

NOTE



Predicted distribution of plains spotted skunk in Arkansas and Missouri

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Abstract

The plains spotted skunk (*Spilogale interrupta*) is of conservation concern because of widespread population declines and is being considered for listing under the United States Endangered Species Act. Although the taxon is relatively rare and difficult to study, recent research and reports provided some information about spotted skunks in Arkansas and Missouri, USA. Using this information, we employed full and simplified multivariate species distribution models to evaluate cover type associations and identify regions of high predicted presence for plains spotted skunks. The simple model contained percent forest and percent development within 5 km, land cover category, and distance to water. Percent forest within 5 km was the most important variable based on permutation importance in both models, indicating that plains spotted skunk habitat may persist in contiguous forest at the landscape scale. Regions predicted to have high presence occurred in northern, western, and southern Arkansas and southern Missouri, totaling >300,000 ha. The resulting plains spotted skunk distribution map can be used for research and management efforts in areas of high probability of occurrence, and future statewide survey efforts may validate our results.

KEYWORDS

distribution, MaxEnt, mesocarnivore, plains spotted skunk, predicted presence, species distribution model, *Spilogale interrupta*



The plains spotted skunk (*Spilogale interrupta*, formerly *S. putorius interrupta*; McDonough et al. 2022) is a rare and cryptic taxon of conservation concern that underwent a population decline since the mid-1900s (Gompper and Hackett 2005, Gompper and Jachowski 2016, Sasse 2021). The United States Fish and Wildlife Service (USFWS) has been petitioned to list the taxon for protection under the United States Endangered Species Act (USFWS 2012). Problematically, the exact cause of the long-term and widespread plains spotted skunk population decline remains unknown (Gompper and Hackett 2005, Gompper 2017). Potential explanations range from disease to overharvest to rapidly changing landscapes (Choate et al. 1973, DeSanty 2001, Schwartz and Schwartz 2001, Gompper 2017), and unknown threats that pressured plains spotted skunks during their range-wide decline may continue to put the species at risk. An understanding of where plains spotted skunks persist is necessary to conduct targeted research that will assist managers in conserving the taxon, identify potential threats to spotted skunk populations, and guide the petition for listing.

Most recent research efforts have focused on identifying resource needs of eastern (*S. putorius*) and plains spotted skunk populations (Lesmeister et al. 2009, Lombardi et al. 2016, Harris et al. 2020, Higdon and Gompper 2020). Many studies have concluded that forest structure is important for eastern and plains spotted skunks (Hackett 2008, Lesmeister et al. 2009, Thorne et al. 2017, Perry et al. 2018). In particular, dense understory cover appears to play a major role in rest and den site selection (Lesmeister et al. 2008, 2009; Thorne et al. 2017; Sprayberry and Edelman 2018; Eng and Jachowski 2019a; Harris et al. 2020). With a handful of exceptions (Martin et al. 2017, Fino et al. 2019, Harris et al. 2020), eastern and plains spotted skunks are rarely observed in open landscapes (Lesmeister et al. 2009). Similarly, both species tend to avoid human development and rarely occur in agricultural landscapes (Hackett 2008), despite their historical occurrence on family farms (Crabb 1948).

While research on habitat needs continues to grow and coarse-scale distribution information is available (Perry et al. 2021), research on the status and fine-scale state-level distribution of eastern and plains spotted skunks is necessary. Further, these areas are highlighted as priority research areas by the Eastern Spotted Skunk Cooperative Study Group (Eastern Spotted Skunk Cooperative Study Group 2020). In Arkansas, USA, plains spotted skunks are considered imperiled, although harvests were historically recorded across most of the state (Eastern Spotted Skunk Cooperative Study Group 2020, Perry et al. 2021). Recently, harvests come primarily from the Ozark and Ouachita regions with a handful harvested from across southern Arkansas (Sasse and Gompper 2006). Similarly, in Missouri, USA, the species is considered endangered, although it was historically widespread (Schwartz and Schwartz 2001, Gompper 2017, Eastern Spotted Skunk Cooperative Study Group 2020). Recent sighting records are restricted to the southern, Ozark region of Missouri (Missouri Natural Heritage Program 2019). An updated distribution model of eastern and plains spotted skunks would provide insight into where these species likely occur statewide in Arkansas and Missouri, further clarify habitat requirements, and highlight probable areas for refined studies on abundance, population dynamics, disease ecology, and other knowledge gaps.

We identified the current potential distribution of the remaining populations of the plains spotted skunk within Arkansas and Missouri. Our aim was to build a plains spotted skunk distribution map to guide future survey efforts and to identify environmental variables that could anchor future management for plains spotted skunks in Arkansas and Missouri. Building a distribution model in these 2 states was appropriate as they appear to include the core remaining range of the taxon (although populations are known to persist in other states) and are the states where most research on the plains spotted skunk has occurred (Hackett et al. 2007; Hackett 2008; Lesmeister et al. 2009, 2013; Higdon and Gompper 2020). We predicted that plains spotted skunk presence would be positively related to forested land because associations between both eastern and plains spotted skunks and forested regions have routinely appeared in habitat selection studies (Hackett 2008; Lesmeister et al. 2009, 2013; Thorne et al. 2017; Perry et al. 2018). Conversely, we expected a negative relationship between abundance of agricultural land and plains spotted skunk presence because modern agricultural practices are considered a contributing factor to the decline of eastern and plains spotted skunks, and because plains spotted skunks tend to avoid open pasture (Choate et al. 1973, DeSanty 2001, Schwartz and Schwartz 2001, Lesmeister et al. 2009, Gompper 2017). We expected variables



associated with dense forest understory cover to correlate positively with plains spotted skunk presence because research on home ranges, rest site selection, and occupancy have revealed associations between both plains and eastern spotted skunks and such habitat characteristics (Lesmeister et al. 2008, 2009; Thorne et al. 2017; Sprayberry and Edelman 2018; Eng and Jachowski 2019a; Harris et al. 2020). We expected distance to water to correlate negatively with plains spotted skunk presence because areas closer to water can offer better foraging quality and cover (Eng and Jachowski 2019b). Finally, we expected the amount of developed land to negatively influence presence because plains spotted skunks are not found in developed areas in the Ozark region (Hackett 2008).

STUDY AREA

This study focused on Arkansas and Missouri, totaling 31,829,399.9 ha, and data used in the study were collected between 1999 and 2019. Elevation ranges from 16 m to 839 m in Arkansas and 70 m to 540 m in Missouri. The topography ranges from flat in southern and eastern Arkansas and northern Missouri to hilly and rugged in the western Arkansas Ouachitas and in the Ozark Mountain region shared by both states. The Mississippi River borders the eastern portion of both states. Both states experience 4 seasons, including hot, humid summers (Jun–Aug) and mild winters (Dec–Feb) annually; mean annual temperature in Arkansas is 16.1°C and is 13.2°C in Missouri, and precipitation averages 156.9 cm and 114.8 cm annually in Arkansas and Missouri, respectively.

Prior to the plains spotted skunk population decline in the mid-1900s, the species occurred across the majority of Arkansas and Missouri (Gompper and Hackett 2005, Sasse and Gompper 2006, Gompper 2017, Sasse 2017). Many recent occurrences of plains spotted skunks have been reported from the Arkansas and Missouri Ozarks (Hackett et al. 2007, Higdon and Gompper 2020), the Arkansas Ouachitas (Lesmeister et al. 2009), and in general, from southern and eastern Arkansas (Sasse and Gompper 2006, Sasse 2018). In eastern Arkansas and northern and southeastern Missouri, row crop agriculture dominates the landscape, although pastured livestock agriculture is interspersed in the mountainous portions of both states. Northern Arkansas and southern Missouri hold the majority of the Ozark Mountains, a region characterized by oak (*Quercus* spp.) and mixed oak-pine (*Pinus* spp.) forests interspersed with open glades and rocky, steep terrain. In the Ouachita Mountain region of central and western Arkansas, open pine forests dominate, but hardwood forests are also present. The mesocarnivore guild, which may act as predators or competitors to plains spotted skunks, is characterized by coyotes (*Canis latrans*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), and gray fox (*Urocyon cinereoargenteus*). Avian predators, including great horned owl (*Bubo virginianus*) and barred owl (*Strix varia*), are also present (Lesmeister et al. 2010, Hassler et al. 2021). Black bears (*Ursus americanus*) are common throughout northern and western Arkansas and parts of southern Missouri.

METHODS

We used maximum entropy (MaxEnt) modeling to build a predictive distribution for the plains spotted skunk. Maximum entropy models are often employed to build species distribution models for rare or cryptic species because of their high performance when sample sizes are low and information is incomplete (Phillips et al. 2006, Pearson et al. 2007, Wisz et al. 2008, Aubry et al. 2017). Species distribution models (SDMs) are widely used to predict potential distributions using spatially explicit environmental data layers thought to reflect species-habitat relationships (Phillips et al. 2006). Abundant literature exists on best practices and tools for building SDMs, and they are a widely accepted method for building predictive species distribution maps (Phillips and Dudík 2008, Elith et al. 2011, Hijmans 2012, Merow et al. 2013, Radosavljevic and Anderson 2014).



Training datasets, testing datasets, and environmental variables

For our training dataset, we gathered presence data from a random sample (e.g., point data from track plate and motion-sensitive camera surveys), which produces a reliable prediction of relative presence (Fithian and Hastie 2012, Merow et al. 2013). We obtained the training data from 3 large-scale surveys for plains spotted skunks in Arkansas and Missouri (Figure S1, available in Supporting Information). The first Arkansas survey occurred in 2006–2007 and used track-plate surveys to evaluate plains spotted skunk habitat selection (Lesmeister et al. 2013); it resulted in 57 records of plains spotted skunks in the Ouachita National Forest. The second Arkansas survey took place in 2017–2018 within the Ozark National Forest and the Gene Rush Wildlife Management Area (Higdon and Gompper 2020). The survey, which consisted of a large-scale camera grid designed to identify plains spotted skunk locations for future live-trapping efforts, contributed 4 plains spotted skunk locations to the presence dataset. For the Missouri survey, which occurred in 2005–2006, Hackett (2008) used motion-sensitive cameras and track-plate surveys across the Missouri Ozarks to evaluate mesocarnivore occupancy and interactions in the region, recording plains spotted skunks at 15 sites.

We strengthened our SDM by validating the predictive model built with the training data using a second, independent dataset of test points (Araújo and Rahbek 2006, Phillips et al. 2009). The contemporary availability of presence data collected through citizen science initiatives and reports of incidental captures by other field researchers can serve as an important source for test data (MacPherson et al. 2018). In recent years, several state wildlife agencies reached out to community members for location information on eastern and plains spotted skunks (Dowler et al. 2017, Eastern Spotted Skunk Cooperative Study Group 2020). Point data collected from field research, community reports, and agency information on incidental captures provide reliable data for validating a predicted distribution of remaining populations of the species (Hefley et al. 2014, MacPherson et al. 2018). Incorporating a second, independently collected dataset for model validation reduces bias because it measures the model's ability to predict species presence without depending on a subset of the same dataset that was used to build the model (Araújo and Rahbek 2006, Phillips et al. 2009). We incorporated incidental captures and citizen science reports of plains spotted skunks from 1999–2019 in Arkansas and Missouri into the testing dataset. Citizen science reports are expected to produce point locations that differ in biases from standardized sampling (described above for the training datasets) in fundamental ways, including proximity to more disturbed areas (urban centers and agricultural lands) and lands subject to greater hunting or trapping pressures (and thus subject to the use of traplines and game cameras for other species). A model more reflective of a species' true distribution is produced by including a second dataset with different biases (Radosavljevic and Anderson 2014). For the testing dataset, we solicited 49 data points from the Arkansas Game and Fish Commission (D. B. Sasse, Arkansas Game and Fish Commission, unpublished data) and the Missouri Department of Conservation Natural Heritage Database (Missouri Natural Heritage Program 2019; Figure S1). These included incidental captures, observations, and reports from community scientists. All occurrences used in our model were confirmed by a researcher or biologist familiar with spotted skunk identification because data quality and misidentification of target species can affect the accuracy of the SDM (Aubry et al. 2017).

We identified 9 environmental variables that may be important for plains spotted skunk distribution based on the existing literature (Table 1). We used QGIS version 3.2.2 (QGIS.org) to align raster layers to a size of 250 × 250-m pixels, using the bilinear resampling method for continuous variables and the nearest neighbor method for categorical variables.

MaxEnt species distribution model

Maximum entropy assesses correlations between broad-scale environmental predictors (e.g., precipitation, temperature, elevation) with presence-only point locations, allowing us to identify a refined predicted distribution for the plains spotted skunk. We used MaxEnt SDM software (Phillips et al. 2019) and known locations of plains



TABLE 1 List of environmental variables used to predict plains spotted skunk distribution in Arkansas and Missouri, USA, 1999–2019, their description and data source, research justifying their selection, our hypothesized response, and the test area under the receiver-operator curve (AUC) associated with a univariate maximum entropy (MaxEnt) model. Test AUC < 0.5 indicates the variable was worse than random at predicting plains spotted skunk presence

Environmental variable	Description	Source	Justification	Expected response	Test AUC
Downed wood	Dead or downed wood (2.03 m dbh; metric tons carbon/ha)	Derived from Forest Inventory and Analysis (FIA)/Moderate Resolution Imaging Spectrometer (MODIS) imputation methods (Wilson et al. 2012)	Eng and Jachowski (2019a); Sprayberry and Edelman (2018)	Positive	0.764
Small stem density	Stems/ha	Derived from FIA/MODIS imputation methods (Wilson et al. 2012)	Lesmeister et al. (2008); Sprayberry and Edelman (2018); Eng and Jachowski (2019a)	Positive	0.786
Basal area	Basal area (m ² /ha)	Derived from FIA/MODIS imputation methods (Wilson et al. 2012)	Lesmeister et al. (2009)	Positive	0.783
Distance to water	Distance (m) to water, includes streams and waterbodies	Based on United States Geological Survey (USGS) National Hydrography Data	Eng and Jachowski (2019b)	Negative	0.709
Agriculture	Percent of agriculture land within a 5-km radius, includes all agricultural types	Derived from National Land Cover Data (Homer et al. 2015)	Choate et al. (1973); DeSanty (2001); Schwartz and Schwartz (2001); Lesmeister et al. (2009)	Negative	0.830
Forest	Percent of forested land within a 5-km radius	Derived from National Land Cover Data (Homer et al. 2015)	Hackett (2008); Lesmeister et al. (2009); Lesmeister et al. (2013); Thorne et al. (2017)	Positive	0.850
Development	Percent of developed land within a 5-km radius	Derived from National Land Cover Data (Homer et al. 2015)	Hackett (2008)	Negative	0.600
Edge density	Percent of land at the interface of forested and non-forested cover types	Derived from National Land Cover Data (Homer et al. 2015)	Lesmeister et al. (2009); Thorne et al. (2017)	Positive	0.487
Land cover class	Land cover classification	National Land Cover Data	Lesmeister et al. (2009); Hackett (2008)	Positive with forested land classes	0.685



spotted skunks to evaluate the environmental data layers as predictors of distribution and to identify regions with a higher predicted presence of plains spotted skunk. To reduce bias from occurrence data (e.g., observations closer to open areas such as roads, trails, or rivers where individuals might be easier to see), we relied on MaxEnt's pseudo-absence points, or background points, where presence or absence of the target species is unknown (Phillips and Dudík 2008, Phillips et al. 2009).

We set MaxEnt to randomly select a set of 10,000 pseudo-absence locations across the landscape with the objective of sampling the full range of environmental conditions available to plains spotted skunk (Phillips and Dudík 2008, Phillips et al. 2009, Elith et al. 2011). To ensure a conservative estimate, we randomly selected pseudo-absence locations without replacement and; therefore, pseudo-absence locations may include some points where presence was recorded.

Because SDMs can be spatially biased in predicting presence in regions where heavy sampling occurred (Phillips et al. 2009, Merow et al. 2013, Syfert et al. 2013, Beck et al. 2014), we created a bias file using a 2-dimensional kernel density estimator developed in R (R Core Team 2017) and packages raster (Hijmans 2021), MASS (Venables and Ripley 2002), magrittr (Bache and Wickham 2016), and mapproj (Bivand and Lewin-Koh 2021). The bias file reduces biases associated with clustered points and heavily surveyed regions by limiting the spatial area for model building to the vicinity surrounding the training and test points.

We used a multi-step approach to identify the most parsimonious model for predicting plains spotted skunk distribution. We began by using 46 training points and 9 environmental predictors (Table 1) to build univariate MaxEnt SDMs and added the 49 test points to test each model. We selected the automatic features in MaxEnt (linear, quadratic, product, and hinge), the logistic output format, defined the training and test datasets as described above, and used the bias file. We used the test area under the receiver-operator curve (AUC) metric to determine whether each univariate model was able to predict plains spotted skunk presence better than random (i.e., $AUC > 0.5$). We removed those variables from further analysis that were worse than random (i.e., test $AUC < 0.5$) at predicting presence for plains spotted skunks.

To account for collinearity between related environmental variables, we systematically removed variables such that no highly correlated variables were used in the most parsimonious model. We determined whether predictors were highly correlated using the Pearson correlation coefficient (r) option in the layerStats function from the raster package in R (Elith et al. 2011, Merow et al. 2013, Hijmans 2021). Beginning with the variable that was best at predicting plains spotted skunk probable distribution in a univariate model (i.e., had the highest test AUC value), we tested for collinearity with each of the other variables and removed those variables that were highly correlated ($r > 0.7$; Aubry et al. 2017) before moving to the next best variable.

To compare the importance of all environmental predictors and those selected for the most parsimonious model, we built 2 multivariate MaxEnt SDMs. The first was a full model using all environmental predictors, followed by a simple model using only those predictors that were better than random at predicting distribution in univariate models and were not correlated with other predictors. We used the same settings described above and evaluated the models using test AUC in MaxEnt. For both models, we predicted the distribution of plains spotted skunks across Arkansas and Missouri. We used clamping to produce the predictive distribution outside of the area of our bias file because this approach reduces model overfitting by limiting prediction to environmental condition values encountered in the training region (Phillips et al. 2019). Finally, we calculated the area, in hectares, of predicted presence at 4 levels (low = 0–0.24, medium low = 0.25–0.49, medium high = 0.5–0.74, and high = 0.75–1) for the full and simple models using R and packages raster and measurements (Birk 2019, Hijmans 2021).

RESULTS

Of the 9 environmental variables, 8 were better than random at predicting plains spotted skunk distribution in a univariate model. We removed edge density from the simple model because the test AUC was < 0.5 (Table 1). Percent forest within a 5-km radius was best at predicting plains spotted skunk distribution in a univariate model

(Table 2). We removed percent agriculture within a 5-km radius, basal area, small stem density, and downed wood from the variable set for the simple model because they were strongly correlated with percent forest within a 5-km radius. No other strong correlations existed among the remaining 4 variables.

The simple multivariate model included percent forest and development within a 5-km radius, distance to water, and land cover category. This model had a test AUC of 0.839, indicating that it was able to correctly predict presence of plains spotted skunks at test data sites 83.9% of the time. Percent forest within a 5-km radius was also the most important variable based on permutation importance (92.1%; Table 2) and this variable had the highest regularized training gain in a single-variable model in the jackknife test of variable importance (Figure 1). Distance to water was the second most important variable (permutation importance = 6.2%) and the remaining 2 variables had a combined permutation importance of 1.7%, indicating these variables were less important than percent forest within 5 km at predicting plains spotted skunk presence (Table 2; Figure 1).

The full multivariate model included the full suite of environmental predictors (test AUC = 0.828). As with the simple model, percent forest within a 5-km radius was the most important variable based on both permutation importance (88.3%) and the jackknife test of variable importance (Figure 2), followed by percent agriculture within a 5-km radius (permutation importance = 5.2%; Table 2). Downed wood, edge density, land cover category, distance to water, and percent development within a 5-km radius collectively contributed 6.4% to the model, indicating they were less important than the percent forest variable (Table 2). Small stem density and basal area each had permutation importance equal to 0%, indicating no contribution to the model.

Response curves for the variables common between both models indicated that locations of plains spotted skunks were positively correlated with percent forest within a 5-km radius (Figure 3). Response curves for distance

TABLE 2 Permutation importance of environmental variables that remained in the multivariate maximum entropy (MaxEnt) model used to evaluate plains spotted skunk distribution in Arkansas and Missouri, USA, 1999–2019. The test area under the receiver-operator curve (AUC) of the model represents the ability of the model to predict plains spotted skunk presence correctly on the test data set. Mean, minimum, and maximum columns represent the mean and range variable values in the background, or pseudo-absence, and training data points used to build the model

Model	Environmental variable	Permutation importance (%)	Test AUC	\bar{x}	Min.	Max.		
Simple	Forest within 5 km (%)	92.1	0.839	0.41	0	0.98		
	Distance to water (m)	6.2		1,476.37				
	Land cover category	1.2						
	Development within 5 km (%)	0.5		0.07			1	
Full	Forest within 5 km (%)	88.3	0.828	0.41	0	0.98		
	Agriculture within 5 km (%)	5.2		0.47			0.97	
	Edge density (%)	3.5		0.22			0.81	
	Distance to water (m)	1.2		1,476.37			12,773.81	
	Land cover category	0.8						
	Downed wood (metric tons carbon/ha)	0.7		2.13			0	9.30
	Development within 5 km (%)	0.2		0.07			0	1
	Small stem density (stems/ha)	0		2,458.61			0	18,665.14
	Basal area (m ² /ha)	0		7.86			0	39.35

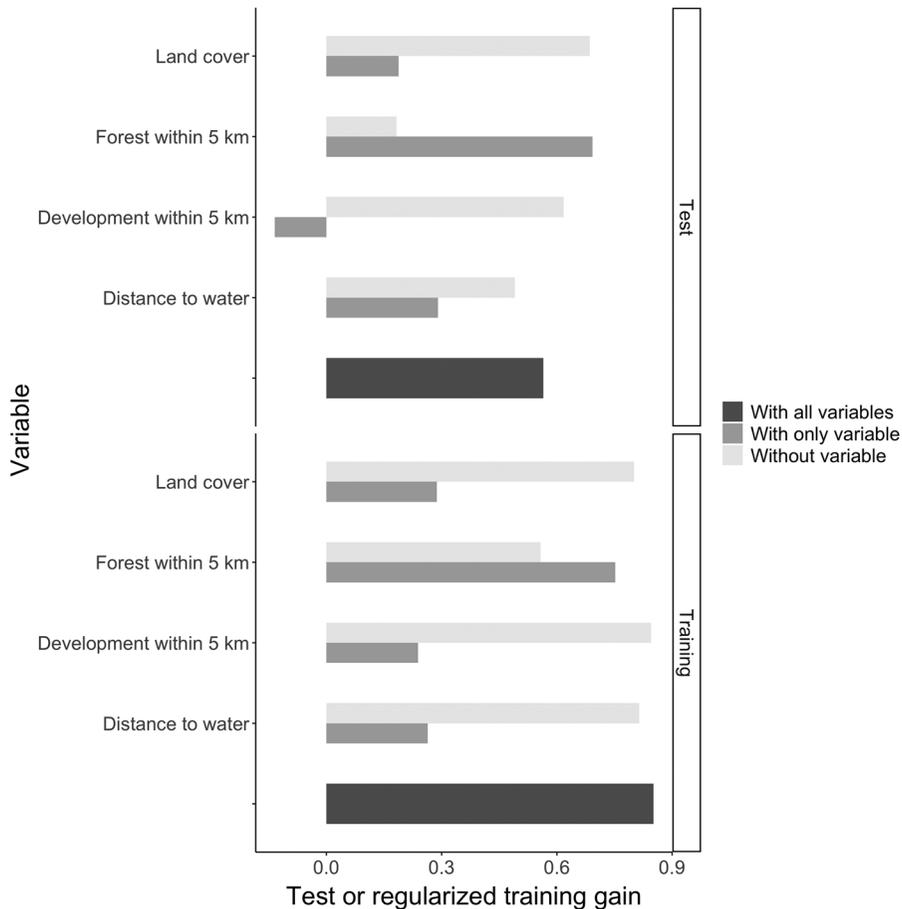


FIGURE 1 Test (top) and regularized training (bottom) gain for variables that remained in the simple multivariate maximum entropy (MaxEnt) model of plains spotted skunk distribution in Arkansas and Missouri, USA, 1999–2019. High gain in a univariate model (with only variable) indicates the variable was more important to the model, while high gain in a model without the variable (without variable) indicates lower importance. The large dark gray bar (with all variables) represents test or training gain for the model including all variables for the test and training datasets, respectively

to water also revealed a positive relationship with plains spotted skunk predicted presence, while percent development within a 5-km radius was negatively correlated with plains spotted skunk locations (Figure 3). Responses to land cover categories reflected relatively low predicted presence associated with most categories, but predicted presence was greater for forested land cover types and the shrub-scrub land cover type than other categories. The developed, open space land cover category also had a slightly greater predicted presence for plains spotted skunk compared to other land cover types but was less than the forested and shrub-scrub categories (Figure 3). Of those predictors unique to the full model, downed wood, small stem density, and basal area response curves revealed positive relationships with plains spotted skunk predicted presence, while there was a negative relationship between predicted presence and both percent agriculture within a 5-km radius and edge density (Figure 3).

Across Arkansas and Missouri, the average predicted presence for plains spotted skunks was 9.4% and 8.16% for the simple and full models, respectively. The MaxEnt model calculated that 317,837.5 ha of land reflected high predicted presence and the majority of the area (>47 million ha) fell below a predicted presence estimate of 50% for the simple model (Figures 4, S1). The full model predicted that 292,912.5 ha of land fell within the high predicted presence category, while >48 million ha were below the 50% predicted presence estimate.

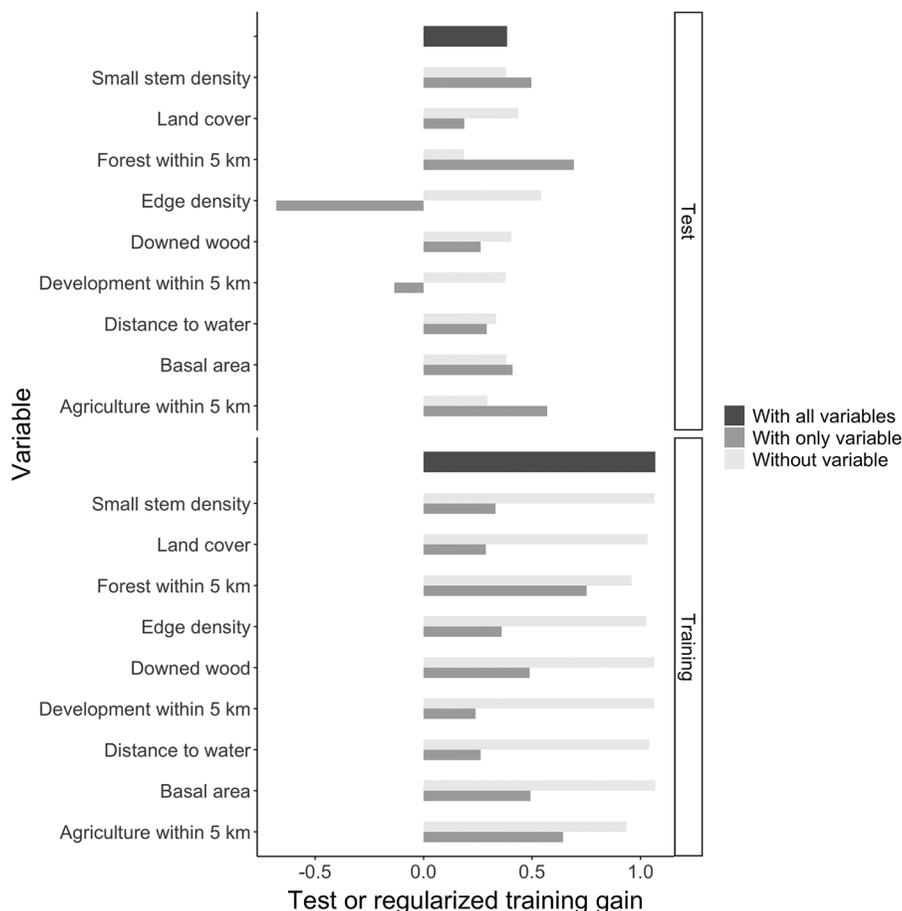


FIGURE 2 Test (top) and regularized training (bottom) gain variables in the full multivariate maximum entropy (MaxEnt) model of plains spotted skunk distribution in Arkansas and Missouri, USA, 1999–2019. High gain in a univariate model (with only variable) indicates the variable was more important to the model, while high gain in a model without the variable (without variable) indicates lower importance. The large dark gray bar (with all variables) represents test or training gain for the model including all variables for the test and training datasets, respectively

According to the predictive map from both models, the plains spotted skunk distribution was heavily concentrated within large blocks of forest, including Mark Twain National Forest, Ozark National Forest, and Ouachita National Forest, with additional high predicted presence regions in portions of north-central Arkansas, southern Arkansas, and southern Missouri (Figure 5; Figure S2, available in Supporting Information). The Mississippi River Alluvial Plain region of eastern Arkansas and southeastern Missouri, and nearly all of northern Missouri were areas of particularly low predicted presence.

DISCUSSION

Our results revealed that large, primarily forested blocks (i.e., sites with higher proportions of forest within a 5-km radius) may be important for remnant populations of plains spotted skunk, which is in agreement with findings from recent studies of habitat associations of both plains and eastern spotted skunks (Hackett 2008;

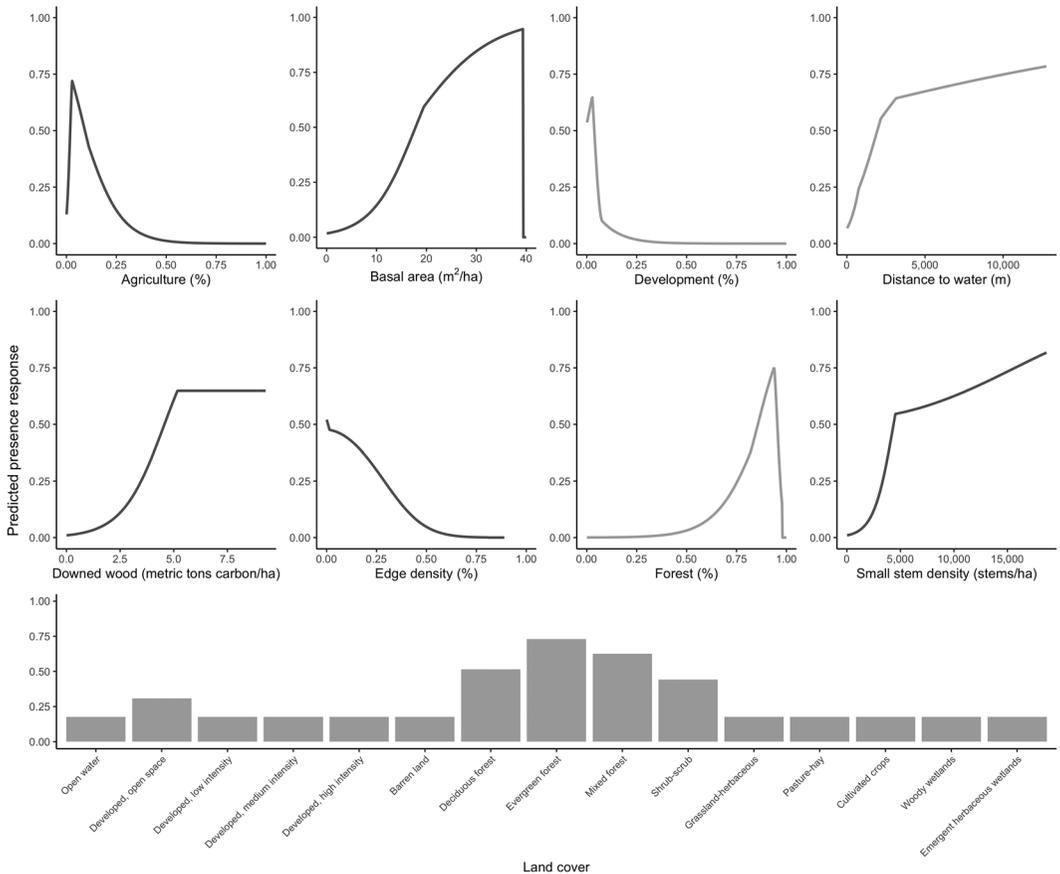


FIGURE 3 Response curves for predictor variables used in maximum entropy (MaxEnt) modeling of plains spotted skunk distribution in Arkansas and Missouri, USA, 1999–2019. Response curves are based on univariate models to prevent collinearity among variables from affecting the relationships shown. Response curves in gray represent those variables that remained in the simple multivariate MaxEnt model. Line graphs represent continuous variables and bar graphs represent categorical variables

Lesmeister et al. 2009, 2013; Thorne et al. 2017). Further, predicted plains spotted skunk presence was greater in forested land cover types than other cover types (Figure 3), although the cover type variable was far less important in both multivariate models than percent forest within a 5-km radius. Our predictions of the responses of plains spotted skunk to 6 of the environmental variables in the multivariate models were supported (Table 1; Figure 3). The relative importance of those responses was overshadowed by the importance of forest at the landscape scale. For example, we predicted that small stem density and downed wood would be important factors, but this prediction was not supported by our full model analysis based on permutation importance (Table 2). Several researchers identified dense understory cover as factors contributing to plains and eastern spotted skunk use of rest and den sites (Lesmeister et al. 2008, Sprayberry and Edelman 2018, Eng and Jachowski 2019a) and home ranges (Hackett 2008; Lesmeister et al. 2009, 2013; Thorne et al. 2017). We suspect that while those factors may play a large role in home range dynamics and rest or den site selection at the local scale (i.e., microhabitat scale), our results indicated that at the landscape scale (i.e., 250-m resolution used in this study), plains spotted skunks inhabiting the Interior Highlands may require contiguous forest. Lesmeister et al. (2010) reported that spotted skunk predation risk was highest in open cover types, due primarily to avian predators, and Lesmeister et al. (2013)

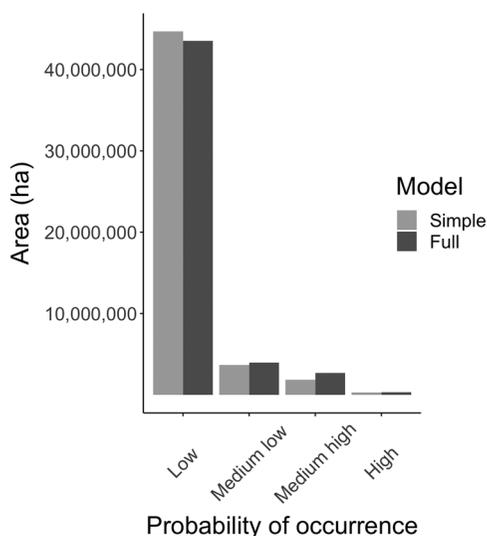


FIGURE 4 Hectares of land that fell within 4 categories of plains spotted skunk predicted presence in the simple (light gray) and full (dark gray) multivariate maximum entropy (MaxEnt) models in Arkansas and Missouri, USA, 1999–2019. For both models, predicted presence for plains spotted skunks most commonly fell in the low category (prediction < 0.25), followed by the medium low ($0.25 \leq \text{prediction} < 0.5$), medium high ($0.5 \leq \text{prediction} < 0.75$), and high ($0.75 \leq \text{prediction}$) categories

suggested that increasing isolation of dense forest stands within a matrix of more open cover types could negatively affect the species.

Our full model indicated that large forest blocks are more important at the landscape level than basal area, even though certain basal area values may promote characteristics suitable for plains spotted skunks, such as understory density. Evaluating the probable distribution of plains spotted skunks within a contiguous forest block, rather than across the entirety of 2 states, may illuminate finer-scale forest characteristics that are important for skunks to fulfill their life-history needs. Although researchers suggest plains spotted skunks may avoid human settlements (Hackett 2008), development was not a strong predictor of presence in either model. A lack of large cities within our sampled area and a corresponding low level of variability in development within a 5-km radius at our sampled sites could explain why development was not an important variable in our analysis.

In contrast to early work on plains spotted skunks that revealed high densities in highly anthropogenic agricultural landscapes (Crabb 1948), most recent researchers have reported that both plains and eastern spotted skunks select for denser forests within large forest stands at the microhabitat scale (Hackett 2008; Lesmeister et al. 2008, 2013; Thorne et al. 2017). We continue to lack a clear understanding of how habitat fragmentation at the landscape level could limit dispersal, which could affect metapopulation dynamics and population persistence across the range (Ims and Andreassen 2002, Sgro et al. 2011, Colyn et al. 2019). Despite high to medium-high predicted presence of the species in large portions of northern, western, and southern Arkansas and southern Missouri predicted by our models, there are significant spatial gaps predicted by our models that suggest remaining populations could be isolated. A handful of testing data points appeared to fall outside areas of high predicted presence in our predictive map. While some eastern and plains spotted skunk populations appear to thrive in treeless environments (Dowler et al. 2017, Harris et al. 2020), or persist in agricultural landscapes (Fino et al. 2019), these point locations could represent dispersing or otherwise transitory individuals in Arkansas and Missouri. Unique biases associated with the testing dataset may also have resulted in observations closer to areas more commonly frequented by humans, such as roads, trails, and agricultural areas. Sampling biases associated with more recent studies of eastern and plains spotted skunks in Arkansas and Missouri, including those data used

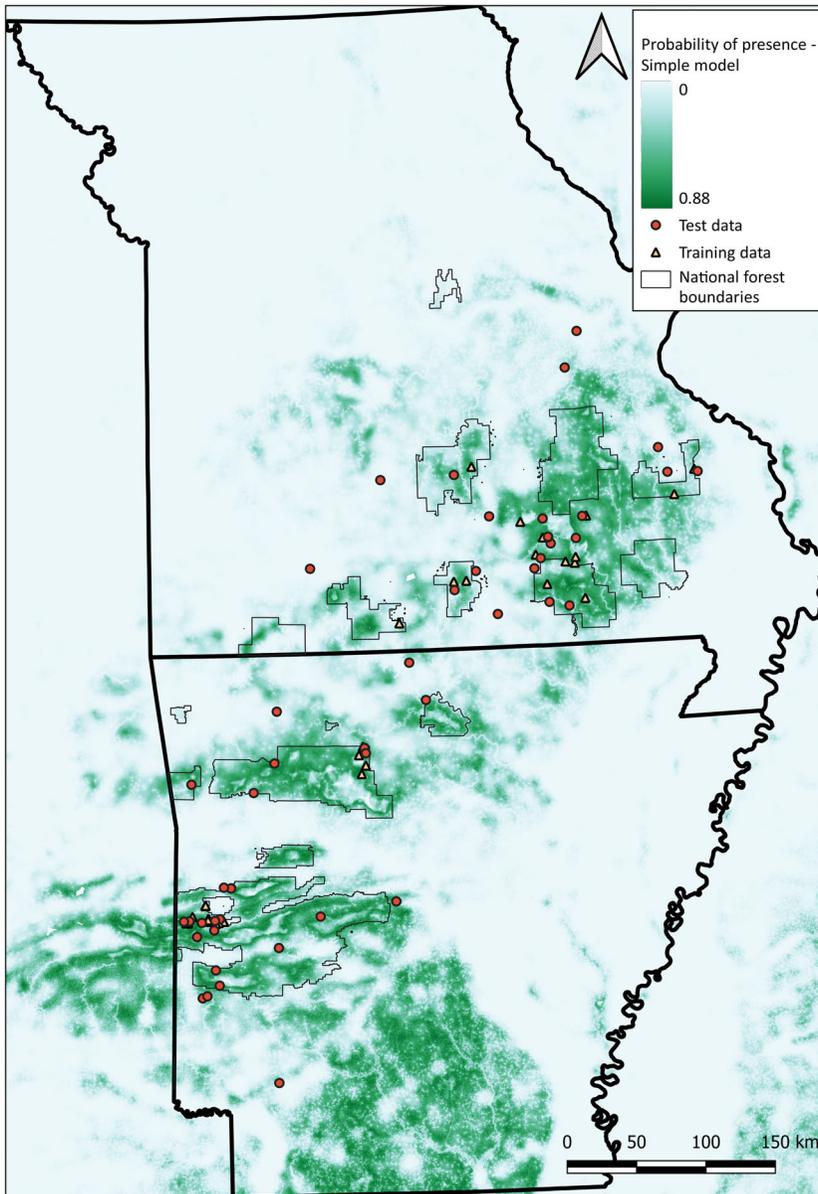


FIGURE 5 Predicted presence of plains spotted skunks in Arkansas and Missouri, USA, 1999–2019, and the surrounding area based on the simple multivariate species distribution model. Dark green regions represent areas of high predicted presence, while light blue represents areas of low predicted presence. Red circles are test data points and yellow triangles are training data points. The dark outline represents the full study area and the thin black lines indicate United States National Forest boundaries

to build our SDM, could have influenced our results as they relate to treeless and agricultural landscapes. Motion-sensitive cameras and track plate sampling occurred primarily on public lands in forested landscapes and may have limited opportunities to detect plains spotted skunks in other land cover types. Still, the use of open landscapes appears primarily transitory in Arkansas and Missouri, and such landscapes are rarely incorporated into home ranges even when available, perhaps because of predation risk (Lesmeister et al. 2009, 2010, 2013).



Two environmental variables that we identified as potentially important predictors for plains spotted skunk distribution performed differently than expected during our analysis. Distance to the nearest drainage channel has been identified as a predictor of eastern spotted skunk presence because of the greater availability of food resources and cover closer to channels (Eng and Jachowski 2019b); therefore, we expected plains spotted skunk presence to be negatively associated with distance to water. Instead, we observed a positive response whereby plains spotted skunks were more likely to be present with increasing distance to water (Figure 3). Eng and Jachowski (2019b) noted, however, that distance to drainage channel was not among the top predictors for eastern spotted skunk detection in the Appalachian Mountains. We suspect that the plains spotted skunks in Arkansas and Missouri may not be limited by cover associated with water because dense cover is readily available within the forested regions identified as plains spotted skunk distribution by our models. We also predicted that edge density would be a factor contributing to plains spotted skunk distribution because brushy cover common along edges is similar to dense forest cover selected by plains and eastern spotted skunks (Lesmeister et al. 2009, Thorne et al. 2017, Perry et al. 2018). There was a negative correlation between edge density and plains spotted skunk predicted presence and we excluded edge density from the simple model because this variable performed worse than random (test AUC = 0.487) in a univariate model. We suspect that selection for forest cover and general avoidance of open areas (Lesmeister et al. 2009) may preclude use of edge adjacent to open areas.

We believe our data were well-suited to a presence-only modeling approach. Although occupancy modeling, which incorporates imperfect detection into probability of occurrence estimates, may yield better predictive models, true absence data is difficult to obtain and assigning inaccurate absence points when modeling rare species could significantly reduce the quality of the SDM (Engler et al. 2004, Rota et al. 2011, Comte and Grenouillet 2013). Although camera and track plate surveys may inherently gather absence data for use in detection models, using these data in the context of a cryptic species like the plains spotted skunk may be inappropriate because probability of detection is generally low (Wilson et al. 2016, Higdon and Gompper 2020, Hayes et al. 2021). In such cases, a presence-only model is more appropriate because these models reduce false positive rates in predictions because absence data is less informative owing to ambiguity between true absence and non-detection despite presence (Rota et al. 2011). While MaxEnt modeling is the norm for SDMs of rare or cryptic taxa like the plains spotted skunk (Phillips et al. 2006, Pearson et al. 2007, Wisz et al. 2008, Aubry et al. 2017), it may not always be the best (Marini et al. 2009). We tailored our approach to employ best practices by using different training and testing datasets (Araújo and Rahbek 2006, Phillips et al. 2009), selecting explanatory variables with ecological relevance to the taxon (M. P. MacPherson, Louisiana State University, unpublished data), limiting model overfitting by accounting for spatial sampling bias (Syfert et al. 2013), and employing clamping when predicting outside of the sampling area (Phillips et al. 2019). Thus, our model reflects a robust and careful approach to creating an appropriate predicted current distribution for the plains spotted skunk.

A leading explanation for the decline of eastern and plains spotted skunk populations since the mid-1900s is that modern agricultural practices and the onset of pesticide use contributed to decreased habitat and food availability (Choate et al. 1973, DeSanty 2001, Schwartz and Schwartz 2001, Gompper 2017). In our full model, agriculture was the second most important variable predicting plains spotted skunk distribution. Our response curve indicated that plains spotted skunks can tolerate some less-intensive agriculture (Figure 3). In the Ozark region, pasture lands are more prevalent than in the Mississippi River Alluvial Valley and northern Missouri, where row crops dominate. It is likely that the type of agriculture plays a role in whether plains spotted skunks will be present, and future research may improve distribution models for the plains spotted skunk by incorporating more detailed layers of agricultural land use. While plains spotted skunks were once common on agricultural landscapes (Crabb 1948), recent research suggests that the remaining extant plains spotted skunk populations do not use pasture typical of the Ouachita Mountain region except to disperse, likely because of enhanced risk of predation (Lesmeister 2007; Lesmeister et al. 2009, 2010). Plains spotted skunks persist in open cropped, pastured, and grassland regions of South Dakota, USA, where structure such as shelter belts, wood piles, and hay bales likely provide cover (Fino et al. 2019). They have also been observed on a Texas, USA, cattle ranch that was managed for



prairie conservation and cattle production (Perkins et al. 2021). As such, agricultural practices that promote farm diversity similar to historical farming practices and that provide structure for cover, such as shelter belts, alley cropping, forest farming, and native prairie species in pastured land, may facilitate plains spotted skunk use of farmland (Crabb 1948, Choate et al. 1973). Although the impacts of these and similar practices are well studied for some taxa (Millsbaugh et al. 2009), an understanding of whether plains spotted skunks would use such agricultural systems remains unclear and warrants further research. Our survey efforts did not incorporate areas of Arkansas and Missouri that are heavily dominated by agriculture, especially row crops and large swaths of pastureland. A statewide survey is necessary to validate our model results.

Historically, plains spotted skunks were widespread across much of Arkansas and Missouri, but our results agree with other evidence that by the early 2000s, they persisted only locally. The extent of land cover and land use change within Arkansas and Missouri over the past several decades likely played a role in the persistence or extirpation of spotted skunks. For example, our models predicted low probability of presence in areas like eastern Arkansas and northern Missouri, which are now dominated by human modifications, primarily row crop agriculture. Areas predicted to have a high probability of plains spotted skunk presence, such as northern Arkansas and southern Missouri, are dominated by natural woodlands interspersed with pasture. Since the early 1900s in Arkansas, plains spotted skunks ranged primarily throughout the northwestern and north-central portions of the state but were harvested broadly across the state throughout the 1900s (Sasse and Gompper 2006, Sasse 2017). More recent incidental harvests of plains spotted skunks in Arkansas (i.e., following large-scale agricultural development) have occurred in the Ozark and Ouachita regions in the northern and western portions of the state, with rare occurrences in east-central and southern Arkansas (Sasse and Gompper 2006, Sasse 2018). Similarly, in Missouri, plains spotted skunks ranged throughout most of the state prior to large-scale agricultural expansion (Schwartz and Schwartz 2001, Gompper 2017). Since the 2000s, no new records have entered the Missouri Natural Heritage Database from northern Missouri, where row crop agriculture dominates the landscape (Missouri Natural Heritage Program 2019). As our sampling scheme did not include all areas of both states, future sampling efforts should include statewide searches for plains spotted skunk that would validate our model predictions. Further, a statewide sampling scheme could provide additional information for plains spotted skunk distribution compared to historical records.

MANAGEMENT IMPLICATIONS

Given the conservation concerns regarding the status of the plains spotted skunk, an understanding of the remaining distribution of the taxa and threats to its persistence are valuable. Our species distribution model can guide urgently needed sampling efforts in forested regions of Arkansas and southern Missouri by researchers seeking to provide information toward the decision for listing plains spotted skunk under the United States Endangered Species Act in the near term. Longer term projects should use our results to focus on sampling in areas of both high and low predicted presence to validate model results and ensure the inclusion of other landscape features that may be important predictors of plains spotted skunk distribution.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICS STATEMENT

All training data were collected following protocols approved by the Institutional Animal Care and Use Committee at the University of Missouri (protocol numbers 3871, 4039, and 8821) and testing data resulted from permitted activities by community members.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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