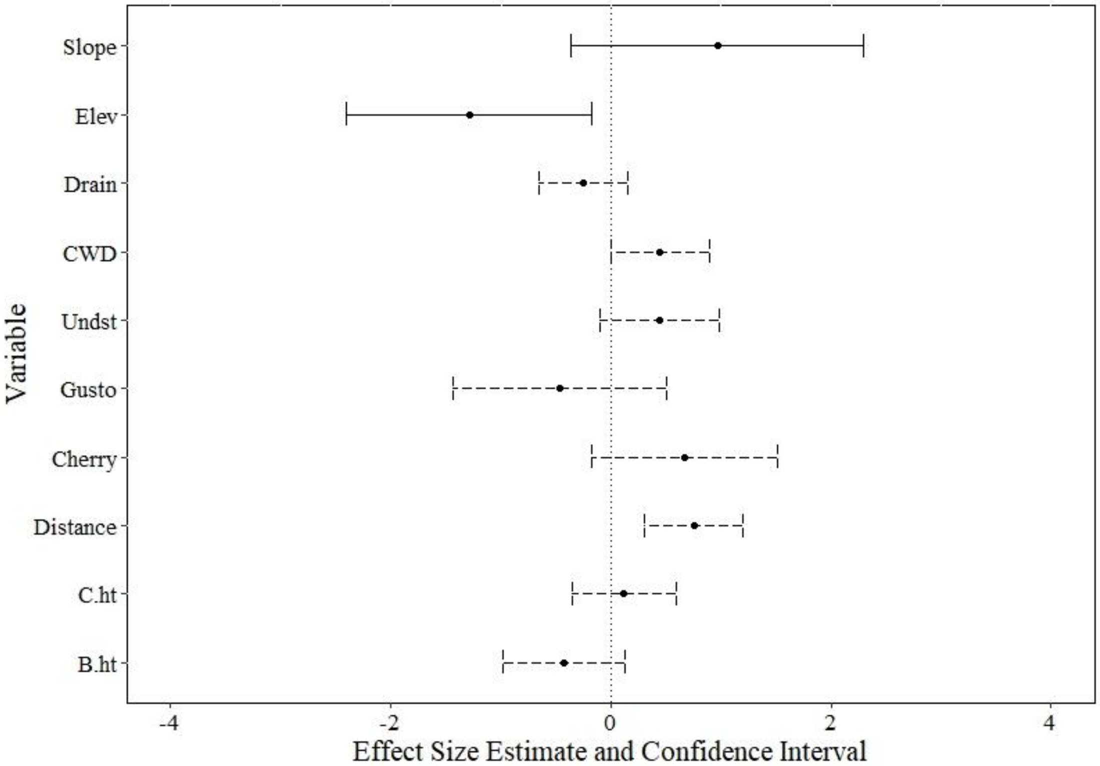

Figure 2 Effect sizes and 95% confidence intervals for covariates from our top *a priori* models evaluating detection and occupancy probability in the southern Appalachians. Solid lines indicate effect estimates and confidence intervals for our site covariates and dashed lines indicate estimates and confidence intervals for our detection covariates. Parameter descriptions can be found in Table 1.

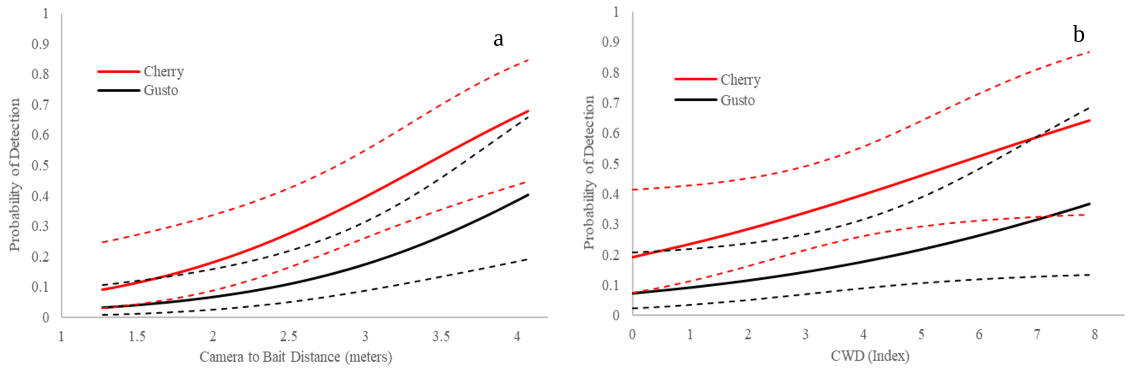

Figure 3 Predictive plots illustrating the effects of our top detection covariates on probability of detection of eastern spotted skunks in the Southern Appalachians. Both figures display effects (solid lines) and 95% confidence intervals (dashed lines) when sites were treated with both Cherry oil (red lines) vs Caven’s Gusto™ (black lines).

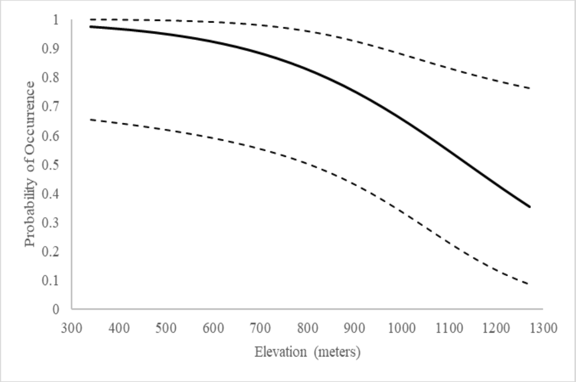

Figure 4 Predictive plot illustrating the effect and 95% confidence interval of elevation, our top site covariate, on the occupancy probability of eastern spotted skunks in our study area of the southern Appalachians.

CHAPTER TWO

UNDERSTORY COVER AND TOPOGRAPHIC FEATURES INFLUENCE REST SITE HABITAT SELECTION BY EASTERN SPOTTED SKUNKS IN SOUTHERN APPALACHIAN HARDWOOD FORESTS

INTRODUCTION

Eastern spotted skunks (*Spilogale putorius*) are a small, nocturnal mesocarnivore species that once ranged throughout much of the eastern United States (Kinlaw 1995). Although spotted skunk fur harvests once exceeded 100,000 per year, records from throughout the 20th century suggest that the species population had declined by over 95% by the end of the century (Gompper and Hackett, 2005). Consequently, many states have listed eastern spotted skunks as a species of conservation concern (Sprayberry and Edelman 2018) and the International Union for Conservation of Nature (IUCN) has upgraded the species' conservation status to "Vulnerable" (Gompper and Jachowski 2016). Although the cause of this dramatic decline remains undetermined, disease outbreaks, over harvesting, and wide-spread changes in agricultural practices are the leading theories that could explain this population crash (Gompper and Hackett 2005). In particular, the transition from small homestead farms to large scale agricultural practices in the 20th century has resulted in the conversion of land to single crop monocultures that provide little cover for resting sites, and has also led to the introduction of wide-spread pesticide use (Dimitri et al. 2005), two factors which may have had dramatic negative effects on eastern spotted skunks (DeSanty 2001, Gompper and Hackett 2005).

Despite indications that the range-wide decline of eastern spotted skunks may be due to habitat loss, recent evidence from across their historic distribution suggests they are moderately versatile in the range of habitats they can occupy. The plains spotted skunk subspecies (*S. p. interrupta)* has been reported to inhabit a diverse variety of wooded habitats, open prairies, and cultivated lands (DeSanty 2001, Lesmeister et al. 2009). The Appalachian subspecies (*S. p. putorius)* has recently been recorded in deciduous and coniferous forests of the southern Appalachians (Sprayberry and Edelman 2018), as well as in the high elevation spruce forests (Diggins et al. 2015) and hardwood forests of the central Appalachians (Thorne et al. 2017). Farther south, the Florida eastern spotted skunk (*S. p. ambarvalis*) occupies coastal scrub or dry prairie vegetation (Kinlaw et al., 1995; S. Harris, Clemson University, Personal communication), and have additionally been reported in more developed suburban areas (Gompper and Jachowski 2016). While these observations suggest that eastern spotted skunks may be habitat generalists at the landscape scale, knowledge of their current distribution, habitat needs, and demographic trends remain unknown. Investigations of fine-scale habitat selection could provide valuable insights about the ecological factors that are driving survival rates in extant populations of eastern spotted skunks throughout their range.

Evaluating fine-scale habitat preferences within an individual's home range can help ecologists and wildlife managers identify specific habitat attributes that may be disproportionately important to a species life history (Johnson 1980). For instance preferred corridors for movement, patches of high forage value, or suitable sites for resting or rearing young may constitute only a small portion of an individual's home range, yet be imperative for its survival (Mayor et al. 2009). For spotted skunks, fine-scale habitat suitability has been associated with dense understory cover, a general habitat feature that may vary in structure and composition depending on the local vegetation (Kinlaw 1995, Lesmeister et al. 2008, Sprayberry and Edelman 2018). However, in pine dominated forests of the southern US, a primary objective of many habitat management practices is to reduce understory cover, which can negatively affect habitat availability for eastern spotted skunks (Lesmeister et al. 2013, Sprayberry and Edelman 2018). Similarly, in southern Appalachian hardwood forests, fuel reductions and attempts to remove recalcitrant layers of understory shrubs are common practices (Waldrop et al. 2016), but their effects have not been considered in respect to the eastern spotted skunk. Thus, an improved understanding of the fine-scale habitat needs of eastern spotted skunks in the southern Appalachians could allow for more precise management regarding primary areas of conservation concern and biological objectives that should be prioritized.

In this study, we investigated summer rest and den site selection by eastern spotted skunks in the hardwood-dominated southern Appalachian forests of South Carolina. Based on results of previous mesocarnivore habitat selection studies, we hypothesized that three general biological factors would drive fine-scale habitat selection by spotted skunks. First, we hypothesized that spotted skunks would select for habitat that provided ample refugia from predators (Fedriani et al. 2000, Vanak and Gompper 2010). Second, we hypothesized that spotted skunks would prefer to use rest sites nearer to abundant sources of prey (Spencer et al. 1983, Litvaitis et al. 1986, Vanak and

Gompper 2010). Finally, we hypothesized that spotted skunks would select rest sites that provided stable temperatures throughout the day to limit thermoregulatory stress (Lesmeister et al. 2008, Aubry et al. 2013). Results from this study will provide new information about the habitat requirements of eastern spotted skunks in southern Appalachian hardwood forests, and will contribute to our understanding of the biological factors that may be driving spotted skunk success or declines throughout the species' range.

METHODS

Study Area

Our study took place in the southern Appalachian hardwood forests of northwestern South Carolina. These forests vary in species composition, but are primarily characterized by four main forest types: northern hardwoods, cove hardwoods, mixed deciduous, and xeric oak-pine forests (Bolstad et al. 1998, Elliott et al. 1999, Turner et al. 2003). In particular, our study took place on 100 km^2 of the Andrew Pickens Ranger District, Sumter National Forest, SC (Figure 1) where a recent study reported detections of eastern spotted skunks (Wilson et al. 2016). This area ranges from 300 to 800 m in elevation, and is primarily comprised of mixed deciduous, cove hardwood, and xeric oak-pine forests. Forest canopies were dominated by oak species (*Quercus spp.),* red maple (*Acer rubrum*), sourwood (*Oxydendrum arboretum*), black gum (*Nyssa sylvatica),* hickory species (*Carya spp.)*, tulip-poplars *(Liriodendron tulipifera*), and pine species (*Pinus spp.*). Understory vegetation was largely comprised of rhododendron

(*Rhododendron maximum)* and mountain laurel *(Kalmia latifolia)*, but was frequently supplemented by deciduous and coniferous tree saplings, American holly (*Ilex opaca*), dog-hobble *(Leucothoe fontanesiana)*, and dense patches of *Vaccinium spp*. Additionally, our study area spanned the Blue Ridge escarpment, a unique area where the Blue Ridge physiographic region abruptly drops several hundred meters into the Piedmont physiographic region of South Carolina (Abella et al. 2003). The nature of the escarpment is such that the hillsides are heavily fragmented by numerous first and second order ravines and streams, creating overall steep and rugged terrain (Prince et al. 2010). These minor headwater ravines and first order streams generally constitute more than half the length of total drainage networks, and are often ephemeral or entirely dry, containing water only during or immediately following heavy rain events (Hansen 2001).

Field Methods

We trapped spotted skunks from January through April of 2016 and 2017. We used single-door Tomahawk live traps (15x15x48 cm) fit with corrugated plastic covers that provided protection from inclement weather or other animals, and set traps along roads surrounded by national forest land where spotted skunks had been detected in previous years (Wilson et al. 2016). We baited traps with canned fish in oil mixed with peanut butter, and applied both cherry oil and Caven's gusto™ (Minnesota Trapline Products, Inc.) as far-reaching scent lures. Once captured, skunks were run into a canvass handling cone to secure the animal for processing. Captured individuals were weighed, sexed, checked for ectoparasites, aged by tooth-wear, ear tagged (Monel ear tags, size

1005-1), and fit with 16g VHF zip-tie radio collars (Advanced Telemetry Systems, model m1545). Collar weight did not exceed 5% of any individual's body weight, and all handling procedures were in accordance with The Institutional Animal Care and Use Committee (IACUC Protocol #2015-042).

From April to August each year we intensively tracked collared skunks during the daylight hours to the immediate structure (e.g., cavity or burrow) where they were resting. We used a hand-held portable telemetry receiver (Communication Specialists, R-1000 Receiver) and a 3-element folding yagi antenna to track each skunk to its rest site approximately once every 6 days (range 2-22; average 6.02) until the skunk perished or collar malfunction inhibited our ability to locate the transmitter signal. Although some of these sites could be distinguished as "den sites" where females were rearing young, we will refer to all locations as "rest sites" for the purpose of this study. If a skunk re-used a rest site or stayed in a single site for more than 5 days, we treated it as an independently selected location. To evaluate habitat selection relative to what was available to our collared skunks, we also identified a random available site (henceforth "random site") for each rest site. Random sites were located along a random bearing between 50 and 200 m from each rest site. We determined an available rest site based on three criteria outlined by Crabb (1948) such that a random site had to (1) exclude sunlight during the daytime hours, (2) provide protection and insulation from external weather conditions, and (3) provide protection from sympatric competitors or predators. We interpreted this last criterion by selecting sites with entrances that did not exceed 30x30 cm and cavities that appeared to extend far enough for a skunk's body to fully fit inside (≥30 cm in length;

Crabb, 1944). The maximum distance of 200 m to a random site was chosen as a value we considered reasonable to represent the nightly-traversable distance for eastern spotted skunks. Post-hoc calculations of the minimum distances traversed per night (distance between consecutive rest sites divided by the number of days between locations) supported this assumption; on average, the minimum distance traversed by spotted skunks in a night was 99 m (range 3-636 m, median 79 m). In 2017, we increased the minimum distance to locate a paired random site from 50 to 80 m in order to decrease the frequency of locating a random site on the same slope or along the same drainage channel where few differences in habitat were evident.

We recorded the location of every rest site and random site using a global positioning system (GPS) unit (Garmin, Kansas City, KA, USA) and measured a suite of surrounding habitat characteristics (Table 1). Within a 10x10 m square centered around each rest site entrance we performed visual estimates of canopy cover, understory cover, and ground cover, and measured an index of coarse woody debris (CWD) abundance. Coarse woody debris was measured on a scale of 0-10, with 0 indicating no CWD >10 cm diameter, and 10 indicating the entire area was covered by CWD. We also counted the number of woody stems present within a 5x5 m square around the rest site entrance. We used ArcGIS 10.5 (ESRI 2017) and a 1/9 arc-second digital elevation model (USGS 2013) to calculate the slope, aspect, and distance to the nearest stream or headwater ravine (henceforth “drainage channels”). Drainage channels were identified using the ‘flow accumulation’ tool and a 1500 cell accumulation threshold in ArcMap (Montgomery and Foufoula-Georgiou 1993); stream order was not differentiated for this study. To determine the land cover type for our sites, we used the 2011 National Land Cover Dataset (NLCD), and grouped land cover categories that were not deciduous, mixed, or coniferous forest into a fourth category considered “open” canopy (Table 1).

Analyses

We used a discrete choice framework to assess relative probability of selection based on comparisons of habitat attributes between rest sites and the paired random sites. These analyses allow for evaluation of the overall perceived “utility” of a habitat patch within an individual’s home range, based on differences in the selected habitat as compared with immediately available but unselected areas (Cooper and Millspaugh 1999, Burnham and Anderson 2002). We used Akaike Information Criterion for small samples sizes (AIC_c) to rank our competing models, and model averaged parameter estimates from the candidate models that comprised a 95% confidence set. We then compared model averaged parameter estimates to determine which habitat characteristics appeared to have the strongest effects on fine-scale eastern spotted skunk habitat selection and use.

We developed 13 *a-priori* models to evaluate support for the three factors we hypothesized would influence rest site selection (Table 2). First, under our prey selection hypothesis, because spotted skunks are known to prey upon salamanders, insects, and small mammals (Crabb 1941, McCullough and Fritzell 1984, Kinlaw 1995, Sprayberry and Edelman 2016, Thorne and Waggy 2017), we predicted spotted skunks would select for rest sites near drainage channels and with abundant CWD where these prey items are likely to be abundant (McMinn and Crossley 1993, Braccia and Batzer 1999, Gompper et al. 2006, Bogan et al. 2013). Second, to minimize thermoregulatory stress, we predicted that spotted skunks would select sites on northwestern facing slopes for their cooler and less humid conditions (Fekedulegn et al. 2004), and would prefer deciduous forests which provide deeper shade than pine, mixed, or open canopies (Lesmeister et al. 2008). Third, under our predation risk hypothesis, we evaluated support for five variables that we predicted would be positively associated with predator avoidance: ground cover, understory cover, canopy cover, slope, and woody stem abundance. Specifically, we predicted that (1) all three sources of vegetative cover would reduce skunk visibility to predators, that (2) steep slopes and woody stems would inhibit mammalian predator maneuverability (Reichman and Aitchison 1981, Litvaitis et al. 1985), and that (3) abundant understory cover alone would provide cover from owls, the primary predator of spotted skunks (Lesmeister et al. 2010). Our candidate set also included six sub-global models, which were combinations of the models described above, and a global model containing all nine habitat variables (Table 2).

We used Program R version 3.4.2 (R Core Team, 2017) to prepare our data for analyses, and used the R package “mlogit” (Croissant, 2013) to evaluate our discrete choice models. Owing to field sampling errors, we were unable to collect ground cover measurements at <10% of sites. To retain this variable in our analysis, we imputed average ground cover values for those sites. All variables were screened for multicollinearity, and no variables were found to have correlation coefficients above 0.32. We transformed the aspect degree values calculated in ArcGIS to a 0-180 linear measure of Southeast-Northwest orientation (respectively) using the equation $asp135 = |asp^{\circ} - 135|$ for aspect measures 0-314.9º, and $asp135 = |asp^{\circ} - 495|$ for measures ≥315º.

All continuous data were scaled linearly to range from approximately 0-10 to allow for comparison between variable effects. Because of limited sample size, we pooled rest site data from all individuals for use in our analyses.

Model Validation

We performed ten iterations of k-fold cross validation to test the predictive performance of our top model (Boyce et al. 2002). We used k=5 for each iteration of validation, such that we used a random subset of 80% of our choice sets (pairs of rest sites and random available sites) to train our top model and the remaining 20% of choice sets to test the predictive capacity of the trained model. For each iteration of model validation, we calculated the relative probability of selection for each rest site and paired available site in our test choice-sets, and then compared these probabilities to determine how often our model would accurately selected a used site over a random available site, as was indicated by a relative probability greater than 0.5 (Bodinof et al. 2012).

RESULTS

We captured 28 eastern spotted skunks between 2016 (n=15) and 2017 (n=13), however due to collar malfunctions, poor collar fits, and mortality events, only 15 spotted skunks (10 males and 5 females) were tracked to rest sites that provided data for this study (for more information refer to Appendix A). We successfully tracked our collared individuals 233 times (63 female and 170 male locations) and collected data for an equivalent number of random-available sites. Of these 233 tracking events, we located 205 unique rest sites, indicating a 12% rate of re-use (n=28). Of those re-used rest sites, 61% were at den sites of the three females known to be rearing kits (n=17). Of all re-used sites, we identified only three locations where spotted skunks were recorded returning to the same structure on non-consecutive tracking events. Only one site was used by two different individuals, and the first occupant was presumed deceased several months prior to when the site was re-used. Structures we identified as random available sites were abundant on the landscape, such that on average, we found a random site less than 100 m from the identified rest site (average 91.8 ± 19.6, range 53-181m).

Spotted skunks utilized a variety of structures for rest sites (Table 3), a majority of which were dependent on trees for structure (e.g. root burrows, tree cavities, or hollow logs; n=164), and a majority of these trees were snags or standing deciduous trees (n=97). We found the most rest sites in root burrows (n=82; 40%), which we characterized as any structure maintained by the presence or decomposition of major tree roots. Tree cavities were the next most frequently identified rest site structures (n=61; 29.8%) and were defined as hollows in live or dead trees, such that the cavity itself was above ground level. We also found many sites in ground burrows (n=40; 19.5%); underground structures that did not appear to be dependent on major tree roots, and were likely created by a small mammal. Finally, we identified several sites in hollow logs (n=22; 10.7% of sites) and on rare occasions under rocky substrate (n=2; <1% of sites) (Figure 2). Of the 17 female denning sites identified, 53.3% were in ground burrows, 35.3% were in root cavities, while CWD and tree cavities were each used only once as den sites. Two of our females spent over a month in their first den site (approximately 50 and 35 days), while our third reproductive female spent over 2 weeks in each of her first two den sites.

Three of our 13 *a priori* models representing forage quality and predator avoidance comprised the 95% confidence set (Table 4). Three parameters, distance to drainage channel, CWD, and understory cover, were present in all three of our top models. Ground cover, canopy cover, slope, and woody stem count were also present in the models of our 95% confidence set, but had very small effect sizes, or parameter estimates that overlapped zero (Table 5). We model averaged parameter estimates to evaluate effect size and direction of the retained covariates. Our results showed a negative relationship with drainage channels, such that relative probability of selection decreased by half for every 50 m farther a site was from a drainage channel. Understory cover and CWD had positive effects on relative probability, such that selection doubled with a 35% increase in understory cover and with a four-times increase in CWD (Figure 3). K-fold cross validation indicated that our model was able to accurately predict if a site was used or random 70% the time.

DISCUSSION

Consistent with previous studies, our results indicated that eastern spotted skunks in southern Appalachian hardwood forests select rest sites in areas where they have increased protection from predators (Lesmeister et al. 2008, Sprayberry and Edelman 2018). Intraguild killing is a major factor that can drive demographic rates of many mesocarnivore species (Palomares and Caro 1999, Terraube and Bretagnolle 2018), and as one of the smallest members of this guild, the threat of intraguild killing may be particularly influential to eastern spotted skunk habitat selection. Although spotted skunks are equipped with a potent olfactory defense mechanism to deter predators in close proximity, there is evidence that spotted skunks first rely on cryptic pelage pattern to reduce their chances of being detected by predators (Caro et al. 2013). In particular, owls are known to be a primary predator of eastern spotted skunks, and understory cover has been associated with a reduced risk of owl predation (Lesmeister et al. 2010). The efficacy of spotted patterns as camouflage is enhanced by dappled lighting (Caro 2005), which leads us to suspect that spotted skunks may not only select for a dense understory because it provides a barrier to direct visibility from owls overhead, but also because it scatters the light in a way that increases their ability to remain cryptic while they move about the forest floor.

Our results supported the hypothesis that prey availability is an important driver of eastern spotted skunk rest site habitat selection. While previous studies have reported other mesocarnivore species select habitat based on prey availability (Spencer et al. 1983, Litvaitis et al. 1986), ours was the first study to find indirect support for this hypothesis for eastern spotted skunks. As dietary generalists showing little rest site fidelity (Crabb 1948, Lesmeister et al. 2008, Sprayberry and Edelman 2018), our results suggest that spotted skunks likely utilize an optimal foraging strategy by selecting rest sites in or near patches of high quality foraging habitat (Macarthur and Pianka 1996). In this study we considered higher availability of CWD and lower distance to drainage channels as proxies for areas with high quality forage. However, a direct investigation of eastern spotted skunk diet in the southern Appalachians would allow for a better interpretation of how prey availability may be influencing habitat selection and behavior of eastern spotted skunks throughout the year. In particular, there is evidence that diet may fluctuate seasonally, with spotted skunks showing a preference for small mammals in the winter and invertebrates in the summer (Crabb 1941, McCullough 1983). Based on our results, we suggest that these fluctuations in prey availability may result in seasonal variation in fine-scale habitat preferences of eastern spotted skunks. In particular, we recommend further investigation of habitat selection during the winter when prey is likely to be limited and deciduous leaf cover is reduced.

In general, CWD likely serves as both foraging habitat and protective structure for eastern spotted skunks in southern Appalachian Hardwood forests, and may warrant greater consideration in regard to its overall ecological value. Both small mammals and invertebrates use CWD throughout the many stages of decomposition (Harmon 1982, Braccia and Batzer 1999, Loeb 1999, Koenigs et al. 2002), thus providing a stable food source for eastern spotted skunks throughout the year. We also recorded many instances of spotted skunks using CWD as rest site structure, suggesting that CWD can provide protection from predators. In particular, CWD may be important as protective structure for spotted skunks in between foraging bouts while handling and consuming prey items, when requirements for protective cover may be less stringent (Crabb 1948). Although it was one of the most important habitat attributes identified in our study, other studies of spotted skunk rest site selection in pine dominated ecosystems have not found strong associations with CWD (Lesmeister et al. 2008, Sprayberry and Edelman 2018). Because hardwood trees tend to decay more slowly and persist on the forest floor for longer than many coniferous softwood species (Moorman et al. 1999), we suggest this contrasting result may be related to differences in overall abundance of CWD between study areas.

Management efforts that maintain large decaying trees and allow for the persistence of some CWD have been successfully implemented in other forested systems (Bull et al. 1997), and we suggest similar practices may be beneficial in southern Appalachian hardwood forests.

Distance to drainage channel was our strongest predictor of eastern spotted skunk rest site selection, and we suggest that this feature may warrant greater consideration as a habitat attribute relevant to many aspects of spotted skunk ecology. Although previous studies have considered distance to water or distance to streams as a predictor of mesocarnivore rest site selection (Spencer et al. 1983, Zielinski et al. 2004, Lesmeister et al. 2008, Purcell et al. 2009), these metrics often exclude consideration of dry or ephemeral first order streams or headwater ravines. In general, dry and ephemeral minor drainage channels are neither well defined nor well studied, despite these features constituting over half the length of stream networks (Hansen, 2001; Montgomery and Buffington, 1997). Furthermore, they play an important role in shaping the topography of mountainous terrain (Prince et al. 2010), and can have strong effects on forest and vegetative composition (Swanson et al. 1982, Bolstad et al. 1998). A better understanding of how eastern spotted skunks use variably sized drainage channels could provide important insights about best management practices, while knowledge of how spotted skunks move or travel within stream networks could provide crucial information about dispersal and connectivity for populations throughout the species' range. For instance, drainage channels are inherently connected with a larger drainage networks and tend to be less steep than the surrounding hillsides, making them possible corridors for dispersal and exploration (Campbell Grant et al. 2007). Confluences of drainage channels of any size could also act as natural hubs for olfactory communication, and may be important for establishing home range boundaries (Campbell Grant et al. 2007). In general, our results suggest there is a need for further research regarding the way animals use drainage networks in mountainous systems and how management practices may be impacting or fragmenting these features.

Spotted skunks in the southern Appalachian hardwood forests appear to be opportunistic in the specific structures they use as rest sites. Nonetheless, when compared with rest site selection studies in conifer-dominated forests (Lesmeister et al. 2008, Sprayberry and Edelman 2018) we observed several differences in use and selection of rest site structures. Our skunks showed distinctly lower rates of site re-use than in other populations (12% vs >40%), suggesting that suitable rest sites may have been more abundant in our study area. In addition, spotted skunks in our study used tree-associated structures (e.g. tree cavities, root burrows, or hollow logs) twice as often and used ground burrows only half as often as was reported in either of the other studies (Lesmeister et al. 2008, Sprayberry and Edelman 2018). This high use of tree-associated structures could be related to the increased proportion of deciduous hardwood trees in the area, which may provide more suitable tree cavities for mammalian carnivores (Paragi et al. 1996). In contrast to previous studies where 14-17.5% of rest sites were found in rocky outcrops (Lesmeister et al. 2008, Sprayberry and Edelman 2018), rocky outcrops were largely absent from our study area and composed <1% of rest sites. Overall, given the variety of structures we detected spotted skunks using as rest sites, it is likely that rest site selection may be more impacted by habitat characteristics of the surrounding area.

While spotted skunk research is ongoing in many systems, our overall knowledge of eastern spotted skunk ecology remains vague. Although progress has been made in determining their current distribution over the past decade, studies of landscape-scale habitat selection have been unable to identify strong predictors of spotted skunk occurrence in their Appalachian range, which may largely be due to the species' low probability of detection, (Chapter 1; Thorne et al., 2017). Thus, further studies like this one that track individual animals may provide the best insights about what composes suitable habitat for this species. In particular, investigation of the fine-scale needs for den sites by reproductive females could illuminate important limitations to recruitment. Many mesocarnivore species show increased selectivity when determining suitable den sites, particularly for parturition and early-rearing when offspring are extremely vulnerable (Brainerd et al. 1995, Paragi et al. 1996, Magoun and Copeland 1998, Bull and Heater 2000, Birks et al. 2005). A better knowledge of the site and structure characteristics preferred by denning eastern spotted skunks would allow for directed efforts to ensure availability of suitable den site structures. Such management efforts could improve rates of spotted skunk kit survival which in turn could benefit the overall demographic trends of this cryptic species. Furthermore, recent studies of eastern spotted skunks have only been carried out in protected areas such as national forest or state protected land (Lesmeister et al. 2008, Wilson et al. 2016, Thorne et al. 2017, Sprayberry and Edelman 2018), resulting in a lack of knowledge about how this species may be interacting with and responding to anthropogenic development. A better understanding of how eastern spotted skunks are responding to anthropogenic influences at multiple scales is crucial to our ability to design effective management objectives for spotted skunk conservation. We also recommend future studies more directly investigate how eastern spotted skunk habitat selection varies over time in response to prescribed fire and other management practices. Overall, while our understanding of spotted skunk ecology has been greatly advanced in the past decade, a better understanding of eastern spotted skunk distribution, habitat associations and demography are still urgently needed to better understand their current status and develop appropriate conservation plans.

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TABLES

Table 1 Variable names, abbreviations, and descriptions of parameters measured to evaluate eastern spotted skunk rest site selection the southern Appalachian hardwood forests in 2016 and 2017.

Variable	Abbreviation	Description
Canopy Cover	Canopy	Percent cover from canopy vegetation greater than 5 m tall within a 10x10 m square around the site.
Understory Cover	Undst	Percent cover from understory vegetation between 1-5 m tall within a 10x10 m square around the site.
Ground Cover	Ground	Percent cover from ground-level vegetation less than 1 m tall within a 10x10 m square around the site.
Coarse Woody Debris	CWD	Index of coarse woody debris abundance within a 10x10 m square around the site. Index ranged from 0-10 with 0 indicating no CWD, and 10 indicating a major blowdown covering the entire area.
Stem Count	Stems	Number of woody stems within 5x5 m square around the site.
Canopy Type	Type	A factor of the dominant cover type, calculated from the 2011 NLDC dataset at 30 m resolution (Deciduous, Mixed, Coniferous, or Open)
Dist to Drainage Channel	Drain	Distance to nearest drainage channel in m. Drainage channels were identified in ArcGIS using flow accumulator with a 1/9 arc-second USGS DEM and a 1500 cell accumulation threshold.
Slope	Slope	Steepness of the slope in degrees, calculated in ArcGIS using a 1/9 arc-second USGS DEM
Aspect	Aspect	Aspect of the slope, calculated in ArcGIS using a 1/9 arc-second USGS DEM and transformed to represent a linear Northwest-Southeast gradient

Table 2 Hypotheses, model structures, predicted parameter responses for the 13 *a-priori* models developed to evaluate eastern spotted skunk rest site selection in the southern Appalachian hardwood forests. See Table 1 for parameter descriptions

Hypothesis	Model Structure	Predicted Response
Primary Hypotheses		
(1) FORAGE: Drainages and abundant CWD will provide good foraging habitat	= ß$_1$(drain)+ß$_2$(CWD)	ß$_1$ < 0, ß$_2$ > 0
(2) THERMOREGULATION: Northwest facing slopes and deciduous forests will produce cooler temperatures and reduce thermoregulatory stress	= ß$_1$(aspect)+ß$_2$(mixed)+ß$_3$(conifer) +ß$_4$(open)	ß$_1$ > 0, ß$_2$ < 0, ß$_3$ < 0, ß$_4$ < 0
(3) PREDATORS: Ground, understory, and canopy cover will decrease visibility; steep slopes and woody stems will reduce predator maneuverability	= ß$_1$(undst)+ß$_2$(canopy)+ß$_3$(ground) +ß$_4$(stems)+ß$_5$(slope)	ß$_1$ > 0, ß$_2$ > 0, ß$_3$ > 0, ß$_4$ > 0, ß$_5$ > 0
(4) PRED.COVER: Ground, understory, and canopy cover will provide reduced visibility from all predators	= ß$_1$(undst)+ß$_2$(ground)+ß$_3$(canopy)	ß$_1$ > 0, ß$_2$ > 0, ß$_3$ > 0
(5) PRED.MOVE: Steep slopes and abundant woody stems will reduce maneuverability for mammalian predators	= ß$_1$(stems)+ß$_2$(slope)	ß$_1$ > 0, ß$_2$ > 0
(6) PRED.UNDST: Dense understory will provide protection from avian predators	= ß$_1$(undst)	ß$_1$ > 0
Sub-Global Models		
(8) THERM+FORAGE	= ß$_1$(aspect)+ß$_2$(mixed)+ß$_3$(conifer) +ß$_4$(open)+ß$_5$(drain)+ß$_6$(CWD)	ß$_1$ > 0, ß$_2$ < 0, ß$_3$ < 0, ß$_4$ < 0, ß$_5$ < 0, ß$_6$ > 0
(9) THERM+PREDATORS	= ß$_1$(aspect)+ß$_2$(mixed)+ß$_3$(conifer) +ß$_4$(open)+ß5(undst)+ß$_6$(canopy) +ß$_7$(ground)+ß$_8$(stems)+ß$_9$(slope)	ß$_1$ > 0, ß$_2$ < 0, ß$_3$ < 0, ß$_4$ < 0, ß$_5$ > 0, ß$_6$ > 0, ß$_7$ > 0, ß$_8$ > 0, ß$_9$ > 0
(7) FORAGE+PREDATORS	= ß$_1$(drain)+ß$_2$(CWD)+ß$_3$(undst) +ß$_4$(canopy)+ß$_5$(ground)+ß$_6$(stems) +ß$_7$(slope)	ß$_1$ < 0, ß$_2$ > 0, ß$_3$ > 0, ß$_4$ > 0, ß$_5$ > 0, ß$_6$ > 0, ß$_7$ > 0
(10) FORAGE+PRED.UNDST	= ß$_1$(undst)+ß$_2$(drain)+ ß$_3$(CWD)	ß$_1$ > 0, ß$_2$ < 0, ß$_3$ > 0
(11) FORAGE+PRED.COV	= ß$_1$(drain)+ß$_2$(CWD)+ß$_3$(undst) +ß$_4$(canopy)+ß$_5$(ground)	ß$_1$ < 0, ß$_2$ > 0, ß$_3$ > 0, ß$_4$ > 0, ß$_5$ > 0
(12) FORAGE+PRED.MOVE	=ß$_1$(drain)+ß$_2$(CWD)+ß$_3$(stems) +ß$_4$(slope)	ß$_1$ < 0, ß$_2$ > 0, ß$_3$ > 0, ß$_4$ > 0
(13) GLOBAL	= ß$_1$(drain)+ß$_2$(CWD)+ß$_3$(undst) +ß$_4$(canopy)+ß$_5$(ground)+ß$_6$(stems) +ß$_7$(slope)+ß$_8$(aspect)+ß$_9$(mixed) +ß$_{10}$(conifer)+ß$_{11}$(open)	ß$_1$ < 0, ß$_2$ > 0, ß$_3$ > 0, ß$_4$ > 0, ß$_5$ > 0, ß$_6$ > 0, ß$_7$ > 0, ß$_8$ > 0, ß$_9$ < 0, ß$_{10}$ < 0, ß$_{11}$ < 0

Table 3 Average values, standard errors, and ranges of values for each parameter measured to describe eastern spotted skunk rest sites and random available sites, and their surrounding habitat in the southern Appalachian hardwood forests of South Carolina in 2016 and 2017. See Table 1 for parameter descriptions.

Variable	Rest Sites Avg±SE (Range)	Random Sites Avg ± SE
Entrances	1.97±1.14 (1-6)	1.27 ± 0.57 (1-5)
Entrance Area (cm^2)	133.65±228.33 (10-2400)	132.53 ± 226.25 (12-2590)
Stem Count	3.72±1.71 (0.5-7.8)	3.46 ± 1.61 (0.5-7)
Canopy Cover (%)	78.89±18.07 (5-100)	82.73 ± 14.26 (25-100)
Undst Cover (%)	72.51±23.03 (5-100)	62.08 ± 25.02 (0-100)
Ground Cover (%)	27.33±28.48 (0-100)	27.26 ± 25.31 (0-100)
CWD	4.36±2.22 (1-10)	3.82 ± 1.92 (1-10)
Aspect(NW)	83.16±52.95 (1-179.2)	73.61 ± 52.77 (0.06-178.51)
Slope (degrees)	20.08±8.72 (1.65-47.56)	18.38 ± 8.02 (2.54-47.72)
Dist to Drain (m)	42.97±37.11 (0.44-156.74)	54.52 ± 39.72 (1.38-186.56)

Table 4 Ranked candidate models developed to predict eastern spotted skunks rest site selection in the southern Appalachian hardwood forests. Models are ranked by AIC_c values. See Table 2 for model descriptions.

Model	Log-Lik	K	AIC_c	Δ AIC_c	w_i
Forage+PredUndst	-137.096	3	280.223	0.000	0.678
Forage+PredCover	-136.110	5	282.300	2.077	0.240
Forage+Predators	-135.226	7	284.600	4.377	0.076
Global	-134.031	11	290.416	10.193	0.004
Forage+PredMove	-142.448	4	292.950	12.727	0.001
Forage	-145.234	2	294.484	14.261	0.001
Thermo+Forage	-142.573	6	297.258	17.035	0.000
PredCover	-145.625	3	297.282	17.059	0.000
Predators	-144.060	5	298.200	17.977	0.000
PredUndst	-148.760	1	299.525	19.302	0.000
Thermo+Predators	-143.590	9	305.420	25.197	0.000
PredMove	-157.519	2	319.053	38.830	0.000
Thermo	-157.877	4	323.807	43.584	0.000

Table 5 Estimates and standard errors of parameters hypothesized to predict eastern spotted skunks habitat selection in the southern Appalachian hardwood forests. Only parameters from the models in a 95% confidence set and model averaged parameters are included, see Table 1 for parameter descriptions.

Model	Dist to Drain	CWD	Understory Cover	Canopy Cover	Ground Cover	Slope	Stems
Forage+Undst	-0.27±0.08	0.17±0.06	0.20±0.05	-	-	-	-
Forage+PredCov	-0.26±0.08	0.16±0.06	0.21±0.06	-0.06±0.07	0.05±0.05	-	-
Forage+Predators	-0.24±0.08	0.16±0.06	0.21±0.06	-0.06±0.07	0.06±0.05	0.10±0.08	-0.01±0.07
Model Average	**-0.26±0.08**	**0.17±0.06**	**0.20±0.06**	**-0.02±0.02**	**0.02±0.02**	**0.01±0.01**	**<-0.01±0.01**

FIGURES

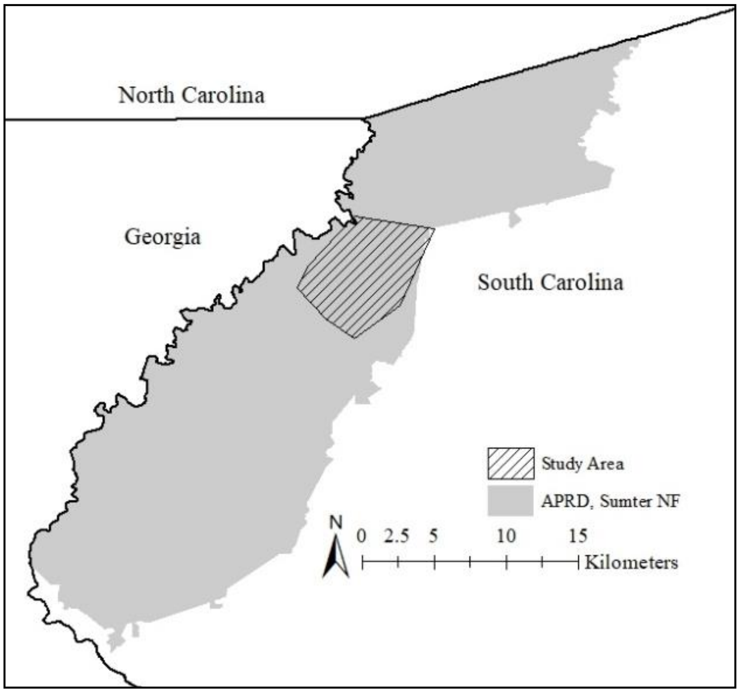

Figure 1 Map of our study area within the Andrew Pickens Ranger District (APRD) of Sumter National Forest where we evaluated eastern spotted skunk rest site selection in 2016 and 2017.

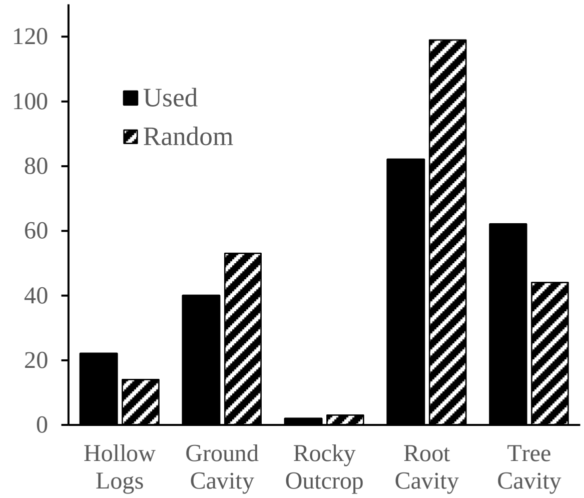

Figure 2 Number of structures used as rest sites by spotted skunks in the southern Appalachian hardwood forests of South Carolina in 2016 and 2017, compared with random sites located in the field

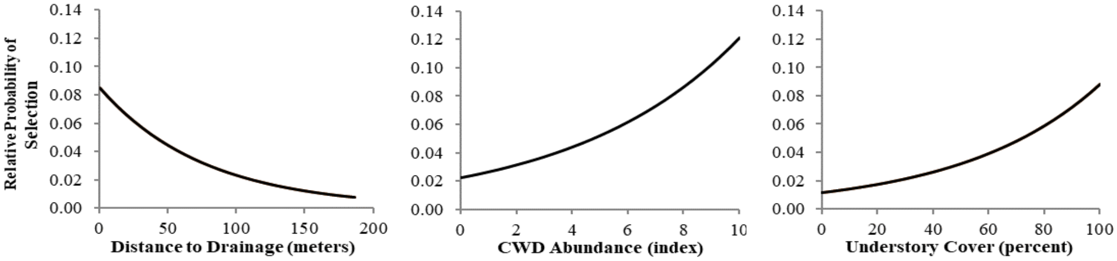

Figure 3 Predictive plots illustrating the change in relative probability of selection for the three top variables predicting eastern spotted skunk rest site selection in 2016 and 2017 in the southern Appalachian hardwood forests of South Carolina. All other covariates were held constant at their mean values for the creation of these plots. See Table 1 for parameter descriptions.

Appendix A

Descriptive data of captured eastern spotted skunks

Appendix A Descriptive data about captured eastern spotted skunks and the outcome of our tracking efforts from April-August in 2016 and 2017 on the Andrew Pickens Ranger District of Sumter National Forest, South Carolina.

Skunk ID	**Capture Date**	**Sex**	**Weight (g)**	**Collar (cm)**	**Outcome**
M01	3/2/2016	M	440	NA	Mortality signal (not retrieved)
M02	3/3/2016	M	510	NA	Mortality signal in tree (not retrieved)
F01	3/10/2016	F	330	NA	Presumed mortality
M03	3/10/2016	M	480	NA	Presumed mortality
M04	3/11/2016	M	450	NA	Survive (re-captured)
M05	3/14/2016	M	570	14.5	Mortality signal in tree (not retrieved)
M06	3/25/2016	M	570	12.8	Mortality signal (not retrieved)
F02	3/27/2016	F	450	NA	Collar slipped
M07	3/28/2016	M	540	11.2	Mortality signal (not retrieved)
M08	3/29/2016	M	530	12.9	Survive (re-captured)
M09	3/29/2016	M	510	12.5	Mortality
M10	3/31/2016	M	430	11.9	Signal lost
M11	4/1/2016	M	440	12.2	Collar clasp broken
F03	4/6/2016	F	390	10.6	Collar failure (not re-captured)
M12	4/12/2016	M	440	11.1	Survive (re-captured)
M13	2/3/2017	M	430	11.5	Mortality signal in burrow (not retrieved)
F04	2/22/2017	F	360	9.8	Presumed mortality
M04	2/23/2017	M	540	10.7	Presumed mortality
M14	2/25/2017	M	630	11.9	Collar slipped
F05	2/26/2017	F	420	9.8	Presumed mortality
M15	2/28/2017	M	560	11	Survived (removed collar)
F06	3/4/2017	F	520	10.7	Presumed mortality
M12	3/4/2017	M	650	11.5	Survived (removed collar)
M16	3/7/2017	M	520	11.4	Signal lost
M17	3/16/2017	M	410	9.8	Collar slipped
F07	3/21/2017	F	360	9.1	Collar clasp broken
M18	3/23/2017	M	590	11.1	Survived (removed collar)
M08	3/29/2017	M	530	11.1	Survived (removed collar)
M19	4/2/2017	M	510	10.7	Survived (removed collar)
F08	4/7/2017	F	420	9.5	Mortality
M20	4/11/2017	M	480	9.9	Collar slipped