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*Research Article*

# Winter Habitat Associations of Eastern Spotted Skunks in Virginia

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**ABSTRACT** Eastern spotted skunk (*Spilogale putorius*) populations have declined throughout much of their range in the eastern United States over recent decades. Declines have been attributed to habitat loss or change, increased competition with sympatric mesocarnivore species, or disease. To better understand the extant distribution of spotted skunks in the Appalachian Mountains of western Virginia, USA, we used a detection-non-detection sampling approach using baited camera traps to evaluate the influence of landscape-level environmental covariates on spotted skunk detection probability and site occupancy. We conducted camera trap surveys at 91 sites from January to May in 2014 and 2015. Spotted skunk occupancy was associated with young-aged forest stands at lower elevations and more mature forest stands at higher elevations. Both land cover types in this region can be characterized as having complex forest structure, providing cover that varies with stand age, species composition, elevation, and management regime. Our results provide insight into factors that influence spotted skunk spatial distribution and habitat selection, information that can be used to generate conservation assessments and inform management decisions.


**KEY WORDS** Appalachian Mountains, camera-trapping, detection, eastern spotted skunks, habitat, mesocarnivore, occupancy, *Spilogale putorius*.

The eastern spotted skunk (*Spilogale putorius*) is a small Mephitid that was once a fairly common furbearer throughout the central and southern United States with annual range-wide harvests of over 100,000 individuals (Gompper and Hackett 2005). Though it has a federal status of least concern, the eastern spotted skunk is listed as vulnerable, imperiled, or critically imperiled in most of the states throughout its historical range (Chapman 2007) and is listed as vulnerable on the International Union for the Conservation of Nature Red List (Gompper and Jachowski 2016). Perceived population declines in the Midwest and upper South, USA, beginning in the 1940s, may be attributed to a decrease in available early successional shrub-scrub, regenerating yellow pine (*Pinus* spp.), and oldfield habitat due to intensive agricultural practices (clean farming) or the maturation of early successional forests (Polder 1968, Gompper and Hackett 2005, Lesmeister et al. 2009). Declines may have also been influenced by increased competition with sympatric mesocarnivore species (e.g., striped skunks [*Mephitis mephitis*], raccoons [*Procyon lotor*], bobcats [*Lynx rufus*], and coyotes [*Canis latrans*]) as a result of declining trapping pressure or range expansions of such species (Chapman 2007, Lesmeister et al. 2010). A series of rabies outbreaks beginning in the 1970s, may have also contributed to Midwest population declines of spotted skunks potentially because of increased mortality and reduced productivity, an effect that has been observed in striped skunks (Greenwood et al. 1997).

In Virginia, an analogous reduction of early- to mid-successional habitat associated with forest maturation occurred in the Appalachians in the later portion of the twentieth century (Yarnell 1998). Within the central and southern Appalachians, forest maturation occurred, as a result of succession from earlier harvesting in the industrial logging period, and decreased timber harvest on federally owned lands, which may have led to diminished habitat quality for spotted skunks. A raccoon rabies enzootic also spread throughout much of Virginia by the 1980s following a translocation of infected raccoons from Florida to the

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mid-Atlantic region to replenish hunting stock in the late 1970s (Torrence et al. 1992, Real et al. 2005). The amalgamation of habitat change, increased competition with sympatric carnivores, and spread of the rabies virus, similar to the potential causes of spotted skunk declines in the Midwest, may have affected the current spatial distribution and habitat associations of spotted skunk populations in Virginia.

Little is known about the spatial distribution or ecology of eastern spotted skunks in the central and southern Appalachians. In the Blue Ridge portion of the southern Appalachians of Tennessee, spotted skunk populations have been associated with rhododendron (*Rhododendron maximum*) thickets near high elevation emergent rock outcrops (Reed and Kennedy 2000). Similarly, in South Carolina, spotted skunks were detected predominantly in areas of mixed softwood-hardwood forest containing dense understory (Wilson et al. 2016). In the central Appalachians of West Virginia and Virginia, spotted skunks have been incidentally captured during surveys of other rare Appalachian wildlife near emergent rock outcrops (Webster et al. 1985) and in a high elevation red spruce (*Picea rubens*) forest (Diggins et al. 2015). It is currently unknown whether emergent rock outcrops and ericaceous shrubs, such as rhododendron or mountain laurel (*Kalmia latifolia*), represent primary spotted skunk habitat in the Appalachians. These apparent associations may be an adaptive response to decreased amount of early successional forest habitat, as seen in other areas where spotted skunks occur (Lesmeister et al. 2013), or may be random occurrences not reflective of spotted skunk habitat preferences.

Currently, the species is classified as vulnerable in Virginia with anecdotal evidence suggesting that it has been rare or largely absent throughout the central and southern Appalachian portions of the state where it formerly was believed abundant and widespread (M. L. Fies, Virginia Department of Game and Inland Fisheries, personal communication). However, anecdotal information from an ongoing multistate, golden eagle (*Aquila chrysaetos*) wintering distribution study in the Appalachians using baited camera stations has recorded spotted skunks in West Virginia in the Peters-Potts Mountain, Shenandoah Mountain, and Great North Mountain areas along the Virginia-West Virginia border, and within Shenandoah National Park to the east (T. E. Katzner, U.S. Geological Survey, unpublished data). These recent records suggest that spotted skunks remain extant in areas throughout the Appalachians.

Our first objective was to identify landscape-level environmental characteristics associated with eastern spotted skunk habitat occupancy. Specifically, we intended to ascertain whether spotted skunks habitat associations in the central and southern Appalachians remain consistent with those reported in other parts of its range (Lesmeister et al. 2013). Our second objective was to create a predictive spotted skunk occurrence model for the Appalachian region of Virginia to determine eastern spotted skunk distribution across the Appalachians of Virginia. We hypothesized spotted skunk predicted occupancy would be higher in forested areas of early to mid-successional growth with increased occupancy at high elevations as reported in other studies (Webster et al. 1985, Lesmeister et al. 2013, Diggins et al. 2015).

## STUDY AREA

We conducted our study in the central and southern Appalachian Mountains of western Virginia, in the Ridge and Valley and Blue Ridge physiographic subprovinces in 10 counties (Fig. 1) extending from the North Carolina state line north to the eastern boundary of West Virginia, primarily on the George Washington and Jefferson National forests (GWJNF). The Ridge and Valley and the Blue Ridge regions are characterized by long mountain ridges with steep side slopes and narrow to moderately broad valleys. Elevations range from 350 m to 1,460 m. Including private land, the entire study area predominately is forested (67%), intermixed with pasture or hay production in the valleys (22%), and limited areas of row-crop agriculture, residential, and urban development (Homer et al. 2015). The climate is cool-temperate with a mean annual temperature of 6.1°C, annual mean minimum temperature of −10.6°C in January, and mean maximum of 27.5°C in June (National Oceanic Atmospheric Administration, public data 2015; www.noaa.gov). With the exception of the southernmost portion of the Blue Ridge, annual precipitation is approximately 110 cm as much of the area is in the rain shadow created by the Allegheny Mountains along the West Virginia border (Ford et al. 2006). Because of this, the dominant forest types over much of the area on ridges and side slopes are relatively xeric hardwood oak-hickory or oak-pine associations dominated by white oak (*Quercus alba*), chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), black oak (*Q. velutina*), red maple (*Acer rubrum*), pitch pine (*Pinus rigida*), table mountain pine (*Pinus pungens*), and mountain laurel. Hardwood non-oak forests occurred on north-facing, sheltered landforms and were dominated by yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and sugar maple (*A. saccharum*). The montane riparian areas were commonly composed of white pine (*Pinus strobus*)-eastern hemlock (*Tsuga canadensis*) associations, often with dense rhododendron understories. At the highest elevations, small amounts of northern hardwood-montane boreal forest dominated by yellow birch (*Betula alleghaniensis*), sugar maple, American beech, and red spruce were present (Braun 1950, Simon 2011, 2013). Common mammalian fauna in the study area include American black bear (*Ursus americanus*), bobcat, coyote, eastern chipmunck (*Tamias stiatus*), gray fox (*Urocyon cinereoargenteus*), gray squirrel (*Sciurus carolinensus*), raccoon, red fox (*Vulpes vulpes*), striped skunks, Virginia opossum (*Didelphis virginiana*), and white-tailed deer (*Odocoileus virginianus*; Morin et al. 2016).

## METHODS

We conducted baited camera trapping surveys from January through April in 2014 and 2015, deploying 91 camera stations spatially grouped into 9 clusters throughout the study area (Fig. 1). We used a stratified random sampling

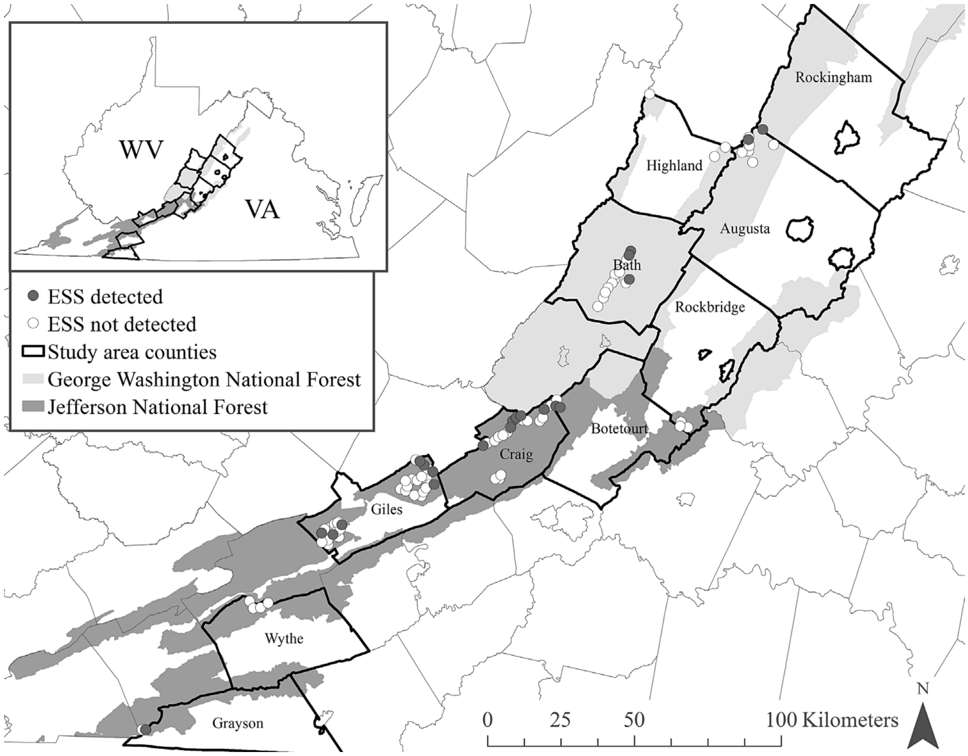


**Figure 1.** Study area across the Appalachian Mountain region of western Virginia, USA, showing the George Washington and Jefferson National Forests. Study area includes Augusta, Bath, Botetourt, Craig, Giles, Grayson, Highland, Rockbridge, Rockingham, and Wythe counties. We detected eastern spotted skunks (ESS) at 19 of 91 camera trap sites from January to April in 2014 and 2015.

approach to sample 3 broadly characterized forest types (i.e., oak-dominated, non-oak dominated, and mixed oak-pine) in proportion to their availability on the landscape (Gasaway et al. 1986). To minimize false absences, we concentrated our surveys in the dormant season because Hackett et al. (2007) reported highest detection rates using camera traps from October through May with little to no trap success during summer in Arkansas. Moreover, our use of bait also constrained our effort at that time to avoid interference to cameras and bait by American black bear.

Our camera trap stations consisted of 1 remote-sensing, motion-activated camera with light-emitting diode (LED) flash. We mounted Reconyx HyperFire HC500 infrared (Reconyx, Holeman, WI, USA), Bushnell Trophy Cam Model 119436, and Bushnell Trophy Cam HD Model 119739 (Bushnell, Overland Park, KS, USA) cameras to trees approximately 1 m above ground level following methods of Jachowski et al. (2015). We secured road-killed white-tailed deer carcasses to the ground with rebar approximately 3–4 m in front of the camera (Jachowski et al. 2015). We spaced camera stations within study sites >1.5 km apart to exceed the diameter of the average male spotted skunk winter home range (Lesmeister et al. 2009) to limit the possibility of detecting a single skunk at multiple camera stations, to promote independence of camera stations, and to maximize forest type coverage. Hackett et al. (2007) observed a 7.2-day latency to initial detection using baited camera traps; therefore, we deployed each camera for ≥8 uninterrupted days to increase probability of detecting skunks in truly occupied habitat patches. We checked cameras weekly to ensure proper function and bait availability. We defined sampling occasions as 24-hour intervals and a detection as any number of spotted skunks photo-captured at an individual camera (Fig. 2). This research was approved by the Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee (protocol number 13-119-FIW).

To assess habitat associations, we related probability of occurrence to landscape-level attributes (based on remotely

**Figure 2.** Example of baited camera station with photo-captured eastern spotted skunk in the George Washington and Jefferson National forests, Virginia, USA, January–April 2014–2015.

sensed geographic information system layers) derived using ArcMap 10.2.2 (ESRI, Redlands, CA, USA). We derived elevation (meters above sea level), slope (degrees), aspect (sine-transformed) using 30-m digital elevation models (DEM; U.S. Geological Survey 2000). We calculated a topographic exposure index (TEI), where higher TEI values indicate greater topographic exposure, using the zonal statistics tools in ArcMap, by subtracting the average elevation of a 1.75-$km^2$ circular area around each camera (Evans et al. 2014, Ford et al. 2015). We buffered each camera location based on average male winter home range estimate for the species (1.75 $km^2$; Lesmeister et al. 2009). Within each of these buffers, we classified land cover type as oak-dominated, non-oak, and mixed oak-pine forests using the Northeast Terrestrial Wildlife Habitat Classification System (Gawler 2008). We used the 2011 National Land Cover Database (NLCD) classification system (Homer et al. 2015) and ArcMap 10.2.2 to measure distance to nearest primary road, water source, and agricultural or pastoral area. We used 2011 NLCD Tree Canopy analytical data to estimate mean percent canopy cover within the 1.75-$km^2$ buffer (U.S. Forest Service 2011). We also used the United States Forest Service landclass inventory data for the GWJNF to determine stand age ($\bar{x}$ age of stand since last harvest) and stand size (area of distinct stand type) for each camera station.

We used a likelihood-based, information-theoretical modeling framework to estimate detection probability ($p$) and probability of site occupancy ($\Psi$) to compare models that included site and survey covariates (MacKenzie et al. 2006). We standardized all continuous site covariates to a mean of 0 and standard deviation of 1 to compare influence of covariates on $\Psi$ and $p$. Camera locations differed between 2014 and 2015 samples, so we included an effect of year in our candidate model set. We combined all data and used a single-species, single-season modeling framework using Program R (R Development Core Team 2014) with package unmarked (Fiske and Chandler 2011). We compared models using Akaike's Information Criterion (AIC) corrected for small sample sizes ($AIC_c$) to rank all $p$ and $\Psi$ models to determine the best-fit models for detection-non-detection data. We considered models competing if $\Delta AIC_c < 2.0$.

We first estimated $p$ (holding $\Psi$ constant) to determine which environmental factors most influenced detection. These factors included average daily temperature, rainfall, snowfall, snow depth, and percent moon illumination (moon surface fraction illuminated) at each camera site. We acquired daily climate data from the National Weather Service (www.weather.gov, accessed 25 May 2015) and percent moon illumination data from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php, accessed 25 May 2015). Because occasionally deep snow at the higher elevations prevented access to many camera stations throughout the study and occasional camera malfunctions, length of time camera stations remained operational at study sites varied from 8 to 62 days. To account for a large range of survey length on detectability of spotted skunks, we included survey effort (no. days camera station was operational) as a detection covariate. Additionally, we included ordinal date to account for temporal variability throughout the study period for each sample year, and daily capture rate (no. photographs captured/day) of bobcats, coyotes, raccoons, striped skunks, and Virginia opossums) to account for effect of other carnivore species presence on spotted skunk detection. We ranked $p$ models based on $AIC_c$, the difference between the model with the lowest $AIC_c$ and the $AIC_c$ of the $i$th model ($\Delta_i$), and Akaike weights ($w_i$), to select the most supported $p$ model (Burnham and Anderson 2002, MacKenzie et al. 2006). We selected the model with the lowest $AIC_c$ value and highest $w_i$ as most supported (Burnham and Anderson 2002). After identifying the most supported $p$ model, we examined relationships between $\Psi$ and environmental factors using a suite of 17 *a priori* models. We examined all covariates for multicollinearity using Spearman's rank correlation with an exclusion criterion of $|r_s| > 0.7$. Additionally, we conducted a parametric bootstrap analysis using 10,000 iterations to assess goodness of fit of the most parameterized model and to ensure the underlying model fit the data (MacKenzie et al. 2002). Using our best model we created a map of eastern spotted skunk predicted $\Psi$ in the GWJNF.

## RESULTS

We detected eastern spotted skunks at 19 of 91 camera stations, 13 out of 50 in 2014 and 6 out of 41 in 2015, resulting in a naïve occupancy (survey sites with skunk detection/no. survey sites) of 0.21 (Fig. 1). Mean survey period length was 38.7 days (±1.4 days [SE]). Eighty percent of camera stations were located in oak-dominated forest stands, 14% in non-oak cove, northern hardwood or riparian stands, and 6% in mixed oak-pine stands. Percent canopy cover at camera stations ranged from 81.7% to 98.9% ($\bar{x} = 92.1 \pm 0.04\%$). Elevation at our stations ranged from 349.0 m to 1,468.1 m ($\bar{x} = 942.7 \pm 22.3$ m). Topographic exposure index (TEI) values varied from −75.1 to 107.3 ($\bar{x} = 8.2 \pm 4.6$). Mean distances from camera stations to nearest primary road, water source, and agricultural or pastoral area were 5.4 ± 0.3 km, 2.1 ± 0.1 km, and 2.4 ± 0.2 km, respectively. Forest stand age varied from 26 years to 164 years ($\bar{x} = 91.9 \pm 3.1$ yr) and stand size varied from 2.4 ha to 231.0 ha ($\bar{x} = 49.4 \pm 5.1$ ha), though in most cases absolute forest patch size was large (>1,000 ha).

No significant multicollinearity occurred between covariates and we retained all covariates for $\Psi$ and $p$ analysis. Additionally, we found no effect of sample year on $\Psi$ for the combined 2014 and 2015 data. Our top detection model, indicated a negative influence of percent moon illumination on spotted skunk detection ($\beta = -0.7$, 95% CI = −0.5 to −0.1) with no competing models based on $AIC_c$ score and Akaike weight (Table 1). Detection probability generally was low and was estimated to decline from 0.14 on nights with 0% moon illumination (new moon) to 0.04 on nights with 100% moon illumination (full moon; Fig. 3).

The stand age and elevation interaction best predicted occupancy based on $AIC_c$ score and $w_i$ (Table 2). The

**Table 1.** Model selection results for detection probability ($p$) of eastern spotted skunks in the George Washington and Jefferson National forests, Virginia, USA, January–May, 2014–2015. We held occupancy constant and fit survey data from 91 camera stations to the candidate model set to estimate $p$. Models ranked based on Akaike's Information Criterion corrected for small sample sizes ($AIC_c$).

| Model | $AIC_c$ | $\Delta_i$[a] | $w_i$[b] | $K$[c] |
|---|---|---|---|---|
| $p$ (moon illumination) | 454.68 | 0.00 | 0.8751 | 3 |
| $p$ (Virginia opossum) | 459.82 | 5.14 | 0.0668 | 3 |
| $p$ (snow depth) | 463.08 | 8.40 | 0.0131 | 3 |
| $p$ (temp) | 464.12 | 9.44 | 0.0078 | 3 |
| $p$ (bobcat) | 464.55 | 9.87 | 0.0063 | 3 |
| $p$ (.) | 464.76 | 10.08 | 0.0057 | 2 |
| $p$ (rainfall) | 464.98 | 10.30 | 0.0051 | 3 |
| $p$ (coyote) | 465.14 | 10.46 | 0.0047 | 3 |
| $p$ (raccoon) | 466.13 | 11.45 | 0.0029 | 3 |
| $p$ (survey effort) | 466.16 | 11.48 | 0.0028 | 3 |
| $p$ (accumulated snowfall) | 466.19 | 11.51 | 0.0028 | 3 |
| $p$ (striped skunk) | 466.22 | 11.54 | 0.0027 | 3 |
| $p$ (canopy cover) | 466.68 | 12.00 | 0.0022 | 3 |
| $p$ (ordinal date) | 466.76 | 12.08 | 0.0021 | 3 |

[a] Difference in $AIC_c$ of given model and top model.
[b] Akaike weight.
[c] Number of parameters.

**Table 2.** Model selection results for occupancy probability ($\Psi$) of eastern spotted skunks in the George Washington and Jefferson National forests, Virginia, USA, January–May 2014–2015. All models included percent moon illumination as a detection ($p$) covariate based on the best detection model. We fit survey data from 91 camera stations to the candidate model set to estimate $\Psi$. Models ranked based on Akaike's Information Criterion corrected for small sample sizes ($AIC_c$).

| Model | $AIC_c$ | $\Delta_i$[a] | $w_i$[b] | $K$[c] |
|---|---|---|---|---|
| $\Psi$ (stand age × elevation) | 451.61 | 0.00 | 0.3681 | 6 |
| $\Psi$ (stand size) | 454.07 | 2.46 | 0.1076 | 4 |
| $\Psi$ (.) | 454.96 | 3.35 | 0.0690 | 3 |
| $\Psi$ (slope) | 455.16 | 3.55 | 0.0624 | 4 |
| $\Psi$ (stand age) | 455.31 | 3.70 | 0.0579 | 4 |
| $\Psi$ (yr) | 455.51 | 3.90 | 0.0524 | 4 |
| $\Psi$ (elevation) | 455.70 | 4.09 | 0.0476 | 4 |
| $\Psi$ (area × elevation) | 456.63 | 5.02 | 0.0299 | 6 |
| $\Psi$ (canopy cover) | 456.11 | 4.50 | 0.0388 | 4 |
| $\Psi$ (aspect) | 456.20 | 4.59 | 0.0371 | 4 |
| $\Psi$ (age × area) | 456.78 | 5.17 | 0.0278 | 6 |
| $\Psi$ (TEI)[d] | 456.99 | 5.38 | 0.0250 | 4 |
| $\Psi$ (distance to agriculture) | 457.08 | 5.47 | 0.0239 | 4 |
| $\Psi$ (land cover)[e] | 457.09 | 5.48 | 0.0238 | 6 |
| $\Psi$ (distance to roads) | 457.37 | 5.76 | 0.0207 | 5 |
| $\Psi$ (.)$p$(.) | 459.22 | 7.61 | 0.0082 | 2 |
| Global | 474.26 | 22.65 | 0.0000 | 17 |

[a] Difference in $AIC_c$ of given model and top model.
[b] Akaike weight.
[c] Number of parameters.
[d] Topographic exposure index was calculated by subtracting the average elevation of a 1.75-$km^2$ circular area around each camera.
[e] Land cover type was classified as oak-dominated, non-oak, and mixed oak-pine forests using the Northeast Terrestrial Wildlife Habitat Classification System.

evidence ratio of $w_i$ between our 2 highest ranking models indicated 3.4 times more support for the top model over the second highest ranking model. Additionally the difference between $AIC_c$ score of the 2 highest ranking models exceeded 2. Therefore, we did not average occupancy models. Occupancy decreased as stand age and elevation at camera stations increased (Fig. 4). The 95% confidence intervals on the beta for the interaction of stand age and elevation ($\beta = 0.6$; 95% CI = 0.1–1.1) did not contain 0, which suggested an important effect of both on $\Psi$. The map of spotted skunk predicted $\Psi$ revealed small, spatially disjunct patches of high predicted occupancy surrounded by large patches of moderate to low predicted occupancy (Fig. 5). Approximately 2.65% of the study area consisted of high predicted occupancy habitat (predicted $\Psi \geq 0.90$) and 3.14% of the study area consisted of moderate predicted occupancy habitat (predicted $\Psi = 0.75$–$0.89$).

# DISCUSSION

Detection probability for eastern spotted skunks was generally negatively influenced by percent moon illumination. Detection probability peaked at new moon (0–25% illuminated), which agreed with many studies of nocturnal small-mammal response to moon phase (Wolfe and Summerlin 1989, Orrock et al. 2004, Kotler et al. 2010, Read et al. 2015). Moonlight increases the conspicuousness of small mammals to nocturnal predators such as owls, bobcats, and coyotes, which in turn leads to greater predation risk (Wolfe and Summerlin 1989, Orrock et al. 2004, Kotler et al. 2010). Lesmeister et al. (2010) reported aerial predators, most likely the nocturnal great horned owl (*Bubo virginianus*), and mammalian predators, to be the greatest cause of eastern spotted skunk mortality in the

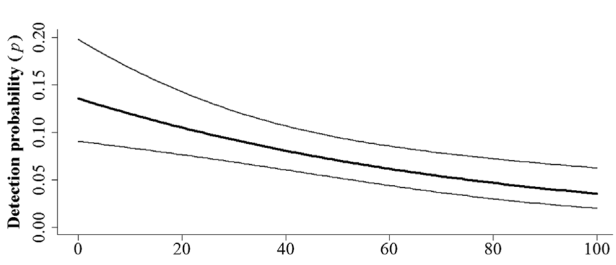


**Figure 3.** Eastern spotted skunk probability of detection (± SE) as a function of percent of moon surface illuminated in the George Washington and Jefferson National forests, Virginia, USA, January–April 2014–2015. We estimated probability from the most supported occupancy model.

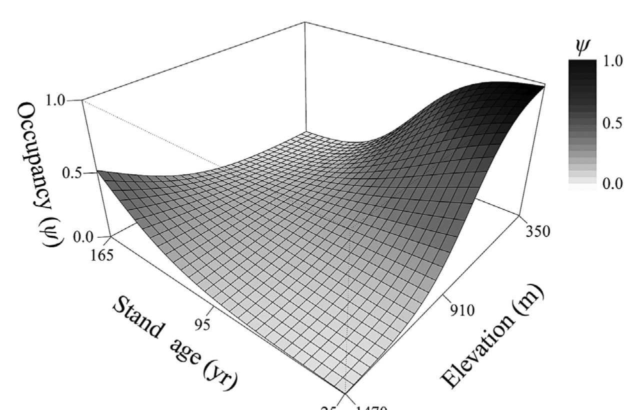


**Figure 4.** Eastern spotted skunk probability of winter occupancy ($\Psi$) as a function of forest stand age and elevation in the George Washington and Jefferson National forests, Virginia, USA, January–May 2014–2015. We estimated probability from the most supported occupancy model.

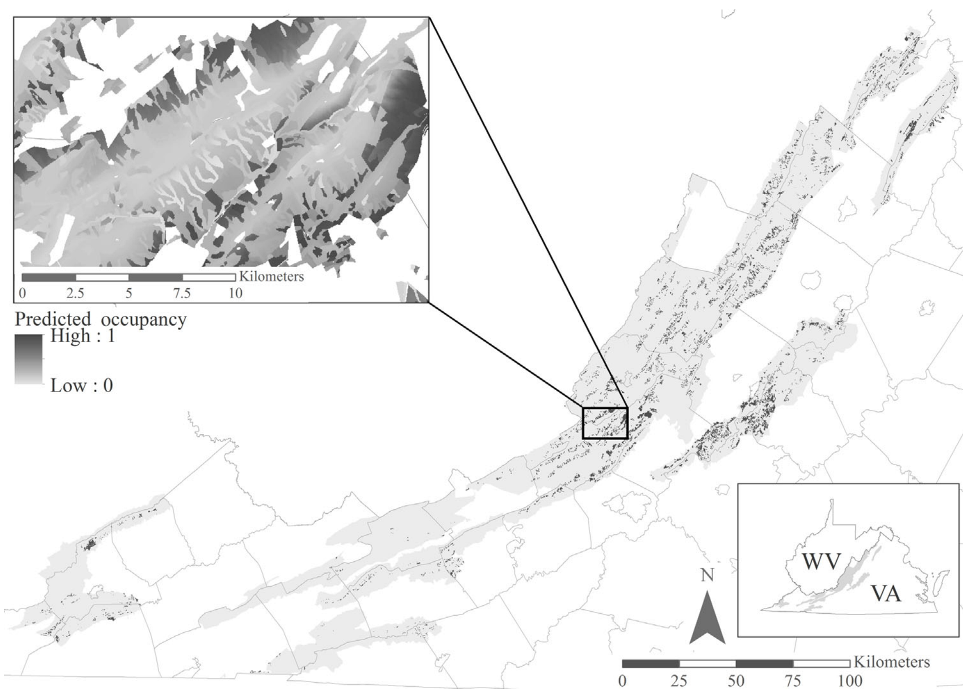


**Figure 5.** Map of predicted eastern spotted skunk winter occupancy ($\Psi$) across the landscape in the George Washington and Jefferson National forests, Virginia, USA, January–May 2014–2015. Areas of >50% predicted occupancy are shown in dark gray and areas of <50% occupancy are shown in light gray. Inset demonstrates patchy distribution of small, spatially disjunct areas of high predicted occupancy (>90%) surrounded by large areas of moderate to low predicted occupancy. We developed the occupancy map by applying our most supported occupancy and detection ($p$) model, $\Psi$ (stand age $\times$ elevation) $p$ (moon illumination), to each pixel.

Ouachita Mountains of western Arkansas. We suspect the negative association of spotted skunk detection probability with percent moon illumination in our study is suggestive of predator avoidance and risk reducing behaviors.

The indices for nocturnal illumination may not be accurate because we did not measure light intensity directly in our study. However, average daily temperature, rainfall, snowfall, and percent canopy cover had no effect on spotted skunk detection probability. Therefore, overcast skies from inclement weather or shade from canopy cover may not be affecting the response of spotted skunks to moon illumination. In areas of variable percent canopy or forest type, activity patterns and detectability of nocturnal animals may be influenced by light intensity irrespective of moon phase (Vignoli et al. 2014); however, our study was unable to distinguish between the effects of light intensity and moon phase. We found no strong effect of survey effort on detectability, which suggests the variation in survey length among sites likely did not bias spotted skunk detection probability. Ordinal date also showed no effect, which suggests no temporal variation in detection probability throughout the study period. Additionally, capture rates of other carnivore species had little effect on spotted skunk detection probability.

An interaction between forest age and elevation best predicted spotted skunk winter habitat occupancy throughout the study area. Probability of occupancy was highest in early to mid-successional forest stands (<50 yr old) at elevations <525 m and tended to decrease as forest age and elevation increased. Forest age is likely not the ultimate factor influencing spotted skunk winter habitat selection *per se* but rather the structural characteristics of forests associated with age. In eastern North America, forest structure tends to be more important for many wildlife species than plant species composition for a variety of taxa (Greenburg et al. 2011). Newly regenerated Appalachian forests often are characterized by high woody stem density prior to the stem exclusion phase of succession (Swanson et al. 2011, Wilson et al. 2014). In the central and southern Appalachians, a variety of species benefit from such complex forest structure such as ruffed grouse (*Bonasa umbellus*), where populations in habitats with greater forest cover and high understory cover reach higher densities than populations in mature forests with lower understory cover (Thompson and Dessecker 1997, Devers et al. 2007). Similarly, Lesmeister et al. (2010) reported higher spotted skunk mortality from avian predators in lower quality spotted skunk habitat consisting of mature shortleaf pine (*Pinus echinata*) stands with open canopy and little understory cover. Relationships between spotted skunk occupancy and forest age have been observed in the Ouachita Mountains (Lesmeister et al. 2008, 2009, 2010, 2013) and in the Missouri Ozarks (Hackett et al. 2007). Furthermore, for many species in the Appalachian region including migrating songbirds, rodents, white-tailed deer, and American black bears, young forests provide increased foraging opportunities through greater quantities of fungi, hard and soft mast, and invertebrate food sources (Harlow 1984, Loeb 1996, Mitchell and Powell 2003, McDermott and Wood 2010, Wilson et al. 2014).

Though our top model suggests spotted skunks are occupying habitat associated with young forests at low elevations, we detected eastern spotted skunks in a high elevation virgin red spruce forest type in the Whitetop Mountain area of Grayson County (second, smaller peak in Fig. 4). The year-round, closed canopy and dense rhododendron thickets characteristic of old growth red spruce forests may provide thermal cover and protection from aerial predators in a way that is functionally similar to younger hardwood forests. Whereas this forest type is limited to isolated patches in the southwestern-most region of the Appalachians in Virginia, relatively large and continuous patches persist in the central Appalachians of West Virginia and the southern Appalachians of Tennessee and North Carolina (Nowacki et al. 2010). These larger forest patches may potentially provide habitat for persistence of spotted skunk populations and travel corridors that allow movement between selected habitat patches separated by mountain ridgetops. This dichotomy of habitat selection suggest that, given enough structural cover, spotted skunks may show plasticity in elevational and forest type use when selecting for habitat.

Our predictive map of spotted skunk occupancy shows a fragmented distribution of small, high occupancy areas surrounded by a matrix of moderate to low occupancy areas (Fig. 5). Loss of early and mid-successional habitat to forest maturation and reduced harvesting, and declines in natural and anthropogenic disturbance regimes in forests of eastern North America (i.e., fire; Brose et al. 2001, King and Schlossburg 2013) may explain the patchy distribution of occupied habitat in the central and southern region of the Appalachians. In the GWJNF, annual timber harvest objectives total approximately 2,100 ha, whereas annual prescribed burn objectives total approximately 17,000 ha, of which selected areas of repeated treatment account for only 13% of the 287,691 ha of forest designated suitable for active management (U.S. Forest Service 2004, 2014). Currently, the majority of timber stands in the GWJNF are in the 90–130-year-old age class, which is either at, or exceeding, specified rotation ages of 80–100 years, in comparison to 11% of forest in the $\leq$50-year-old age classes (U.S. Forest Service 2004, 2014). Eastern spotted skunk populations may experience reduced winter habitat availability as production and maintenance of early- to mid-successional habitat remains low in much of the National Forest land in the central and southern Appalachians.

Habitat loss and fragmentation has been reported to be the cause of population declines and reduced habitat occupancy for various sensitive mesocarnivore species across a variety of habitats throughout North America, including western spotted skunks (*Spilogale gracilis*) and long-tailed weasels (*Mustela frenata*) in the Southwest (Crooks 2002) and fishers (*Martes pennanti*) in the Pacific Northwest (Marshall 1992, Zielinski et al. 1995) and the Northeast (Brander and Books 1973, Powell 1993). Loss of young forest habitat in the GWJNF over time, due to maturation of forests on public lands, possibly has reduced winter habitat availability for eastern spotted skunks. If vegetative cover as a means of predator avoidance and thermal protection is influencing spotted skunk winter habitat selection, this species may be vulnerable to environmental changes that reduce the structural complexity of forests. Populations experiencing declining winter habitat availability, reduced habitat patch size, and increased patch isolation are highly susceptible to the negative consequences of demographic, environmental, and genetic stochasticity (Lawton and May 1995, Boyce et al. 2005, Frankham 2006). As a result, there is potential for eastern spotted skunk populations to remain relatively rare or experience further decline in Virginia, and other parts of the central and southern Appalachians, as forest fragmentation increases and availability of young forest declines regionally.

Although, the use of bait at camera sites may potentially bias occupancy results by increasing detection rates for some species, unbaited camera surveys may fail to detect small, rare, and elusive carnivores in occupied habitat patches. For example, within the same region, Kelly and Holub (2008) were unable to detect eastern spotted skunks using unbaited sampling, whereas we detected spotted skunks at 4 baited camera stations from 2014 to 2015 where they had previously sampled. Moreover, fewer than 6 spotted skunks were detected throughout all the Appalachian region of Virginia throughout >10 years of unbaited camera surveys (M. J. Kelly, Virginia Tech Department of Fish and Wildlife Conservation, unpublished data). Baited camera sampling methods may increase precision of population estimates of small carnivores by increasing recapture rate, particularly when population sizes are small (Gerber et al. 2012, 2014). Therefore, we did not suspect the use of bait in our study to have influenced spotted skunk detection probability or patch occupancy estimates. Lastly, limiting our work to the dormant season may also have introduced another source of bias. Causes of seasonal variation in detectability of eastern spotted skunks are unclear. However, patterns of detectibly and capture success of many carnivore species, including other species of skunk, may be attributed to season shifts in resource availability, home range size, habitat use, and foraging ability (Bailey 1971, Bixler and Gittleman 2000, Zapata et al. 2001, Cantú-Salazar et al. 2005, Doty and Dowler 2006).

Future research on eastern spotted skunk should assess the effects of creating additional early- to mid-successional habitat through forest management (e.g., stand thinning, prescribed burning) with the goal of increasing patch connectivity that may reduce or prevent further population decline and aid in recovery. Maintaining habitat for spotted skunks will require more detailed knowledge of spotted skunk ecology, micro-habitat selection, movement patterns, and genetic health of the population. Although occupancy analysis is a suitable method for predicting habitat associations at the landscape level, detection-non-detection methods are limited in scope because of the inability to identify individual spotted skunks for abundance or density estimates, home range analysis, sex segregation, or detailed movement patterns. Intensive capture-recapture efforts combined with the use of radio telemetry are necessary to further understand eastern spotted skunk habitat requirements. In addition, effective population monitoring and sampling methods are necessary for implementing successful management practices.

## MANAGEMENT IMPLICATIONS

The overall low availability of selected habitat (predicted $\Psi \geq 0.90$) throughout the GWJNF indicates a potential need to consider this species when generating conservation and management assessments in forested areas. The baited remote-sensing camera methods used in this study are an effective technique for detecting spotted skunks and may provide a relatively low cost method for long term, large-scale monitoring. Managers should also consider the dichotomous forest types that spotted skunks use throughout their range, which may require separate assessments of habitat associations and adaptable management practices at local scales. Additionally, non-habitat factors may influence spotted skunk spatial distribution and habitat use. Further research is needed to investigate the effects of sympatric carnivore interactions, including competition, predation, and potential zoonotic disease transfer on eastern spotted skunk populations, habitat use, and spatial distribution at both the local and regional scales.

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