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Landscape Ecology of Eastern Spotted Skunks in Habitats Restored for Red-Cockaded Woodpeckers

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Abstract

Although examples are rare, conflicts between species of conservation concern can result from habitat restoration that modifies habitat to benefit a single taxon. A forest restoration program designed to enhance habitat for endangered red-cockaded woodpeckers (*Picoides borealis*) may be reducing available habitat for the eastern spotted skunk (*Spilogale putorius*), a forest-adapted sympatric species of conservation concern that occurs in the Ouachita National Forest, Arkansas, U.S.A. At small scales, eastern spotted skunks select early successional forest with structural diversity, whereas red-cockaded woodpeckers prefer mature pine (*Pinus* spp.) habitat. We surveyed for eastern spotted skunks at 50 managed forest stands, modeled occupancy as a function of landscape-level habitat factors to examine how features of restoration practices influenced occurrence, and compared known occupied forest stands to those where active red-cockaded woodpecker nesting clusters were located. The most-supported occupancy models contained forest stand age (negatively associated) and size (positively associated); suggesting eastern spotted skunks primarily occupy large patches of habitat with dense understory and overhead cover. Red-cockaded woodpecker nesting clusters were located in smaller and older forest stands. These results suggest that increased overhead cover, which can reduce risk of avian predation, enhances occupancy by small forest carnivores such as eastern spotted skunks. Management activities that increase forest stand rotation length reduce the availability of young dense forest. The practice may enhance the value of habitat for red-cockaded woodpeckers, but may reduce the occurrence of eastern spotted skunks. Implementing plans that consider critical habitat and extinction risks for multiple species may reduce such conservation conflict.

Key words: conservation conflict, forest structure, Ouachita Mountains, *Picoides borealis*, pine-bluestem, *Spilogale putorius*.

Introduction

At large spatial scales, ecosystems are typically composed of habitats that may be roughly similar in taxonomic composition, but vary in successional stages. For example, periodic perturbations to a forest community may result in stands of young or dense forest within a broader matrix of older forest. Conversely, restoration efforts may result in stands of protected older forest within a younger or more degraded forested landscape. Large forest ecosystems, by providing diversity in forest composition or structure, likely enhance the diversity of the animal community therein, because in a fixed area species richness is positively related to habitat diversity (Kallimanis et al. 2008).

In some cases, habitat restoration or modification is used as a tool to support populations of conservation concern, whereby an attempt is made to enhance habitat characteristics that may limit the target population. Implicit in this management decision is that habitat characteristics may simultaneously, and perhaps negatively, influence non-target taxa, perhaps including other taxa of conservation concern. Therefore, to reduce conservation conflict it is important to consider critical habitat and extirpation risks for multiple species in management plans (Lambeck 1997; Nicholson & Possingham 2006). However, while potential conflicts involving the management of threatened taxa have been reported (Roemer & Wayne 2003; Livezey 2010), these typically involve direct manipulations of the taxa rather than habitat restoration efforts. Conflicts mediated by habitat restoration efforts are, to our knowledge, rare. Here, we show how ecosystem restoration efforts undertaken to restore populations of an endangered bird (red-cockaded woodpecker, *Picoides borealis*) may negatively affect the presence of a second species of conservation concern (eastern spotted skunk, *Spilogale putorius*).

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The carnivore community of North America has changed dramatically over the past century. While the loss of large carnivores from most regions is recognized, and the causes of these declines are reasonably well understood (Woodroffe 2001), several small carnivore species have also declined in abundance and the causes for these declines are often unclear. The eastern spotted skunk, one of the smallest (generally <1 kg) North American carnivores, was historically common throughout much of the southeastern and central United States, but for unknown reasons populations have declined precipitously and the species is now of conservation concern throughout much of its range (Gompper & Hackett 2005). Recent work on local-scale resource selection in western Arkansas suggested that eastern spotted skunks select early forest successional habitat to reduce predation risk (Lesmeister et al. 2009; Lesmeister et al. 2010), although at larger landscape scales such work has not been conducted. Predation by owls was a primary source of mortality for eastern spotted skunks, and predation events were more likely to occur in mature forest patches that contained an open understory (Lesmeister et al. 2010).

Large tracts of forested habitat occur throughout the range of the eastern spotted skunk, but these areas are subject to a variety of management strategies. Notably, timber harvest and controlled burning to alter forest age and understory community structure are commonly used to enhance the value of the habitat for other wildlife species. Manipulation of forest age and structure to increase red-cockaded woodpecker populations represents an ecosystem management program instituted to improve the likelihood of species persistence. The red-cockaded woodpecker is federally listed as endangered and prefers forest comprised of open, frequently burned, mature pine (*Pinus spp.*), with sparse midstory and a high herbaceous understory (Porter & Labisky 1986; Engstrom & Sanders 1997; Walters et al. 2002). Indeed, managers and researchers generally consider the species a near obligate of mature pine forest. These mature pine areas provide a food source because red-cockaded woodpeckers feed primarily on bark-dwelling arthropods of trees in their preferred pine-dominated habitats. Furthermore, only mature trees older than 70 years have sufficient heartwood to contain a cavity chamber and a greater prevalence of fungal heart rot (*Phellinus pinii*) infection, facilitating cavity construction for nesting and roosting (Bukenhofer et al. 1994). The majority of red-cockaded woodpecker populations exist on federal lands, which are subject to habitat restoration as directed by the United States Endangered Species Act. To enhance the availability of this forest community, ecosystem-scale conservation efforts involving intensive removal of hardwoods, pine thinning, and prescribed fire [commonly known as pine-bluestem (*Andropogon* spp. and *Schizachyrium* spp.) restoration] have been applied. This management strategy may also benefit other taxa that are adapted to mature open forest (Wilson et al. 1995; Masters et al. 1998), but it is unknown how the habitat restoration practice influences many species, particularly those that rely on early successional forest.

The structure of the landscape, and thus management techniques that manipulate that structure, are important factors in carnivore patch use (Ruggiero et al. 1994; Mortelliti & Boitani 2008). Therefore, we contrasted occupancy models based on forest habitat characteristics and restoration strategies for an eastern spotted skunk population in the Ouachita Mountains of Arkansas, U.S.A. that co-occurs with a red-cockaded woodpecker population managed through pine-bluestem restoration efforts (Bukenhofer et al. 1994; Lesmeister et al. 2008, 2009). The long-term dynamics of eastern spotted skunks in Arkansas reflect the pattern of decline observed range-wide (Sasse & Gompper 2006). As part of an ultimate goal of determining the processes that threaten the persistence of an eastern spotted skunk population in the Ouachita Mountains, our objective was to quantify which management techniques used during restoration best predicted eastern spotted skunk occurrence in this forested region. In addition, we compared attributes of areas known to be occupied by eastern spotted skunks to forest stands where active nesting clusters of red-cockaded woodpeckers were located. We designed contrasting models that considered macrohabitat features of the region that were subject to management, including forest stand age, forest stand size, the composition of the surrounding habitat, and the burning history of the forest stand. Manipulation of these variables is the primary management and restoration approach applied in this region as well as in many forested habitats across the United States.

Methods

Study Site

We conducted this study within a large-scale pine-bluestem project in the Ouachita Mountain physiographic region of west-central Arkansas, U.S.A. Forest stands were selected in the Poteau Ranger District (PRD; 96,755 ha), Ouachita National Forest (ONF; 690,000 ha; lat 34°48′N, long 94°21′W; Fig. 1). Mean annual temperature and precipitation for PRD are 17°C and 105 cm, with a general climate of warm winters and hot, dry summers. The ONF is comprosed of east-west trending sandstone mountain ridges (maximum elevations of about 790 m) interspersed with rich alluvial soil bottomlands of the valleys. Valleys and north aspects of the mountains are dominated by pines and by oaks and hickories (*Quercus* spp. and *Carya* spp.). At the time of this study, approximately 73% of the PRD was managed as shortleaf pine (*Pinus echinata*) stands.

Shortleaf pine historically covered as much as 40% of the southwest aspects of the Ouachita Mountains. Naturalists who explored the Ouachita highlands in the early 1800s described the forest cover as primarily pines interspersed with oak, hickory, and dogwood (*Cornus* spp.; Strausberg & Hough 1997). Accounts also described a variety of vines and grass in the understory, and dense vegetation in forests with infrequent burns. Indigenous peoples were believed to clear portions of the forest for small-scale cultivation and set fires in fall or winter to attract game to young grass during spring. However,

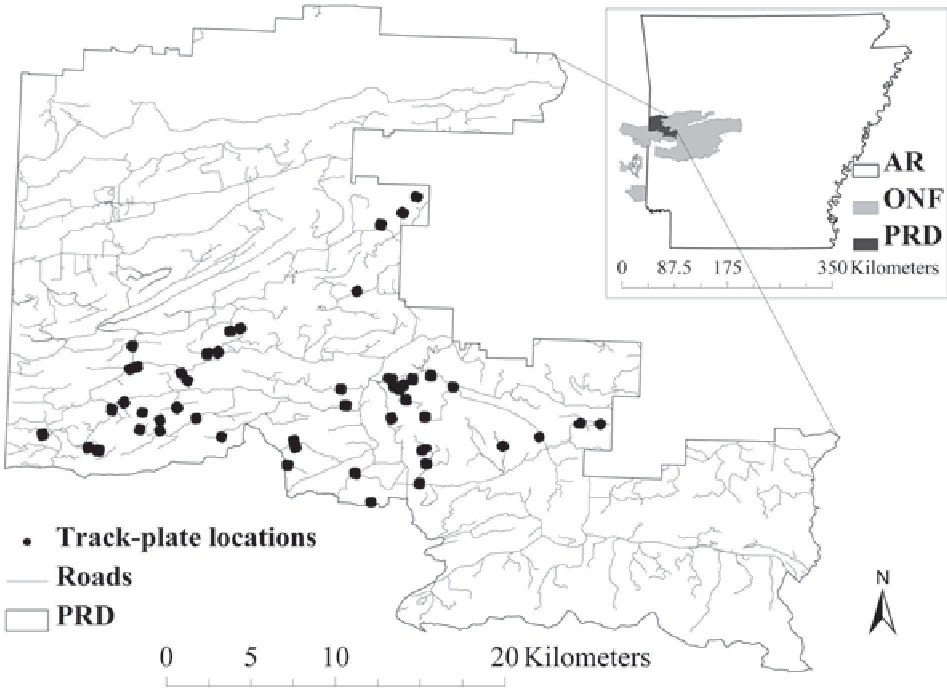

Figure 1. Locations of track-plate survey forest stands for eastern spotted skunks (*Spilogale putorius*) in the Poteau Ranger District (PRD), Ouachita National Forest (ONF), expanded from Arkansas (AR), U.S.A., 2006–2007.

the scale at which the landscape was regularly impacted by fires is unknown. Although various timber harvest regimes were used in the ONF throughout the 1900s, the United States Forest Service (USFS) maintained a strict policy of fire suppression that continued into the 1980s (Strausberg & Hough 1997).

To restore forest conditions to those putatively occurring prior to settlement by non-indigenous peoples, the ONF initiated large-scale restoration efforts for the shortleaf pine-bluestem ecosystem. The restoration project covered 62,730 ha and was overseen by the USFS (USDA 2005). Following the recovery plan for red-cockaded woodpeckers (USFWS 2003), the primary objective of the restoration project was to create an open canopy with herbaceous vegetation in the understory (Fig. 2), thereby providing habitat for species associated with mature, open pine forest (Masters et al. 1998; USDA 2005). The USFS accomplishes ecosystem restoration and maintenance by reducing tree basal areas through commercial and non-commercial thinning of shortleaf pine stands and increasing use of prescribed fire to a 3-year rotation. To facilitate cavity creation, the USFS increased stand rotation age from 70 to 120 years to increase the number of fungal heart rot-infected shortleaf pine trees (Bukenhofer et al. 1994). The maximum size of pine regeneration areas is 16 ha if within 1.6 km of an active red-cockaded woodpecker cavity tree cluster, or 32 ha otherwise; and 4 ha for hardwood-dominated stands (USDA 2005). Forest stands in PRD are well delineated and monitored by the USFS. Restored mature (>70 years old) shortleaf pine stands (58% of PRD) have a more open canopy and are typically 10–13 times less dense in understory woody vegetation compared to young (<30-years old) shortleaf pine forest (4% of PRD; Perry, unpublished data; Masters 2007; Table 1). An additional management technique used in the PRD is retention of hardwood stands and streamside management zones (natural hardwood forest stands retained along streams; 25% of PRD) within the intensively managed shortleaf pine forest mosaic (USDA 2005).

Field Techniques

Local-scale patterns of habitat use by radio-collared animals indicated that habitat selection by eastern spotted skunks was based on forest age and stand structure (Lesmeister et al. 2008, 2009). Therefore, at the much larger spatial scale of this study we selected forest stands to survey that differed in structure due to differences in age, management techniques, species composition, and burn history (control, burned mature, unburned mature, burned young, and unburned young) where active pine-bluestem restoration occurred (Table 1). Burned mature stands were considered fully restored, and while unburned mature stands were thinned to appropriate residual basal area, they were not considered fully restored because of the lack of prescribed burns, which created a denser woody understory. We surveyed 50 forest stands (7 control, 15 burned mature, 8 unburned mature, 10 burned young, and 10 unburned young) for eastern spotted skunks using track-plate stations from September 2006 to February 2007 (Fig. 1). The season for surveys was selected to maximize detection probabilities for the species (Hackett et al. 2007). At surveyed stands, we established a 3 × 3-station grid with

Figure 2. Photos of (a) early successional forest and (b) mature shortleaf pine forest restored to meet the pine-bluestem restoration objective in the Ouachita National Forest (ONF), Arkansas, U.S.A., 2006–2007.

approximately 100 m between stations, designed to maximize detections and accommodate the small size of some forest stands. Track-plates were 24 × 100 × 0.32-cm solid plastic sheeting with carbon toner as tracking medium, contact paper to collect footprints, and sardines as bait. We placed track-plates within a corrugated plastic housing to protect against weather (Gompper et al. 2006). We checked, rebaited, and replaced contact paper of track-plates every 3 days, and left track-plates deployed for 12 days, which provided four survey samples (four opportunities to detect the species) per forest stand.

Data Analyses

We estimated survey-specific detection probability (p) and forest stand occupancy (ψ) of eastern spotted skunks. There were three possible outcomes of surveys: (1) the stand was occupied and ≥1 eastern spotted skunk was detected, $\psi \times p$; (2) the species was present but not detected, $\psi \times (1 - p)$; and (3) the species was not present and therefore was not detected, $1 - \psi$. We verified that occupancy was closed throughout the study period using the Robust-design models suggested by MacKenzie et al. (2006).

Table 1. Descriptions of forest stand types surveyed for eastern spotted skunks (*Spilogale putorius*) using track-plates, Ouachita Mountains, Arkansas, U.S.A., 2006–2007.

Forest Stand Type	*Description*
Control	Mixed forest stands ≥70-years old with no management treatments applied
Burned young	Shortleaf pine (*Pinus echinata*) stands 10- to 25-year-old treated with pre-commercial thinning and ≥1 burn within 10 years
Unburned young	Shortleaf pine stands 10- to 25-year-old treated with pre-commercial thinning and no burns within 10 years
Burned mature	Shortleaf pine stands ≥70 years old treated with commercial thinning and wildlife stand improvement to residual basal area of about 13.8 m^2/ha and ≥1 burn within 10 years
Unburned mature	Shortleaf pine stands ≥70 years old treated with commercial thinning and wildlife stand improvement to residual basal area of about 13.8 m^2/ha and no burns within 10 years

We used a two-stage process in a likelihood-based modeling framework to estimate p and ψ (MacKenzie et al. 2006). First, we assumed that p and ψ were constant across time and space, which provided a comparison to models with habitat and survey covariates. To reduce bias in predicted ψ, we assessed factors that might affect eastern spotted skunk p by holding the proportion of stands occupied constant ($\psi(\cdot)$) and developed a set of 11 candidate p models (Table 2). We constructed p models with combinations of the variables such as date, burns, stand age, survey-specific detections (separate p estimated for each survey sample), habitat type, temperature, and previous detections. The latter represents a detection history to account for potential likelihood of an animal revisiting a baited track-plate because of knowledge of the availability of bait.

In the second stage of our modeling procedure, we used the most-supported p model and combinations of several habitat factors (forest stand age and size, burn or not burned within 10 years, buffer mature, and buffer young) that may affect eastern spotted skunk ψ to develop a candidate set of 11 a priori ψ models. We used USFS records for age, burn history, and size of stands. For the covariates buffer mature and buffer young, we calculated the percentage of mature forest (>70 years old) and young forest (10 to 25 years old) within buffers surrounding the central track-plate at surveyed forest stands that corresponded to the mean home range size (3.12 km^2) for eastern spotted skunks (Lesmeister et al. 2009). Using program PRESENCE 2.3, we ranked both p and ψ models based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) values and Akaike weights (w_i) to select the most-supported model (Burnham & Anderson 2002; Hines 2006; MacKenzie et al. 2006). The w_i for each model represents the

Table 2. Model selection results for per survey detection probability (p) of eastern spotted skunks (*Spilogale putorius*) using track-plate surveys in the Ouachita Mountains, Arkansas, U.S.A., 2006–2007.

Model	AIC_c	ΔAIC_c	w^a	K^b	*Deviance*[c]
p(.)	101.24	0.00	0.244	2	97.24
p(date)	102.06	0.82	0.159	3	96.06
p(burn)	102.19	0.95	0.149	3	96.19
p(age)	102.25	1.01	0.144	3	96.25
p(previous detection)	103.21	1.97	0.086	3	97.21
p(temperature)	103.28	2.04	0.082	3	97.28
p(date + age)	103.33	2.09	0.081	4	95.33
p(survey)	104.65	3.41	0.038	5	94.65
p(habitat)	105.73	4.49	0.019	6	93.73
p(survey + date)	107.25	6.01	0.004	6	95.25
p(fully parameterized)[d]	111.08	9.84	0.000	20	71.08

We held occupancy constant [ψ(.)] and fit encounter history data from 50 forest stands to the candidate model set to estimate p.
Ranking was based on Akaike Information Criterion for small samples (AIC_c).
[a] Akaike weight.
[b] Number of parameters.
[c] Difference in 2log(Likelihood) of current model and −2log(Likelihood) of the saturated model.
[d] Survey-specific date, age, burn, temperature, and recapture.

probability of that model being the best approximating model of those evaluated. We created a map of eastern spotted skunk ψ in the PRD based on most-supported models.

To contrast the eastern spotted skunk ψ models with the habitat used by red-cockaded woodpeckers, we measured the size and age of forest stands where active red-cockaded woodpecker nesting clusters ($n = 86$) were located by USFS researchers in 2006 (Montague, unpublished data). We used the Mann–Whitney U test to statistically assess the significance of differences in size and age of stands where eastern spotted skunks were detected and where active red-cockaded woodpecker nesting clusters were located.

Results

We recorded 126 eastern spotted skunk detections across 11 different forest stands ($\psi \pm SE = 0.220 \pm 0.059$; $p \pm SE = 0.794 \pm 0.062$). Stands where eastern spotted skunks were detected were 1.6 times larger and 1.8 times younger than those where the species was not detected (Fig. 3). Similarly, eastern spotted skunks were detected in stands that were 1.9 times larger ($U = 667$, p-value = 0.06) and 2.2 times younger ($U = 205$, p-value < 0.01) than those where red-cockaded woodpecker nesting clusters were located (Fig. 3). Ranking of p models revealed that the constant detection model, p(.), was the most supported (Table 2). While a variety of other models fell within 2 AIC_c units of the top-ranked model, none performed better than the p(.) model, suggesting variability in detections were not explained by survey covariates. Therefore, we used the p(.) in all occupancy models.

Ranking of occupancy models indicated that the size and age of forest stands were the best predictors of occupancy ($w = 0.51$; Table 3). The second highest ranked model included stand age as the only habitat covariate ($\Delta AIC_c = 2.38$), but

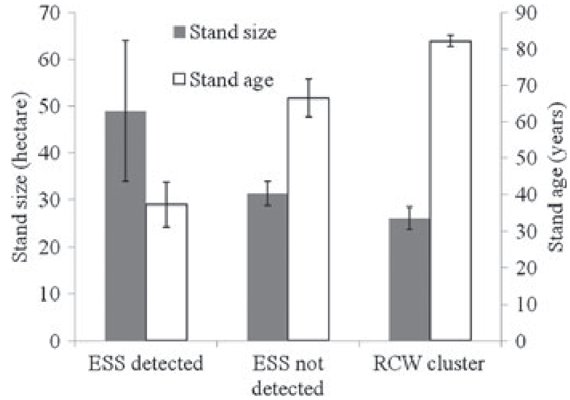

Figure 3. Mean (SE) stand age and stand size of shortleaf pine (*Pinus echinata*) forest stands of known red-cockaded woodpecker (RCW; *Picoides borealis*) nesting cluster locations ($n = 86$), and where eastern spotted skunks (ESS; *Spilogale putorius*) were ($n = 11$) and were not ($n = 39$) detected during track-plate surveys in the Poteau Ranger District (PRD), Ouachita National Forest (ONF), Arkansas, U.S.A., 2006–2007.

this model had considerably less support ($w = 0.16$) relative to the top-ranked model, indicating a strong combined effect of the two predictor variables. Age of a forest had a negative influence on occupancy (Fig. 4a), and was present in each of the top five models. Modeling stand size by itself, as well as the burn history provided little insight ($w < 0.02$) toward predicting the likelihood of occupancy. However, there was a positive relationship between stand size and predicted occupancy (Fig. 4b).

Mapping eastern spotted skunk ψ based on stand age and size indicated a patchy distribution of high use areas (Fig. 5). Most nesting clusters of red-cockaded woodpeckers were located in areas where the predicted occupancy of eastern spotted skunks was low ($\psi \pm SE$; 0.035 ± 0.003; Fig. 5).

Discussion

Forest age was the most important parameter for predicting habitat occupancy by eastern spotted skunks, with the probability of occurrence declining in older forests. The importance of forest age has been repeatedly observed for eastern spotted skunks in the Ouachita Mountains, with support for this finding derived from local-scale studies of den site selection (Lesmeister et al. 2008), home range habitat use (Lesmeister et al. 2009), survival analyses (Lesmeister et al. 2010), and now a broader scale assessment of habitat occupancy and comparisons to areas occupied by red-cockaded woodpeckers. This preference for younger forest in ONF is striking, as this habitat type was strongly selected over older forest despite comprising only a small portion (4 vs. 58% for mature forest) of the study region. Forest age, however, must also be viewed in the context of forest stand size. Even if sufficient resources are available, patch size and isolation play important roles in carnivore habitat use (Mortelliti & Boitani 2008). Small stands were less likely to contain eastern spotted skunks even when

Table 3. Model selection results for forest stand occupancy (ψ) by eastern spotted skunks (*Spilogale putorius*) using track-plate surveys in the Ouachita Mountains, Arkansas, U.S.A., 2006–2007.

Model	*AIC$_c$*	*ΔAIC$_c$*	w^a	K^b	*Deviance^c*
Ψ(size + age)	94.59	0.00	0.514	4	86.592
Ψ(age)	96.97	2.38	0.156	3	90.966
Ψ(age + burn)	97.76	3.17	0.105	4	89.757
Ψ(buffer mature + age)	98.62	4.03	0.069	4	90.622
Ψ(burn + age + size + size^2 + buffer mature + buffer young)	99.22	4.63	0.051	8	83.219
Ψ(buffer mature)	100.64	6.05	0.025	3	94.645
Ψ(size)	101.11	6.52	0.020	3	95.114
Ψ(.)	101.24	6.65	0.019	2	97.236
Ψ(buffer young)	101.25	6.66	0.018	3	95.252
Ψ(size + size^2)	102.13	7.54	0.012	4	94.131
Ψ(burn)	102.18	7.59	0.012	3	96.176

We held probability of detection constant [$p(.)$] and fit encounter history data from 50 forest stands to the candidate model set to estimate ψ.
Ranking was based on Akaike Information Criterion for small samples (AIC$_c$).
^{a} Model weight.
^{b} Number of parameters.
^{c} Difference in 2log(Likelihood) of current model and -2log(Likelihood) of the saturated model.

those patches were younger forest and would otherwise be considered excellent habitat for the species.

Predation risk has a powerful role in the space use of meso- and small-bodied carnivores, such that they avoid areas of high risk (Ruggiero et al. 1994; Buskirk 1999; King & Powell 2007). Three non-exclusive explanations, each related to predation, may underlie the lower likelihood of eastern spotted skunk occurrence in smaller forest stands. First, smaller patches may contain a greater edge-to-core ratio, thus animals are increasingly susceptible to predators when they enter the edge portion of their habitat with increased openness (Lesmeister et al. 2010). Second, males have large seasonal increases in home range size during the breeding period when they quest for mating opportunities (Lesmeister et al. 2009). In large patches, these increases in home range size may be conducted within young forest. For individuals inhabiting smaller patches, however, such increases in home range size can only occur by entering suboptimal habitat and thereby increasing exposure to predators. Third, and by similar reasoning, once local extinction occurs, recolonization can only occur when an individual crosses the hostile matrix of mature open forest, with increased likelihood of avian-caused mortality.

Detailed assessment of eastern spotted skunk habitat has only been conducted in the ONF of western Arkansas. Hackett (2008) observed that proportion of forest cover was the most influential variable in predicting the species' occupancy in the Missouri Ozarks (primarily oak-hickory forests). However, Hackett's work lacked the detailed habitat information to assess whether eastern spotted skunk occupancy varied with forest structure and composition. The importance of having such a detailed and nuanced understanding of the role of forest structure has become increasingly clear. For example, Kays et al. (2008) found that coyote (*Canis latrans*) abundance in forests of the northeastern United States varied as a function of forest structure and diversity. In the case of the eastern spotted skunk, forest age per se may not ultimately drive habitat selection. Rather, it is the complexity and density of the understory that enhances predator avoidance. Such habitat structural components likely also occur in other ecosystems that contain forests of diverse ages and compositions.

The strong habitat preferences of eastern spotted skunks are ultimately explained by considering their susceptibility to predators as well as the habitat characteristics that mediate trophic and competitive interactions. Although the woody component to the understory of unburned mature forest stands may provide some protection from avian predators, the reduced risk is likely not enough to overcome the availability of avian predator roost sites. Young forest provides access to prey, thermal microenvironments for reproduction and resting, enhanced predator avoidance, and may meet a "psychological need" for overhead cover (Ruggiero et al. 1994; King & Powell 2007). This suggests a fundamental difference in the drivers of habitat occupancy for large and small carnivores, where the importance of habitat structure seems to be body-size dependent. Space use by large predators is best understood through a focus on prey availability, which is why they individually may not serve well as "umbrella" species (Carroll et al. 2001). In contrast, smaller carnivores are subject to both bottom-up limitation (i.e. resource availability) as well as top-down limitation (i.e. intraguild competition and predation). Understanding the interplay of these two factors will allow an enhanced appreciation of how habitat restoration activities may modify space use by small carnivores.

Pine-bluestem restoration effort in the ONF is primarily focused on providing preferred habitat for a single species, the red-cockaded woodpecker, and commenced well before knowledge of eastern spotted skunk habitat use was available;

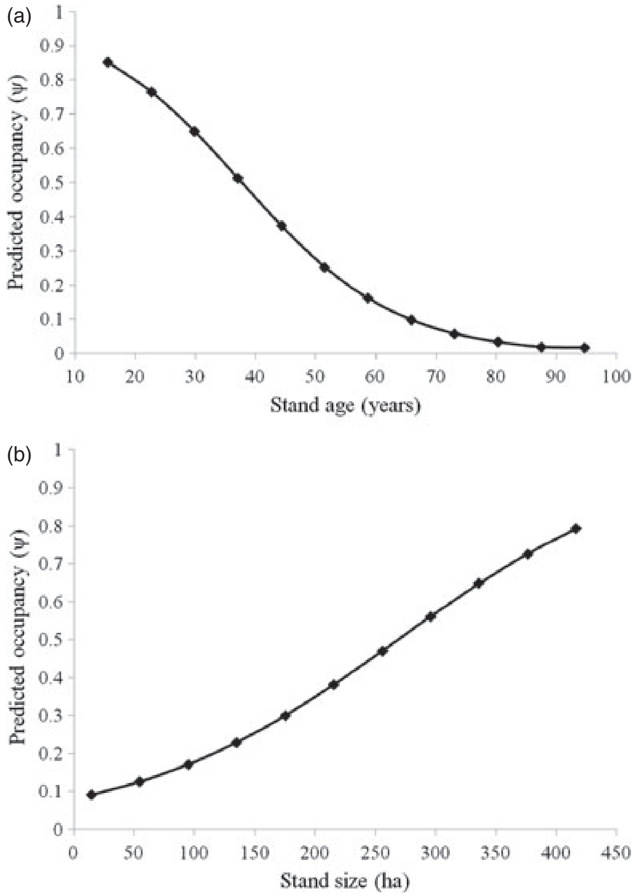

Figure 4. Influence of the (a) forest stand age and (b) forest stand size on the probability of eastern spotted skunk (*Spilogale putorius*) occupancy (ψ) in the Poteau Ranger District (PRD), Ouachita National Forest (ONF), Arkansas, U.S.A., 2006–2007. Probabilities were calculated using model-averaged estimates of the two most-supported occupancy models.

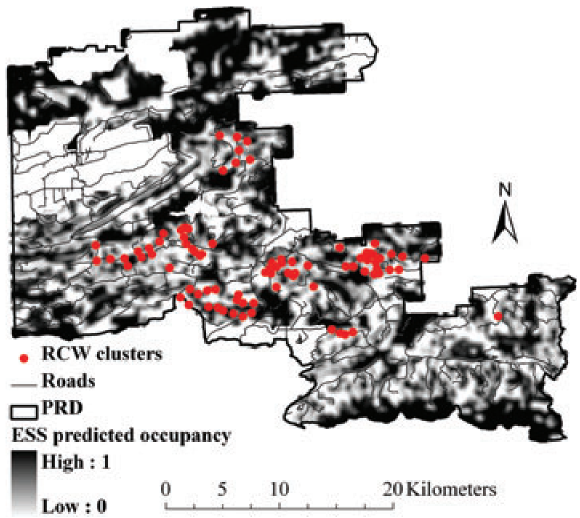

Figure 5. Map of known red-cockaded woodpecker (RCW; *Picoides borealis*) nesting cluster locations (n = 86) and predicted occupancy of eastern spotted skunks (ESS; *Spilogale putorius*) in the Poteau Ranger District (PRD), Ouachita National Forest (ONF), Arkansas, U.S.A., 2006–2007. Probabilities were calculated using forest stand age and size coefficient estimates derived from occupancy models.

thus limited information was available to forewarn of potential management conflict. Our data suggest these two species use vastly different habitats in the ONF. Therefore, large-scale habitat restoration for red-cockaded woodpeckers may be deleterious for eastern spotted skunks for multiple reasons, all related to mortality risk from predators. First, increasing stand rotation from 70 to 120 years will continue to increase the dominance of mature forest on the landscape, thereby decreasing availability of early successional communities and increasing available habitat for avian predators. Second, the maximum pine regeneration stand size of 32 ha is much smaller than the 80 ha average home range of female eastern spotted skunks (Lesmeister et al. 2009). Therefore, each individual requires several patches and must traverse dangerous areas between selected habitats. Third, removal of midstory reduces the structural complexity of a stand, preventing the stand from meeting the eastern spotted skunks' need for overhead cover. Fourth, a 3-year prescribed fire rotation reduces woody understory (Waldrop et al. 1992), which is particularly important for predator avoidance by small carnivores during fall and winter because raptors and larger mammalian predators are less maneuverable in dense vegetation (Clevenger 1994; Forsey & Baggs 2001). Although streamside management zones may serve as corridors because eastern spotted skunks use hardwood stands to the extent available (Hackett 2008; Lesmeister et al. 2009), the continued isolation of small early successional forest will negatively influence populations in the ONF.

Despite the fact that this study was conducted in a short-leaf pine-bluestem ecosystem, eastern spotted skunks and red-cockaded woodpeckers occur sympatrically in other ecosystems [e.g. longleaf pine (*Pinus palustris*)-wiregrass (*Aristida stricta*)] subject to similar management techniques (Van Lear et al. 2005; Means 2006). Consequently, potential conflict in managing for both species is likely not restricted to the ONF. However, while we have extensive knowledge of red-cockaded woodpecker habitat requirements, our in-depth understanding of eastern spotted skunk landscape ecology is primarily limited to the ONF. If abundant habitat for eastern spotted skunks occurs in other regions where red-cockaded woodpeckers cannot persist, then assessing the needs of the two species on a broader spatial scale may help alleviate the apparent conflicting local habitat needs.

Implications for Practice

- To reduce conservation conflict, forest ecosystem restoration plans should consider forest mosaic structure and recognize that different taxa have different life-history needs, and some species may be negatively influenced if habitat diversity is decreased.

- Sufficient spatially and structurally diverse young forest to sustain a viable population of eastern spotted skunks will be necessary for the species' persistence in pine-bluestem ecosystems.
- Increasing maximum size of regeneration areas will provide more stands that meet the minimum size requirement for an individual female eastern spotted skunk home range without negatively affecting red-cockaded woodpeckers.
- Reducing isolation of 10- to 25-year-old stands by limiting distance between and connecting with hardwood stands retained along streams will reduce danger for eastern spotted skunks moving between selected patches without negatively affecting red-cockaded woodpeckers.

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LITERATURE CITED

Bukenhofer, G. A., J. C. Neal, and W. G. Montague. 1994. Renewal and recovery: shortleaf pine/bluestem grass ecosystem and red-cockaded woodpeckers. Journal of the Arkansas Academy of Science **48:**243–245.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York.

Buskirk, S. W. 1999. Mesocarnivores in Yellowstone. Pages 165–180. in T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the rocky mountain region. Ecological Applications **11:**961–980.

Clevenger, A. P. 1994. Habitat characteristics of Eurasian pine martens Martes martes in an insular Mediterranean environment. Ecography **17:**257–263.

Engstrom, R. T., and F. J. Sanders. 1997. Red-cockaded woodpecker foraging ecology in an old-growth longleaf pine forest. The Wilson Bulletin **109:**203–217.

Forsey, E. S., and E. M. Baggs. 2001. Winter activity of mammals in riparian zones and adjacent forests prior to and following clear-cutting at Copper Lake, Newfoundland, Canada. Forest Ecology and Management **145:**163–171.

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. E., R. W. Kays, J. C. Ray, S. D. Lapoint, D. A. Bogan, and J. R. Cryan. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin **34:**1142–1151.

Hackett, H. M. 2008. Occupancy modeling of forest carnivores in Missouri. Ph.D. dissertation. University of Missouri, Columbia.

Hackett, H. M., D. B. Lesmeister, J. Desanty-Combes, W. G. Montague, J. J. Millspaugh, and M. E. Gompper. 2007. Detection rates of eastern spotted skunks (Spilogale putorius) in Missouri and Arkansas using live-capture and non-invasive techniques. American Midland Naturalist **158:**123–131.

Hines, J. E. 2006. PRESENCE 2.0—Software to estimate patch occupancy and related parameters. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.

Kallimanis, A. S., A. D. Mazaris, J. Tzanopoulos, J. M. Halley, J. D. Pantis, and S. P. Sgardelis. 2008. How does habitat diversity affect the species–area relationship? Global Ecology and Biogeography **17:**532–538.

Kays, R., M. Gompper, and J. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications **18:**1014–1027.

King, C. M., and R. A. Powell. 2007. The natural history of weasels and stoats: ecology, behavior, and management. Oxford University Press, New York.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11:**849–856.

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:**18–25.

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.

Livezey, K. B. 2010. Killing barred owls to help spotted owls I: a global perspective. Northwestern Naturalist **91:**107–133.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, New York.

Masters, R. E. 2007. The importance of shortleaf pine for wildlife and diversity in mixed oak-pine forests and in pine-grassland woodlands. Pages 35–46 in Proceedings of shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium.

Masters, R. E., R. L. Lochmiller, S. T. McMurry, and G. A. Bukenhofer. 1998. Small mammal response to pine-grassland restoration for red-cockaded woodpeckers. Wildlife Society Bulletin **26:**148–158.

Means, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems.Pages 157–213. in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York.

Mortelliti, A., and L. Boitani. 2008. Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. Landscape Ecology **23:**285–298.

Nicholson, E., and H. P. Possingham. 2006. Objectives for multiple-species conservation planning. Conservation Biology **20:**871–881.

Porter, M. L., and R. F. Labisky. 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. Journal of Wildlife Management **50:**239–247.

Roemer, G. W., and R. K. Wayne. 2003. Conservation in conflict: the tale of two endangered species. Conservation Biology **17:**1251–1260.

Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, J. Lyon, and W. J. Zielinski, editors. 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine in the western United States. Gen. Tech. Rep. RM-GTR-254. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 184 p.

Sasse, D. B., and M. E. Gompper. 2006. Geographic distribution and harvest dynamics of the eastern spotted skunk in Arkansas. Journal of the Arkansas Academy of Science **60:**119–124.

Strausberg, S., and W. A. Hough. 1997. The Ouachita and Ozark—St. Francis National Forests: a history of the lands and USDA Forest Service tenure. General Technical Report SO-121. U. S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, 45 pp.

U.S. Department of Agriculture (USDA). 2005. Revised land and resource management plan: Ouachita National Forest, Arkansas and Oklahoma. Management Bulletin R8-MB 124 A. U. S. Forest Service, Hot Springs, Arkansas. 175 pp.

U.S. Fish and Wildlife Service (USFWS). 2003. Recovery plan for the red-cockaded woodpecker (Picoides borealis): second revision. U.S. Fish and Wildlife Service, Atlanta, Georgia. 296 pp.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management **211:**150–165.

Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. Forest Ecology and Management **47:**195–210.

Walters, J. R., S. J. Daniels, J. H. Carter, and P. D. Doerr. 2002. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. Journal of Wildlife Management **66:**1064–1082.

Wilson, C. W., R. E. Masters, and G. A. Bukenhofer. 1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. Journal of Wildlife Management **59:**56–67.

Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. Pages 61–92. in J. L. Gittleman, S. M. Funk, D. Macdonald, and R. W. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.