Journal of Mammalogy, 100(4):1295–1304, 2019
DOI:10.1093/jmammal/gyz075

Summer rest site selection by Appalachian eastern spotted skunks

Robin Y. Y. Eng* and David S. Jachowski

Clemson University, Department of Forestry and Environmental Conservation, Clemson, SC 29634, USA

* *Correspondent: reng@g.clemson.edu*

Eastern spotted skunks (*Spilogale putorius*) have suffered a dramatic range-wide decline leading to concern that the species is likely vulnerable to extinction, but were recently discovered to persist in a portion of the southern Appalachian Mountains (United States). For 2 years we investigated habitat selection by eastern spotted skunks to develop an understanding of their habitat and conservation needs in northwestern South Carolina. We used a discrete choice modeling framework to evaluate vegetative and topographic features that we predicted would influence rest site selection by male and female spotted skunks. Using VHF telemetry, we tracked 15 spotted skunks (10 males and 5 females) to 215 day-time rest sites between the months of April and August. Spotted skunks selected rest sites in close proximity to drainage channels, where the relative probability of selection decreased 18% and 50% with every 20-m increase in distance to a drainage channel for males and females, respectively. Relative probability of selection by female spotted skunks increased 30% for every one-unit increase in coarse woody debris (CWD), and relative probability of selection by male spotted skunks increased 25% for every 10% increase in understory cover. These results are consistent with previous studies that have identified cover as important for protection from predators; however, we additionally identified CWD and drainage channels as important to habitat selection by spotted skunks. These latter attributes are likely selected based on prey availability, but alternate ecological functions of these features warrant further investigation. Preservation of understory vegetation and CWD within drainage networks might benefit conservation of eastern spotted skunks in the southern Appalachians.

Key words: civet cat, discrete choice, habitat selection, mesocarnivore, small carnivore, South Carolina, Southern Appalachia, *Spilogale putorius*

Small and mid-sized mammalian carnivore species (mesocarnivores) are prevalent in forested ecosystems throughout the United States. The distribution, demographic trends, and habitat requirements of many mammalian mesocarnivores have yet to be investigated, despite increasing evidence of their substantial impacts on ecosystem structure and function (Roemer et al. 2009). For smaller mesocarnivore species (<1,000 g), our ability to understand elements of their life histories and ecological roles is further inhibited by weight restrictions when considering use of modern wildlife tracking technology (Blackie 2010; Moriarty and Epps 2015). Owing to these logistic difficulties and lack of previous attention, the smallest species of the mesocarnivore guild are often overlooked as research priorities.

Eastern spotted skunks (*Spilogale putorius*) have experienced dramatic range-wide declines. Among the smallest of the mesocarnivore guild, eastern spotted skunks generally weigh between 200 and 800 g, are typically nocturnal, and are known to prey upon insects, reptiles, amphibians, bird eggs, and small mammals (Crabb 1941; McCullough and Fritzell 1984; Kinlaw 1995; Sprayberry and Edelman 2016; Thorne and Waggy 2017). Eastern spotted skunks once ranged throughout much of the eastern United States (Kinlaw 1995); however, harvest records from throughout the 20th century suggest that the species had declined in abundance 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 decline remains unknown, disease outbreaks, over-harvesting, wide-spread changes in agricultural practices, the loss of early to mid-successional forests, and changes in the predator community are thought to be reasons for this population crash (Gompper and Hackett

2005; Gompper and Jachowski 2016; Thorne et al. 2017; Sprayberry and Edelman 2018).

Despite indications that the range-wide decline of eastern spotted skunks might be at least partially due to habitat loss and change, recent evidence from across their historic distribution suggests that 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, rocky outcrops, and cultivated lands (DeSanty 2001; Lesmeister et al. 2009; Boulerice and Zinke 2017). The Appalachian subspecies (*S. p. putorius)* occurs 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), and has been reported in more-developed suburban areas (Gompper and Jachowski 2016). While these observations suggest that eastern spotted skunks might be habitat generalists at the landscape scale, investigations of fine-scale habitat selection could provide valuable insights about the ecological factors influencing the occurrence of eastern spotted skunks in portions of their range where they are still extant.

Evaluating fine-scale habitat preferences within an individual's home range can help ecologists and wildlife managers identify specific habitat attributes that might 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 might constitute only a small portion of an individual's home range, yet might be imperative for its survival (Mayor et al. 2009). For spotted skunks, fine-scale habitat suitability has previously been associated with dense understory cover, a general habitat feature that might vary in structure and composition depending on the local vegetation (Kinlaw 1995; Lesmeister et al. 2008; Sprayberry and Edelman 2018). In pine-dominated forests of the southern United States, management efforts to promote habitat for the endangered red-cockaded woodpecker (*Leuconotopicus borealis*) often aim 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 managers attempt to mitigate wildfire hazards by reducing dry woody debris and dense layers of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*—Waldrop et al. 2016), but these management practices have not been considered with respect to their effects on the eastern spotted skunk.

In this study, we investigated summer rest site selection by eastern spotted skunks in the hardwood-dominated southern Appalachian forests of South Carolina. Based on results of previous studies of habitat selection by mesocarnivores, we hypothesized that three general biological factors would drive fine-scale habitat selection by spotted skunks. First, we hypothesized that spotted skunks would select habitat with dense understory cover that can provide refugia from predators (Fedriani et al. 2000; Lesmeister et al. 2010; 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 provide new information about the habitat requirements of eastern spotted skunks in southern Appalachian hardwood forests, and contribute to our understanding of the biological factors that might influence the occurrence of eastern spotted skunks in this portion of the species' range.

Materials and Methods

Study area.—Our study took place in the southern Appalachian 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, 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 arboreum*), black gum (*Nyssa sylvatica)*, hickory species (*Carya* spp.), tulip-poplars *(Liriodendron tulipifera*), and pine species (*Pinus* spp.). Understory vegetation was largely comprised of rhododendron and mountain laurel, 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, 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 bisected by numerous headwater ravines and first and second order streams, creating overall steep and rugged terrain (Prince et al. 2010). These minor drainages features—such as headwater ravines that are often entirely dry, and many first order streams that are ephemeral and contain water only during or immediately following heavy rain events—generally constitute more than half the length of total drainage networks (Hansen 2001). The average nighttime low temperature in the Andrew Pickens Ranger District during our field season was 16.9°C and ranged from 10.5° to 21.0°, while the average daytime high temperature was 28.5°C and ranged between 23.5° and 34.6° (National Centers for Environmental Information, https://www.ncdc.noaa.gov/).

Field methods.—We trapped spotted skunks from January through April of 2016 and 2017. We used single-door live traps

(Tomahawk Live Trap, Pro Series Model 103SS, Hazelton, Wisconsin) 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, Pennock, Minnesota) to nearby tree branches as far-reaching scent lures. Once captured, skunks were run into a canvas handling cone to secure the animal for processing. Captured individuals were weighed, checked for ectoparasites, and ear-tagged (National Band and Tag Company, Newport, Kentucky; Monel ear tag size 1005-1); sex was determined and age was estimated by tooth wear. All individuals were then fitted with 16-g VHF zip-tie radio collars (Advanced Telemetry Systems, Isanti, Minnesota; model m1545) before release at the capture site. 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 of Clemson University (IACUC Protocol #2015-042) and met guidelines of the American Society of Mammalogists for use of wild mammals (Sikes et al. 2016).

From April to August each year, we tracked and monitored collared skunks 5–6 days per week during daylight hours. We performed ground-based telemetry using a hand-held portable telemetry receiver (Communication Specialists, Orange, California; R-1000 Receiver) and a 3-element folding yagi antenna to track collared skunks to the immediate structure (e.g., cavity or burrow) where they were resting. We were able to locate each spotted skunk at a rest site approximately once every 6 days ($\bar{X}$ = 6.02; range 2–22) until the skunk perished, the collar was removed, or collar malfunction inhibited our ability to locate the transmitter signal. Similar to previous studies (Lesmeister et al. 2008; Harris 2018; Sprayberry and Edelman 2018), spotted skunks changed their use of day resting sites frequently. Thus, although some of these sites could be distinguished as "den sites" where females were rearing young, we were unable to identify when parturition occurred and could not accurately determine if a location was a central den for rearing pups or just a site being used during exploratory periods. Therefore, we will refer to all locations as "rest sites" for the purpose of this study. If a skunk returned to a previously used rest site after being located elsewhere, or repeatedly used a single site after at least 5 days had elapsed, we treated that site as an additional independently selected location. To evaluate habitat selection, we also identified a random available site (henceforth "random site") for each occasion we tracked an individual to a rest site. Random available sites were located along a random bearing between 50 and 200 m from each rest site. Once we were 50 m from the rest site along the random bearing, we began searching for the first available suitable site along the same bearing. Suitable random available sites were identified 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 competitors and predators. We interpreted these criteria by identifying available rest sites that were enclosed on three sides, had an entrance that did not exceed 30 × 30 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 straight-line distances traversed per night (distance between consecutive rest sites divided by the number of days between locations) supported this assumption; on average, the minimum straight-line distance traversed by spotted skunks in a night was 99 m (range: 3–636 m, median: 79 m, third quartile: 118 m), and distance traversed only exceeded 200 m on 15 of 170 tracking intervals. Further, because of the relatively high rate of changing rest sites and large average inter-rest site movement distance, in 2017 we increased the minimum distance to locate a paired random site from 50 to 80 m in order to increase the representation of the variation in habitat that was available for selection. We conducted a post hoc chi-square test to evaluate if there was a significant difference in the type of available rest site we identified between year one when we used a 50-m threshold, and year two when we used an 80-m threshold. We observed no significant difference in the type of available rest site identified between years (P = 0.496); therefore, we pooled data from both years for future analysis.

We recorded the location of every rest site and random site using a global positioning system (GPS) unit (Garmin, Kansas City, Kansas) and measured a suite of surrounding habitat characteristics (Table 1). Within a 10 × 10 m square centered around

Table 1.—Variable names, abbreviations, and descriptions of parameters measured to evaluate summer rest site selection by eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017.

Variable	Abbreviation	Description
Canopy cover	Canopy	Percent cover from canopy vegetation greater than 5 m tall within a 10 × 10 m square around the rest site
Understory cover	Undst	Percent cover from understory vegetation between 1–5 m tall within a 10 × 10 m square around the rest site
Ground cover	Ground	Percent cover from ground-level vegetation less than 1 m tall within a 10 × 10 m square around the rest site
Coarse woody debris	CWD	Index of coarse woody debris abundance within a 10 × 10 m square around the rest site
Stem count	Stems	Number of woody stems within a 5 × 5 m square around the rest site
Canopy type	Type	The dominant canopy cover type, calculated from the 2011 NLDC dataset as either Deciduous, Mixed, Coniferous, or Open–nonforested
Drainage	Drain	Distance to nearest drainage channel in m
Slope	Slope	Steepness of the slope in degrees
Aspect	Aspect	Aspect of the slope, transformed to represent a linear northwest–southeast gradient

each rest site entrance, we performed visual estimates of canopy cover, understory cover, and ground cover, and measured an index of abundance of coarse woody debris (CWD). For each field measurement, to establish consistency between surveyors (n = 3), all surveyors were trained by a single lead surveyor at a series of "test" rest sites. In addition, we used a consensus-based approach among paired surveyors who measured attributes at each site. CWD was measured on a scale of 0–10 by walking transects in four cardinal directions from the center of the study plot, with 0 indicating no CWD >10 cm diameter and 10 indicating the entire area was covered by CWD. We also counted the number of all woody stems greater than 75 cm tall and present within a 5 × 5 m square around the rest site entrance, and did not include low-forking branches near the base of a tree or shrub as additional stems. We used ArcGIS 10.5 (ESRI 2017) and a 1/9 arc-second digital elevation model (United States Geological Survey 2013, www.usgs.gov) 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 1,500-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; https://www.mrlc.gov/nlcd11_data.php), 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). A priori models based on hypotheses were evaluated separately for males and females and we used the Akaike information criterion for small samples sizes (AIC_c) to rank our competing models, and also calculated ΔAIC_c values and model weights (w_i) to compare model support (Burnham and Anderson 2002).

We developed 14 a priori models to evaluate support for the three factors we hypothesized would influence summer rest site selection (Table 2). First, 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, 2) steep slopes and woody stems would inhibit maneuverability of mammalian predators (Reichman and Aitchison 1981; Litvaitis et al. 1985), and 3) abundant understory cover alone would provide cover from owls, the primary predator of spotted skunks (Lesmeister et al. 2010). Second, under our prey selection hypothesis, we predicted spotted skunks would select rest

Table 2.—Hypotheses, model structures, and predicted parameter responses for the 13 a priori models developed to evaluate summer rest site selection by eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017. See Table 1 for parameter descriptions. Note that models 2, 3, and 4 are specific subsets of the overall PREDATORS model.

Hypothesis	Model structure	Predicted response
1) PREDATORS: Ground, understory, and canopy cover will decrease visibility; steep slopes and woody stems will reduce predator maneuverability	$= \beta_1$(undst) + β_2(canopy) + β_3(ground) + β_4(stems) + β_5(slope)	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0, \beta_4 > 0, \beta_5 > 0$
2) PRED.COVER: Ground, understory, and canopy cover will provide reduced visibility from all predators	$= \beta_1$(undst) + β_2(ground) + β_3(canopy)	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0$
3) PRED.MOVE: Steep slopes and abundant woody stems will reduce maneuverability for mammalian predators	$= \beta_1$(stems) + β_2(slope)	$\beta_1 > 0, \beta_2 > 0$
4) PRED.UNDST: Dense understory will provide protection from avian predators	$= \beta_1$(undst)	$\beta_1 > 0$
5) FORAGE: Drainages and abundant CWD will provide good foraging habitat	$= \beta_1$(drain) + β_2(CWD)	$\beta_1 < 0, \beta_2 > 0$
6) THERMOREGULATION: Northwest facing slopes and deciduous forests will produce cooler temperatures and reduce thermoregulatory stress	$= \beta_1$(aspect) + β_2(mixed) + β_3(conifer) + β_4(open)	$\beta_1 > 0, \beta_2 < 0, \beta_3 < 0, \beta_4 < 0$
7) THERM+FORAGE	$= \beta_1$(aspect) + β_2(mixed) + β_3(conifer) + β_4(open) + β_5(drain) + β_6(CWD)	$\beta_1 > 0, \beta_2 < 0, \beta_3 < 0, \beta_4 < 0, \beta_5 < 0, \beta_6 > 0$
8) ASPECT+PRED.COV	$= \beta_1$(aspect) + β_2(undst) + β_3(canopy) + β_4(ground)	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0, \beta_4 > 0$,
9) ASPECT+PRED.MOVE	$= \beta_1$(aspect) + β_2(stems) + β_3(slope)	$\beta_1 > 0, \beta_2 > 0, \beta_3 > 0$
10) ASPECT+PRED.UNDST	$= \beta_1$(aspect) + β_2(undst)	$\beta_1 > 0, \beta_2 > 0$
11) FORAGE+PRED.UNDST	$= \beta_1$(undst) + β_2(drain) + β_3(CWD)	$\beta_1 > 0, \beta_2 < 0, \beta_3 > 0$
12) FORAGE+PRED.COV	$= \beta_1$(drain) + β_2(CWD) + β_3(undst) + β_4(canopy) + β_5(ground)	$\beta_1 < 0, \beta_2 > 0, \beta_3 > 0, \beta_4 > 0, \beta_5 > 0$
13) FORAGE+PRED.MOVE	$= \beta_1$(drain) + β_2(CWD) + β_3(stems) + β_4(slope)	$\beta_1 < 0, \beta_2 > 0, \beta_3 > 0, \beta_4 > 0$
14) GLOBAL	$= \beta_1$(drain) + β_2(CWD) + β_3(undst) + β_4(canopy) + β_5(ground) + β_6(stems) + β_7(slope) + β_8(aspect) + β_9(mixed) + β_{10}(conifer) + β_{11}(open)	$\beta_1 < 0, \beta_2 > 0, \beta_3 > 0, \beta_4 > 0, \beta_5 > 0, \beta_6 > 0, \beta_7 > 0, \beta_8 > 0, \beta_9 < 0, \beta_{10} < 0, \beta_{11} < 0$

sites near drainage channels and with abundant CWD where prey items were likely to be abundant. CWD has been associated with higher abundance of small mammals and invertebrates (Harmon 1982; McMinn and Crossley 1996; Braccia and Batzer 1999; Loeb 1999; Koenigs et al. 2002), while drainage channels accumulate leaf litter that provides suitable conditions for both terrestrial and aquatic invertebrate decomposers and their reptilian predators (Jaeger 1980; Smock et al. 1989; Bogan et al. 2013), all of which are known to be prey for eastern spotted skunks (Crabb 1941; McCullough and Fritzell 1984; Kinlaw 1995; Sprayberry and Edelman 2016; Thorne and Waggy 2017). Third, to minimize thermoregulatory stress during the heat of the summer, 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). 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 analysis, and used the R package "mlogit" (Croissant 2013) to evaluate our discrete choice models. All variables were screened for multicollinearity, and no variables were found to have correlation coefficients above 0.32. We transformed the circular aspect degree values to a linear measure where aspects of Southeast and Northwest had a value of 0 and 180, respectively, and no differentiation was determined between Southwestern and Northeastern differences (i.e., each would have a transformed value of 90). To make this conversion, we used the equation converted.asp = $|asp° - 135|$ for circular aspect measures 0°–314.9°, and converted.asp = $|asp° - 495|$ for measures ≥315°. All continuous data were scaled linearly to range from approximately 0–10 to allow for comparison between variable effects. Because of limited sample size, for each sex we pooled rest site data from individuals in our analyses.

Model validation.—We performed five iterations of k-fold cross validation to test the predictive performance of our top male and female model (Boyce et al. 2002). 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 capability 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 select 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 in 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, and three male skunks were tracked both years. Of 382 active trap-nights, we captured spotted skunks on 59 occasions for a 15.4% trapping success rate. We successfully tracked collared individuals to their rest site 215 times (58 locations for females and 157 locations for males). No individual female skunk contributed more than 30% to its sex's rest site data, and no individual male skunk contributed more than 20% to its sex's rest site data (Table 3). Spotted skunks utilized a variety of structures for rest sites, a majority (n = 164) of which were dependent on trees and CWD for structure (e.g., root burrows, tree cavities, or hollow logs; Fig. 1). We also collected habitat data for an equivalent number of random available sites. Of these 215 tracking events, we located 187 unique rest sites, indicating a 13% rate of reuse (n = 28). Of those re-used rest sites, 61% were rest sites of the three females known to be rearing kits (n = 17). Of all reused sites, we identified only three locations when spotted skunks returned to the same structure on nonconsecutive 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 reused. 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 ($\bar{X} \pm SE$ = 91.8 ± 19.5, range: 53–181 m).

We found that our top predictive model for rest site selection by females was the thermoregulation and forage subglobal model that included aspect, distance to drainage, CWD, and NLCD cover type as covariates (Table 4). This model contained over three times more support than the second-ranking model based on AIC weights, and indicated that females preferred rest sites in close proximity to drainage channels and higher levels of CWD (Table 5). The relative probability of selecting a rest site decreased by 50% for every 20-m increase in the distance from a drainage channel, and increased 30% for every one-unit increase in CWD (Fig. 2). Despite a majority (74%) of rest sites occurring in deciduous forest, which was

Table 3.—Distribution of summer rest sites identified and the number of occasions each collared skunk was tracked during this study evaluating summer rest site selection by eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017.

Skunk ID	Number of sites	Occasions tracked
F01	9	17
F03	14	17
F04	5	5
F05	11	17
F06	2	2
M02	1	1
M03	1	1
M04[a]	23	24
M08[a]	29	30
M12[a]	29	31
M15	13	14
M16	9	11
M17	9	10
M18	16	17
M19	16	18

[a]Skunks tracked for two summer seasons.

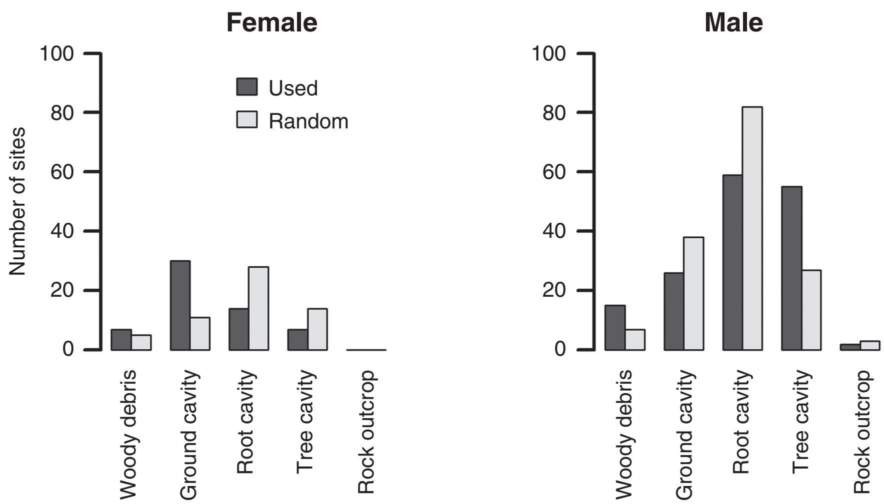

Fig. 1.—Number of rest site structures used by eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017, compared with random-available structures located in the field.

Table 4.—Ranked candidate models developed to predict summer rest site selection by female and male eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017. Models are ranked by ΔAIC_c and only models that contributed to 0.95 of the total model weight are reported. See Table 2 for model descriptions.

Sex	Model	K[a]	ΔAIC_c[b]	w_i[c]	Log-Lik[d]
Females	THERM+FORAGE	6	0.00	0.56	−25.88217
	FORAGE+PRED.COV	5	2.41	0.17	−28.3321
	FORAGE	2	2.81	0.14	−31.9998
	FORAGE+PRED.UNDST	3	4.51	0.06	−31.7366
	FORAGE+PRED.MOVE	4	4.90	0.05	−30.7775
Males	FORAGE+PRED.UNDST	3	0.00	0.59	−90.75984
	PRED.UNDST	1	2.78	0.15	−94.21694
	FORAGE+PRED.COV	5	3.66	0.10	−90.46987
	ASPECT+PRED.UNDST	2	4.49	0.06	−94.04446
	PRED.COVER	3	5.03	0.05	−93.27634

[a]Number of parameters included in the model.
[b]Difference in AICc between the focal model and top-ranked model.
[c]Akaike model weight.
[d]Log-likelihood.

Table 5.—Estimates, standard errors (*SE*), and 95% confidence intervals (*CI*) of parameters in the top model hypothesized to predict summer rest site selection by female and male eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017. See Table 1 for parameter descriptions. The land cover reference category is deciduous.

Sex	Covariate	Estimate	*SE*	*CI*
Female	Aspect	0.183	0.103	−0.023, 0.389
	Drain	−0.701	0.264	−1.229, −0.173
	CWD	0.361	0.148	0.065, 0.657
	Mixed	2.712	1.577	−0.442, 5.866
	Conifer	2.528	0.99	0.548, 4.508
	Open	1.283	0.989	−0.695, 3.261
Male	Undst	0.288	0.07	0.148, 0.428
	Drain	−0.206	0.092	−0.39, −0.022
	CWD	0.089	0.071	−0.053, 0.231

the dominant land cover type in our study area, relative probability of selection suggests that the mixed wood cover type was most preferred (46.8%), followed by conifer (38.9%), open areas (11.2%), and deciduous (3.1%). However, evaluation of 95% confidence intervals of beta estimates suggested that relative probability of selecting conifer over deciduous forest type was the only significant predictor (Table 5). Similarly, while female skunks generally tended to select rest sites on a southeasterly aspect, beta estimate 95% confidence intervals overlapped zero, suggesting this was only a trend and not a significant relationship (Table 5).

The top-performing model for male eastern spotted skunks was the forage-predator-understory model that included distance to drainage, CWD, and percent understory cover as covariates (Table 4). This model contained over four times more support than the second-ranking model based on AIC weights. The relative probability of selecting a rest site increased by 25% for every 10% increase in understory cover. Males, like females, preferred rest sites closer to drainages, with the relative probability of a rest site being selected decreasing 18% for every 20-m increase in distance to a drainage (Fig. 2). Also similar to females, males tended to prefer sites with more CWD, although 95% confidence intervals overlapped zero (Table 5). K-fold cross-validation of models for both females and males indicated that each top model was able to accurately predict if a site was used or random available 75% of the time.

Discussion

We found distance to a drainage channel to be a strong predictor of rest site selection by both male and female eastern spotted skunks, suggesting that this feature warrants greater consideration as a habitat attribute relevant to spotted skunk ecology in the southern Appalachians. Although previous studies have considered distance to water or distance to streams

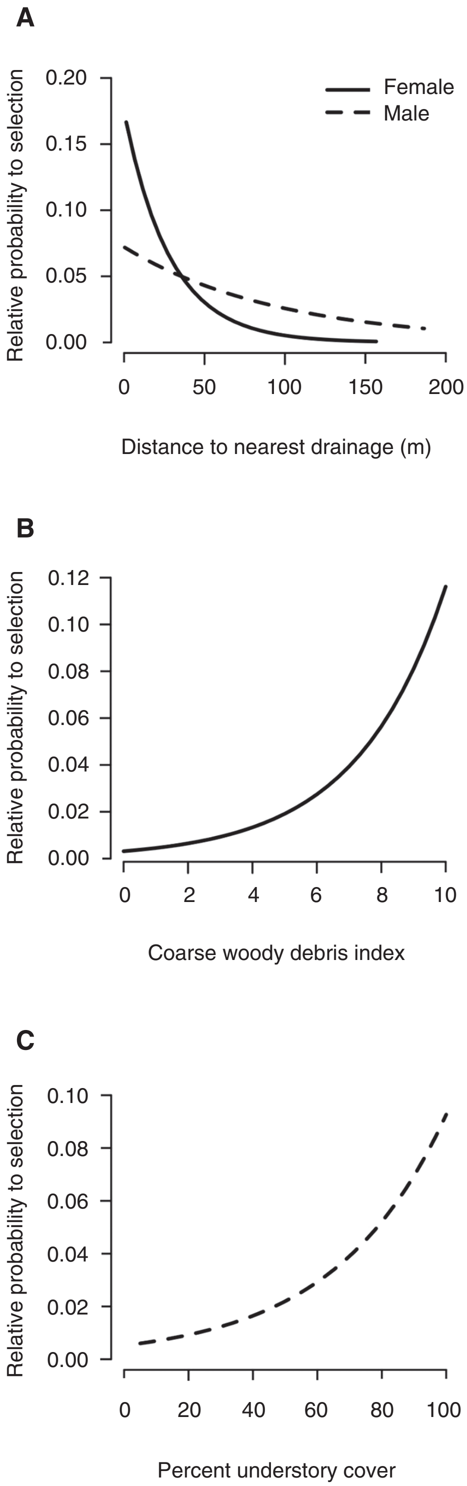

Fig. 2.—Predictive plots illustrating the change in relative probability of rest site selection as a function of distance to nearest drainage (A), coarse woody debris (B), and percent understory cover (C) for summer rest site selection by female and male eastern spotted skunks (*Spilogale putorius*) in the southern Appalachian forests of South Carolina in 2016 and 2017. See Table 1 for parameter descriptions.

as a predictor of rest site selection by mesocarnivores (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, even though they constitute over half the length of stream networks (Montgomery and Buffington 1997; Hansen 2001). Drainage channels 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). In our study system, this was evident from the typically high amount of rhododendron and mountain laurel understory cover compared to the surrounding hillsides that likely provided cover for spotted skunks from avian predators. Furthermore, drainage channels are connected with 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). Thus, our results suggest that a better understanding of how eastern spotted skunks move or travel within stream drainage networks could provide important information about connectivity of populations in this region.

Our finding that female eastern spotted skunks selected areas with higher amounts of CWD suggests that these features might warrant greater consideration in regard to forest management. Both sexes of spotted skunks in our study selected rest sites in woody debris at a high rate relative to its availability on the landscape (Fig. 1). Female spotted skunks selected sites with higher amounts of large (>10 cm) CWD in close (<10 m) proximity during the summer season, suggesting that these conditions could be important for litter rearing. By contrast, previous studies of rest site selection by spotted skunks that quantified CWD did not find it to be associated with rest site selection (Lesmeister et al. 2008; Sprayberry and Edelman 2018). This could be due to those studies being in pine-dominated ecosystems where softwood CWD tends to decay more quickly than the hardwood CWD that dominated our study area (Moorman et al. 1999). Management to maintain large decaying trees and allow for persistence of some CWD has been successfully implemented in other forested systems (Bull et al. 1997), and we suggest similar practices might benefit eastern spotted skunks in southern Appalachian hardwood forests.

Selection by female spotted skunks for rest sites with CWD and in close proximity to drainage channels suggests that prey availability might be important for rest site selection by female eastern spotted skunks. Other mesocarnivore species have been reported to select habitat based on prey availability (Spencer et al. 1983; Litvaitis et al. 1986). Many mesocarnivore species show increased selectivity when choosing sites for rearing offspring, 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 den site characteristics preferred by female eastern spotted skunks with litters, and how den site selection could influence juvenile survival, could help direct conservation efforts. In this study, we considered higher availability of CWD and lower distance to drainage channels as proxies for areas with high-quality forage. Our findings suggest that female spotted skunks, as dietary generalists showing little rest site fidelity (Crabb 1948; Lesmeister et al. 2008; Sprayberry and Edelman 2018), select rest sites that are in or near patches of high-quality foraging habitat. However, without having directly assessed prey availability, it remains unclear whether female spotted skunks were selecting for structure or prey availability, or some combination of both. Direct investigation of the diets of eastern spotted skunks would allow a better interpretation of how prey availability might influence habitat selection. Given evidence that diet fluctuates seasonally, with spotted skunks showing a preference for small mammals in the winter and invertebrates in the summer (Crabb 1941; McCullough 1983), year-round investigations are needed to assess how seasonal fluctuations in prey availability could influence fine-scale habitat preferences of eastern spotted skunks.

Consistent with previous studies (Lesmeister et al. 2008; Sprayberry and Edelman 2018), our results indicate that male eastern spotted skunks in southern Appalachian forests selected rest sites in areas with greater understory cover. Intraguild killing can drive demographic rates of many mesocarnivore species (Palomares and Caro 1999; Terraube and Bretagnolle 2018), including the eastern spotted skunk, where predation by owls and mammalian predators is a leading factor in low (35%) annual survival (Lesmeister et al. 2010). Although spotted skunks have a potent olfactory defense mechanism to deter predators in close proximity, they might rely on a cryptic pelage pattern to avoid being detected by predators (Caro et al. 2013). The efficacy of spotted patterns as camouflage is enhanced by dappled lighting on the forest floor (Caro 2005), which leads us to suspect that spotted skunks might select dense understory not only because it shields them from being detected by owls, but also because it enhances their cryptic appearance under these conditions. However, unlike previous studies (Lesmeister et al. 2008; Sprayberry and Edelman 2018), we did not observe support for an effect of understory cover on rest site selection by female spotted skunks. Future research is needed to investigate the extent to which female spotted skunks could be balancing predation risk and access to foraging areas, and seasonally selecting habitat based on reproductive state.

We found no support for our hypothesis that spotted skunks select sites that support thermoregulation during the heat of summer months, even though previous studies have reported thermoregulation plays a role in rest site selection by spotted skunks (Lesmeister et al. 2008). Our lack of support for this hypothesis might be because the variables of elevation and aspect that we used to represent thermal variation are indirect measures of the thermal environment. Direct measurement of ambient and microsite temperatures across seasons could provide information regarding thermal thresholds for rest site selection.

Given the variety of structures to which we tracked spotted skunks in the southern Appalachian forests, these animals appear to be opportunistic in selecting structures to use as rest sites. We observed several differences in use and selection of rest site structures from studies of rest site selection in conifer-dominated forests (Lesmeister et al. 2008; Sprayberry and Edelman 2018). Our skunks showed lower rates of site reuse (12%) than in other populations (25%—Lesmeister et al. 2008, and 46%—Sprayberry and Edelman 2018), which might be due to a higher abundance of suitable rest sites, lower availability of localized resources, or greater competition or threat from competitors or predators in our study area. Spotted skunks in our study used tree-associated structures (e.g., tree cavities, root burrows, or hollow logs) twice 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 might provide more suitable tree cavities for mammalian carnivores (Paragi et al. 1996). Alternatively, ground conditions at our study area could have been less suitable for rest sites. 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), such outcrops were largely absent from our study area and composed <1% of rest sites. Given the variety of structures spotted skunks used as rest sites in our study, rest site selection might be more impacted by habitat characteristics of the surrounding area. Throughout their range, spotted skunks display great flexibility in the structures they utilize as rest sites (Harris 2018), which suggests that management of the surrounding habitat might be of importance for the conservation of this species.

Our understanding of spotted skunk ecology has been greatly advanced in the past decade, but more knowledge about eastern spotted skunk habitat associations and demography are needed to develop appropriate conservation plans. Recent camera-trap studies of landscape-scale habitat associations have been unable to identify strong predictors of spotted skunk occurrence in their Appalachian range, which might largely be due to the low probability of detecting individuals (Thorne et al. 2017; Eng 2018). Our study establishes that habitat-based factors such as CWD, understory cover, and drainage channels influence the habitat selection of remnant populations of eastern spotted skunks in this region and should be of management concern for conserving this species. However, comparisons to other similar studies suggest rest site selection by spotted skunks is somewhat area- or region-specific, and additional studies are needed to provide insights about suitable habitat for this species in other portions of their range.

Acknowledgments

We thank the South Carolina Department of Natural Resources for their support, which made this project possible, as well as the U.S. Forest Service Oconee Ranger Office, for their permission to access gated property in the field. This research would not have been possible without the assistance of K. Morris and S. Hawthorne in the field, and advice from S. Harris, L. Gigliotti, J. Froehly, and R. Jachowski in revising this paper. We thank C. Bodinof Jachowski, M. Gompper, S. Loeb, and R. Baldwin for their advice throughout the many stages of this project and for their feedback on early versions of this manuscript.

Literature Cited

Abella, S. R., V. B. Shelburne, and N. W. MacDonald. 2003. Multifactor classification of forest landscape ecosystems of

Jocassee Gorges, southern Appalachian Mountains, South Carolina. Canadian Journal of Forest Research 33:1933–1946.

Aubry, K. B., et al. 2013. Meta-analyses of habitat selection by fishers at resting sites in the Pacific coastal region. Journal of Wildlife Management 77:965–974.

Birks, J. D. S., J. E. Messenger, and E. C. Halliwell. 2005. Diversity of den sites used by pine martens *Martes martes*: a response to the scarcity of arboreal cavities? Mammal Review 35:313–320.

Blackie, H. M. 2010. Comparative performance of three brands of lightweight global positioning system collars. Journal of Wildlife Management 74:1911–1916.

Bodinof, C. M., et al. 2012. Habitat attributes associated with short-term settlement of Ozark hellbender (*Cryptobranchus alleganiensis bishopi*) salamanders following translocation to the wild. Freshwater Biology 57:178–192.

Bogan, M. T., K. S. Boersma, and D. A. Lytle. 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. Freshwater Biology 58:1016–1028.

Bolstad, P. V., W. Swank, and J. Vose. 1998. Predicting southern Appalachian overstory vegetation with digital terrain data. Landscape Ecology 13:271–283.

Boulerice, J. T., and B. M. Zinke. 2017. Winter habitat associations for spotted skunks (*Spilogale* spp) in south-central Wyoming. American Midland Naturalist 178:17–28.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Braccia, A., and D. P. Batzer. 1999. Invertebrates associated with coarse woody debris in streams, upland forests, and wetlands: a review. Proceedings of the 1999 Georgia Water Resources Conference, Athens, Georgia, 30–31 March 1999 (Hatcher, K. J., ed.). 299–302.

Brainerd, S. M., J. Helldin, E. R. Lindström, E. Rolstad, J. Rolstad, and I. Storch. 1995. Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. Annales Zoologici Fennici 32:151–157.

Bull, E. L., and T. W. Heater. 2000. Resting and denning sites of American martens in northeastern Oregon. Northwest Science 74:179–185.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs imprtant to wildlife in the Interior Columbia River Basin. USDA Forest Service, Pacific Northwest Reasearch Station, General Technical Report PNW-GTR-391.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York.

Campbell Grant, E. H., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecology Letters 10:165–175.

Caro, T. 2005. The adaptive significance of coloration in mammals. BioScience 55:125–136.

Caro, T., T. Stankowich, C. Kiffner, and J. Hunter. 2013. Are spotted skunks conspicuous or cryptic? Ethology, Ecology and Evolution 25:144–160.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80:566–575.

Crabb, W. D. 1941. Food habits of the prairie spotted skunk in southeastern Iowa. Journal of Mammalogy 22:349–364.

Crabb, W. D. 1944. Growth, development and seasonal weights of spotted skunks. Journal of Mammalogy 25:213–221.

Crabb, W. D. 1948. The ecology and management of the prairie spotted skunk in Iowa. Ecological Monographs 18:201–232.

Croissant, Y. 2013. Mlogit: multinomial logit models. R package version 0.2–4.

DeSanty, J. 2001. A review of plains spotted skunk (*Spilogale putorius interrupta*) throughout its range in North America. Missouri Department of Conservation, Jefferson City.

Diggins, C. A., D. S. Jachowski, J. Martin, and W. M. Ford. 2015. Incidental captures of eastern spotted skunk in a high-elevation red spruce forest in Virginia. Northeastern Naturalist 22:N6–N10.

Elliott, K. J., J. M. Vose, W. T. Swank, and P. V. Boistad. 1999. Long-term patterns in vegetation-site relationships in a southern Appalachian forest. Journal of the Torrey Botanical Society 126:320–334.

Eng, R. Y. Y. 2018. Eastern spotted skunk occupancy and rest site selection in the hardwood forests of the southern Appalachians. M.S. thesis. Clemson University, Clemson, South Carolina.

Esri. 2017. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, Redlands, CA.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fekedulegn, D., J. J. Colbert, J. S. Rentch, and K. W. Gottschalk. 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. Southern Appalachian Botanical Society 69:92–108.

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.

Gompper, M., and D. Jachowski. 2016. *Spilogale putorius*. In IUCN 2017. IUCN Red List of Threatened Species. Version 2017.3. www.iucnredlist.org. Accessed 14 March 2018.

Hansen, W. F. 2001. Identifying stream types and management implications. Forest Ecology and Management 143:39–46.

Harmon, M. E. 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. Oecologia 52:214–215.

Harris, S. N. 2018. Florida spotted skunk ecology in a dry prarie ecosystem. M.S. thesis. Clemson University, Clemson, South Carolina.

Jaeger, R. G. 1980. Microhabitats of a terrestrial forest salamander. American Society of Ichthyologists and Herpetologists 2:265–268.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kinlaw, A. 1995. *Spilogale putorius*. Mammalian Species 551:1–7.

Koenigs, E., P. J. Shea, R. Borys, and M. I. Haverty. 2002. An investigation of the insect fauna associated with coarse woody debris of *Pinus ponderosa* and *Abies concolor* in northeastern California. USDA Forest Service, Pacific Southwest Research General Technical Report PSW-GTR-181.

Lesmeister, D. B., R. S. Crowhurst, J. J. Millspaugh, and M. E. Gompper. 2013. Landscape ecology of eastern spotted skunks in habitats restored for red-cockaded woodpeckers. Restoration Ecology 21:267–275.

Lesmeister, D. B., M. E. Gompper, and J. J. Millspaugh. 2008. Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. Journal of Mammalogy 89:1512–1520.

Lesmeister, D. B., M. E. Gompper, and J. J. Millspaugh. 2009. Habitat selection and home range dynamics of eastern spotted skunks in the Ouachita Mountains, Arkansas, USA. Journal of Wildlife Management 73:18–2518.

Lesmeister, D. B., J. J. Millspaugh, M. E. Gompper, and T. W. Mong. 2010. Eastern spotted skunk (*Spilogale putorius*) survival and cause-specific mortality in the Ouachita Mountains, Arkansas. American Midland Naturalist 164:52–60.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49:866–873.

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.

Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460–471.

Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62:1313–1320.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McCullough, C. 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, Missouri Academy of Science 18:25–32.

McMinn, J. W., and D. A. Crossley. 1996. Biodiversity and coarse woody debris in southern forests. USDA Forest Service, Southern Research Station, General Technical Report SE-94.

Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morpohology in mountain drainage basins. Department of Geological Science 109:596–612.

Montgomery, D. R., and E. Foufoula-Georgiou. 1993. Channel network source representation using digital elevation models. Water Resources Research 29:3925–3934

Moorman, C. E., K. R. Russell, G. R. Sabin, and D. C. Guynn. 1999. Snag dynamics and cavity occurrence in the South Carolina Piedmont. Forest Ecology and Management 118:37–48.

Moriarty, K. M. and Epps, C. W. 2015. Retained satellite information influences performance of GPS devices in a forested ecosystem. Wildlife Society Bulletin 39:349–357.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492–508.

Paragi, T. F., S. M. Arthur, and W. B. Krohn. 1996. Importance of tree cavities as natal dens for fishers. Northern Journal of Applied Forestry 13:79–83.

Prince, P. S., J. A. Spotila, and W. S. Henika. 2010. New physical evidence of the role of stream capture in active retreat of the Blue Ridge escarpment, southern Appalachians. Geomorphology 123:305–319.

Purcell, K. L., A. K. Mazzoni, S. R. Mori, and B. B. Boroski. 2009. Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. Forest Ecology and Management 258:2696–2706.

R Core Team. 2017. R Development Core Team. R: A Language and Environment for Statistical Computing. https://www.r-project.org. Accessed October 2016.

Reichman, O. J., and S. Aitchison. 1981. Mammal trails on mountain slopes: optimal paths in relation to slope angle and body weight. American Naturalist 117:416–420.

Roemer, G. W., M. E. Gompper, and B. Van Valkengurgh. 2009. The ecological role of the mammalian mesocarnivore. BioScience 52:165–173.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. Ecology 70:764–775.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1181–1186.

Sprayberry, T. R., and A. J. Edelman. 2016. Food provisioning of kits by a female eastern spotted skunk. Southeastern Naturalist 15:N53–N56.

Sprayberry, T. R., and A. J. Edelman. 2018. Den-site selection of eastern spotted skunks in the southern Appalachian Mountains. Journal of Mammalogy 99:242–251.

Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. G. Campbell. 1982. Land-water interactions: the riparian zone. Pp. 267–291 in Analysis of coniferous forest ecosystems in the western United States (Edmonts, R.L., eds.). Academic Press, Stroudsburg, Pennsylvania.

Terraube, J., and V. Bretagnolle. 2018. Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale. International Journal of Avian Science 160:693–702.

Thorne, E. D., and C. Waggy. 2017. First reported observation of food provisioning to offspring by an eastern spotted skunk, a small carnivore. Northeastern Naturalist 24:N1–N4.

Thorne, E. D., C. Waggy, D. S. Jachowski, M. J. Kelly, and W. M. Ford. 2017. Winter habitat associations of eastern spotted skunks in Virginia. Journal of Wildlife Management 81:1042–1050.

Turner, M. G., S. M. Pearson, P. Bolstad, and D. N. Wear. 2003. Effects of land-cover change on spatial pattern of forest communities in the southern Appalachian Mountains (USA). Landscape Ecology 18:449–464.

Vanak, A. T., and M. E. Gompper. 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. Journal of Applied Ecology 47:1225–1232.

Waldrop, T. A., D. L. Hagan, and D. M. Simon. 2016. Repeated application of fuel reduction treatments in the southern Appalachian mountains, USA. Implications for achieving management goals. Fire Ecology 12:28–47.

Wilson, S. B., et al. 2016. Recent detections of *Spilogale putorius* (eastern spotted skunk) in South Carolina. Southeastern Naturalist 15:269–274.

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.

Submitted 6 June 2018. Accepted 2 April 2019.

Associate Editor was Bradley Swanson.