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Research Article

Den Site Selection by the Florida Spotted Skunk

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ABSTRACT The eastern spotted skunk (*Spilogale putorius*) is a species of conservation concern in much of its range and has experienced a decline since the early to mid-1990s. But the subspecies that inhabits peninsular Florida, the Florida spotted skunk (*S. p. ambarvalis*), might still be abundant and is an important nest predator of the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*). To gain insight on this little-studied subspecies and inform potential management strategies, we conducted a resource selection study on the Florida spotted skunk. We examined 5 hypotheses for den site selection related to den type, vegetation, and landscape characteristics in a dry prairie ecosystem in central Florida. We tracked 36 individual skunks to 757 den sites. Using discrete choice analysis, we found that male and nonbreeding female skunks at our study site were 5 times more likely to select a mammal burrow over a gopher tortoise (*Gopherus polyphemus*) burrow, that selection of a den site increased 34% for each 1-burrow increase in the number of nearby burrows, and that selection of a den site increased 3% for every 10-cm increase in a visual obstruction index. Similarly, breeding female skunks were more likely to select mammal burrows and shallow depressions over gopher tortoise burrows by 16-fold and 13-fold, respectively, and selection of a den site increased by 75% for every 1-burrow increase in the number of nearby burrows. In contrast to previous studies that occurred in forested, mountainous environments elsewhere in the species' range, our findings suggest that den characteristics might be more important than landscape or vegetation characteristics to Florida spotted skunk den site selection in dry prairie. Additionally, the frequency of prescribed fires on the landscape did not appear to affect Florida spotted skunk den site selection. Thus, Florida spotted skunks in this ecosystem might be landscape generalists, thereby potentially limiting the ability of managers to control nest predation by this subspecies through habitat management.

KEY WORDS den, eastern spotted skunk, Florida, prairie, resource selection, *Spilogale putorius*.

The eastern spotted skunk (*Spilogale putorius*) is a small-bodied skunk that has declined since the early to mid-1900s across much of its range (Gompper and Hackett 2005). Historically, the species ranged east from the Continental Divide through much of the central and southeastern United States, southeastern Manitoba and southwestern Ontario in Canada, and northeastern Mexico (Kinlaw 1995). The reasons for the species' decline are unknown, but hypotheses include the detrimental effects of habitat loss, agricultural industrialization (e.g., reduction in haystacks available for denning), pesticide use, overharvest, and disease (Choate et al. 1973, McCullough 1983, Schwartz and Schwartz 2001, Gompper and Hackett 2005). Most studies on the eastern spotted skunk have focused on forests in mountainous regions (Lesmeister et al. 2008, Thorne et al. 2017, Eng and Jachowski 2019, Sprayberry and Edelman 2018), and there are still knowledge gaps (e.g., current distribution, habitat preferences, evidence supporting reasons for decline) for the species across its range (Gompper and Jachowski 2016).

The Florida spotted skunk (*Spilogale putorius ambarvalis*) is the least studied of the eastern spotted skunk's 3 subspecies (Gompper and Jachowski 2016). This subspecies occurs throughout peninsular Florida, USA, as far south as Lee County (Hamilton 1941), is endemic to the state, and was still thought to be relatively abundant in central and southern Florida in the 1990s (Kaplan and Mead 1991, Kinlaw et al. 1995*b*). The current status of the Florida spotted skunk range-wide is unknown and the only prior dedicated research on the subspecies was conducted on an Atlantic barrier island during the 1970s and 1980s (Kinlaw et al. 1995*a*, *b*) in a coastal strand community dominated by woody shrubs. The Florida spotted skunk has also been reported using suburban areas (Gompper and Jachowski 2016), improved pasture, and native dry prairie (E. L. Hewett Ragheb, Florida Fish and Wildlife Conservation Commission, unpublished data). The

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Florida spotted skunk is a confirmed nest predator of dry prairie ground-nesting birds (Hewett Ragheb et al. 2019*b*), including the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*; Federal Register 1986), an endemic of the dry prairie (Pranty and Tucker 2006). Nest success has been low for Florida grasshopper sparrows (between 10% and 33%), and nest predation has been identified as the primary cause of nest failures (Perkins et al. 2003, Hewett Ragheb et al. 2019*a*), but it is currently unknown how Florida spotted skunks use dry prairie, or how habitat management for Florida grasshopper sparrows (including prescribed fire) influences skunk behavior. Currently, Florida grasshopper sparrow nest predation by Florida spotted skunks and other mammalian predators is mitigated at all known populations through the installation of predator deflection fencing around nests (Hewett Ragheb et al. 2019*b*). Predator deflection (alternatively, exclusion) fencing, which involves fencing off a known ground-nesting bird nest location to prevent terrestrial predators from accessing the nest, increases nest hatching success (Smith et al. 2011). Regardless of the efficacy of fencing nests, there is a need to discover predation management solutions that can be applied at a larger scale and that require less intensive monitoring efforts.

Den sites are an important resource for the eastern spotted skunk, acting as refugia for male and female skunks during periods of inactivity (i.e., daylight hours) and as safe places for parturition and care of young by female skunks (Kinlaw 1995). Den site selection might be vital to the survival of individuals; Crabb (1948) noted some eastern spotted skunk mortalities in Iowa were likely due to poor selection of den sites.

Our objectives were to evaluate support for 5 *a priori* hypotheses examining how habitat (e.g., vegetative cover, distance to landscape features) and den (e.g., den type) characteristics affected den site selection of Florida spotted skunks at a site in south-central Florida dominated by dry prairie. First, we hypothesized that skunk den site selection would be positively associated with the amount of vegetation at potential den sites, as documented for the species in other parts of its range (Crabb 1948, Lesmeister et al. 2008, Sprayberry and Edelman 2018, Eng and Jachowski 2019), because increased cover might allow greater protection from predators. We expected that this positive association with cover would mirror a positive association with time since fire at a potential den site because less frequent fires would allow vegetation to grow for longer periods of time in an area. Second, we hypothesized that skunks would select gopher tortoise (*Gopherus polyphemus*) burrows more than other den types because of previous use records in Florida (Manaro 1961, Toland 1991). In addition, we predicted the number of burrows (of any type) in an area would be positively associated with den site selection because this could indicate an area where soil characteristics were amenable to excavation. Third, we hypothesized that skunks would avoid areas with tall shrubs or trees that could act as perches for raptor predators such as great horned owls (*Bubo virginianus*; Lesmeister et al. 2010). Fourth, we hypothesized that skunks would select den sites with lower flooding risk (i.e., farther from wetlands or at higher elevations) because summer flooding was common at our study site. Fifth, we hypothesized that skunks would select den sites farther from gravel primary roads, which can represent a significant movement barrier to some small-mammal species (Oxley et al. 1974, Swihart and Slade 1984, Merriam et al. 1989), but closer to unpaved, non-gravel secondary roads (including trails and firebreaks) that facilitate movement and more closely resemble natural, vegetated skunk habitat.

STUDY AREA

We conducted our study in the approximately 3,000-ha Route 60 unit of Three Lakes Wildlife Management Area (WMA), Osceola County, Florida (Fig. 1), 2016–2017. This unit contained primarily native vegetation and natural communities, but leading land uses in the surrounding area included agriculture and cattle ranching. Topography at the site was generally flat, with an elevational range of 16–20 m. The climate in this region was humid subtropical (Chen and Gerber 1990) and the region experienced a hot, wet season (~Jun–Sep) and a mild, dry season (~Oct–May) annually (Orzell and Bridges 2006). Average maximum daily temperature in the region ranged from 21.9°C in January to 33.0°C in July and average annual precipitation was 1,320 mm (1981–2010; Kissimmee 2 weather station; National Climatic Data Center 2018).

Dry prairie was the dominant natural community in the Route 60 unit, covering 1,728 ha. Dry prairie is restricted to south-central Florida and has been reduced to <2% of its historical range (Noss et al. 1995, U.S. Fish and Wildlife Service [USFWS] 1999). This natural community consisted primarily of low shrubs and grasses and was maintained by frequent fire (generally every 1–2 yr) and seasonal flooding that kept vegetation heights low and prevented encroachment and establishment of tree species (Platt et al. 2006, Florida Natural Areas Inventory [FNAI] 2010). Soils of the dry prairie primarily consisted of Alfisols and Spodosols with a clayey subsurface layer that delayed drainage and permitted the seasonal flooding events (FNAI 2010). A diverse suite of animal species occurred in the dry prairie, including mammals such as the eastern cottontail (*Sylvilagus floridanus*), hispid cotton rat (*Sigmodon hispidus*), and bobcat (*Lynx rufus*) and herpetofauna such as the eastern box turtle (*Terrapene carolina*), racer (*Coluber constrictor*), rough green snake (*Opheodrys aestivus*), and oak toad (*Anaxyrus quercicus;* USFWS 1999). Besides the Florida grasshopper sparrow, numerous bird species bred in the dry prairie, including the common nighthawk (*Chordeiles minor*), red-winged blackbird (*Agelaius phoeniceus*), eastern meadowlark (*Sturnella magna*), and Bachman's sparrow (*Peucaea aestivalis*; USFWS 1999). Several shorebird, raptor, sparrow, and warbler species also spent time in the dry prairie as migrants (USFWS 1999). Common plant species included wiregrass (*Aristida stricta* var. *beyrichiana*), shiny blueberry (*Vaccinium myrsinites*), gallberry (*Ilex glabra*), dwarf live oak (*Quercus minima*), and a stunted form of saw palmetto (*Serenoa repens*; FNAI 2010). The dry prairie landscape was dotted with permanent depression marshes and was periodically

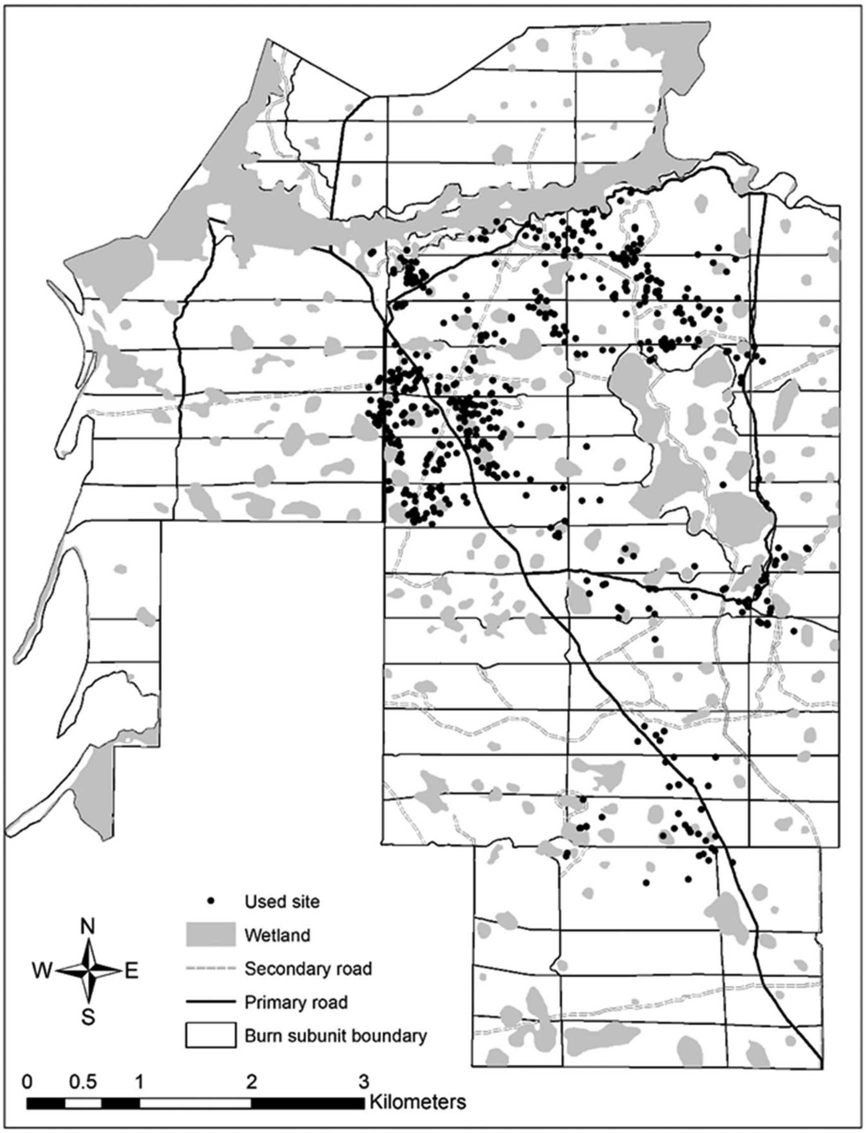

Figure 1. The Route 60 unit of Three Lakes Wildlife Management Area, Osceola County, Florida, USA, where Florida spotted skunk trapping and radio-tracking occurred between February and July in 2016 and 2017. Used sites represent den sites to which we tracked radio-collared skunks during these years.

wet or inundated after seasonal rain events. Other cover types interspersed with the dry prairie at the site included wet prairie and various forest and scrub communities.

Our study area was divided into many smaller management subunits that generally received prescribed fire treatments every 1–3 years to limit recruitment of woody shrubs and trees, creating a landscape with a mosaic of fire return intervals. In addition, trees and cabbage palmettos (*Sabal palmetto*) were occasionally removed from the Route 60 unit mechanically to further prevent hardwood encroachment and to enlarge the size of the prairie.

METHODS

Animal Capture and Processing

We captured Florida spotted skunks in the late winter, spring, and summer of 2016 and 2017 in dry prairie where Florida grasshopper sparrows occurred in recent years. We also trapped skunks in different cover types, along ecotones (e.g., dry prairie–forest edge), in management subunits with differing intervals since the last prescribed fire application, and across a range of distances from roads, trails, firebreaks, and wetlands. We set and baited Havahart double-door live traps (model 1030-B; Havahart, Lititz, PA, USA) with wet cat food in the afternoon and checked them the following morning. We weighed and marked with ear tags (model 1005-1L1; National Band and Tag Company, Newport, KY, USA) each captured individual. We also determined sex and age (adult or juvenile) based on body size and tooth wear (Lesmeister 2007).

We fit adult Florida spotted skunks with very high frequency (VHF) radio-transmitter collars (models M1525 [12 g] and M1545 [18 g]; Advanced Telemetry Systems, Isanti, MN, USA). The collars represented ≤5.5% of each animal's mass (Wilson et al. 1996, Sikes et al. 2016). We attempted to recapture and remove transmitters from every collared skunk before their transmitter batteries died. We followed American Society of Mammalogists guidelines and complied with Clemson University Animal Care and Use Committee protocol (permit AUP2015-042) for all skunk trapping, processing, collaring, and radio-tracking (Sikes et al. 2016).

Tracking

We tracked collared skunks 1–3 times/week from February through July in 2016 and 2017. We divided the hours of daylight per day into 3 equal periods (e.g., 1 = 0700–1059, 2 = 1100–1459, 3 = 1500–1859), alternated our tracking of each skunk between these periods, and waited >24 hours between each tracking attempt. We did not track skunks during evening hours (i.e., 1900–0659) because eastern spotted skunks are primarily nocturnal (Kinlaw 1995) and therefore less likely to use den sites at night.

When attempting to locate a skunk at a den site, we first moved towards its VHF signal until we thought that we were approximately 20–30 m from the skunk's location. We then walked to 2–3 other points at this same distance from the presumed location to help further pinpoint the skunk's exact location. After we felt confident in the general location of the skunk, we homed in to the skunk's exact location and recorded the coordinates of this location with a handheld global positioning system (GPS) unit. If we were unsure of the skunk's location at rest, or if the animal began to flee while we were tracking it, we would abandon the tracking of that skunk for the day.

Den Site Characterization

Within 15 days of the tracking event, we returned to each den site and then walked along a random azimuth from the used site until we identified a potential available site where a skunk could den or rest, ≥50 m and ≤300 m from the used site (Lesmeister et al. 2008). If we did not locate an appropriate site within this distance, we would repeat the procedure with additional random azimuths until we did. We defined a site to be available if it met the 3 requirements Crabb (1948) presented for eastern spotted skunk dens (i.e., provides darkness, shelter from weather, and protection from predators) or was a burrow with an entrance measuring ≥5 cm × 5 cm in size. We categorized dens into 6 types (above-ground, depression, gopher tortoise burrow, hollow trunk, or mammal burrow). A tortoise burrow differed from a mammal burrow in that it usually had a larger diameter entrance, the entrance was generally semicircular in shape (rather than circular), and it had a large sandy apron outside of the entrance. An above-ground site was a location we tracked a skunk to that had no signs of excavation, whereas a depression consisted of a small pit that was excavated and had visible bare soil.

At each used and available den site, we measured habitat and den characteristics (Table 1). Using a 1-m × 1-m modification of the Braun-Blanquet method (Bonham et al. 2004) and a Daubenmire frame (Daubenmire 1959), we estimated the percentage of bare soil and 6 major vegetation cover types (in 5% increments). These cover types included saw palmetto trunks, saw palmetto leaves, graminoids (e.g., grass), non-woody herbaceous plant species (e.g., forbs), oak species (*Quercus* spp.), and non-oak woody shrubs. We recorded an index of visual obstruction by vegetation by placing a 1.5-m Robel pole (marked in 10-cm increments) at the identified den site, kneeling (at a height of 1 m) 4 m north of the den and recording the lowest number visible on the pole from that location (Robel et al. 1970, Doty and Dowler 2006). We recorded Daubenmire plot and visual obstruction measurements at the den site center, 5 m to the east of the center, and 5 m to the west of the center and

Table 1. Covariates measured for each used and available Florida spotted skunk den site at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016–2017.

Variable	Description	Range or categories
Type	Classification of the den site	Above-ground, depression, gopher tortoise burrow, hollow trunk, mammal burrow
Burrows	Number of burrows ≤5 m from the used or available site	0–10
Bare	% of bare soil in plot	0–88
Trunk	% of palmetto trunk in plot	0–62
Leaves	% of palmetto leaves in plot	0–82
Grass	% of graminoids in plot	0–100
Forb	% of non-woody, herbaceous plants in plot	0–82
Oak	% of oak species in plot	0–72
Shrub	% of non-oak woody shrub plants in plot	0–100
VOI	Visual obstruction index using a Robel pole (10-cm increments)	0–150
Clump	Number of woody shrub clumps ≥1.5 m tall within 50 m	0–70
Tree	Number of trees ≥3 m tall within 100 m	0–225
Clump dist	Distance to the nearest woody shrub clump or tree ≤1.5 m tall (m)	0–381
Elev	Elevation at the site (cm)	1,664–1,941
Perch	Relative vegetation height of reclassified natural community	high, low
Forest dist	Distance to nearest forest edge (m)	0–1,131
Water dist	Distance to nearest wetland (m)	0–489
Road dist	Distance to nearest primary road (m)	6–1,240
Trail dist	Distance to nearest secondary road, trail, or firebreak (m)	0–325
Time	Time since the most recent prescribed fire (days)	0–6,321

calculated the average for each site. We stood at the den site center and counted the number of woody shrub clumps ≥1.5 m tall within a 50-m radius of the den site, the number of trees ≥3 m tall within a 100-m radius of the den site, and the distance to the nearest woody shrub clump (≥1.5 m tall) or tree (≥3 m tall). Finally, we systematically searched within a 5-m radius and counted the number of burrows (mammal or gopher tortoise) that could act as den sites as an estimate of local den site density.

We classified the elevation (in cm) and general cover type for used and available den sites based on elevation (Florida Geographic Data Library, www.fgdl.org/metadataexplorer/explorer.jsp, accessed 24 Jan 2017) and natural community (Florida Cooperative Land Cover Map, www.fnai.org/landcover.cfm, accessed 24 Jan 2017) data layers using geographic information system (GIS) software (ArcGIS 10.4, Esri, Redlands, CA, USA). We reclassified natural communities identified in land cover data into 2 categories representing landscapes with typically high or low vertical structure where avian predators could perch (dry prairie, wet prairie, and wetland communities classified as low, forest and scrub communities classified as high). We also determined the distance to forest edge and distance to wetland for each used or available site. We considered all water bodies (e.g., depression marshes, sloughs, borrow pits) as wetlands. We used GIS data layers containing primary roads and secondary roads (including trails and firebreaks; Florida Fish and Wildlife Conservation Commission, Kenansville, Florida) to determine the distance to primary road feature and secondary road feature for each used or available site. We used land management records (S. L. Glass and C. L. Hannon, Florida Fish and Wildlife Conservation Commission, unpublished data) to calculate the number of days since the last prescribed fire for each used and available den site.

Model Development and Validation

After reviewing our raw data, we noticed that we had tracked female spotted skunks during the breeding season (Jun–Jul; i.e., breeding females) to a greater portion of mammal burrows than male skunks overall and female skunks during the nonbreeding season (Feb–May; i.e., nonbreeding females). To address the possibility that den site selection of female skunks may be different during the breeding season, we separated our den site data into 2 groups: 1) breeding females and 2) all males and nonbreeding females. We tested the same hypotheses on each group. We defined our skunk breeding season as starting on 1 June because parturition in the eastern spotted skunk occurs in late May and early June (Mead 1968), and 1 June was approximately 2 weeks prior to our first observations of females with blind, recently born kits. We included all female skunk den site data collected on or after 1 June in the breeding females group because we assumed that all female skunks had reproductive potential given that we were unable to confirm if some females had given birth to young.

We created ≥1 discrete choice models (Cooper and Millspaugh 1999) to represent each of our *a priori* hypotheses (Table 2). We used Pearson's correlation coefficients to determine that none of the covariates included in a model were collinear ($r \geq 0.7$ or $r \leq -0.7$). Although we observed some reuse of den sites, we treated located dens as independent sites every time we encountered them, given that ≥24 hours had elapsed since our previous tracking of an individual (affording the individual an opportunity to move and select a different den site). We did not include any nonlinear forms of covariates in our models because we visually plotted our raw data before fitting models and saw no evidence of nonlinear relationships in our covariates. We included a random effect in each model to account for variation in resource selection between individual skunks. We also fit a global model including all covariates we measured and 2 subglobal models: the first included only those covariates collected ≤5 m from the used or available den site, and the second included all other covariates collected >5 m from the used or available den site (Table 2).

We fit models using package mlogit (Croissant 2015) in the software program R (R Core Team 2017). This package can be used for discrete choice analysis and allowed for the consideration of data derived from individuals (Croissant 2015). We evaluated support for each model using Akaike's Information Criterion with an adjustment for small sample sizes (AIC_c) and determined the best fitting model for each group of skunks to be the one with the highest AIC_c weight (w_i).

To assess the performance of our resultant top models, we validated each top model using cross validation (Boyce et al. 2002). For each model, we randomly selected 80% (with 1:1 choice sets remaining intact) of our data to act as training data for fitting and the remaining 20% of data as test sets to test the newly trained model (Bodinof et al. 2012). We repeated the random split of our data into training and testing sets 10 times. We subsequently used the trained model with our test sets to estimate the relative probability of selection of each used or available point in our choice sets. We pooled across our test sets the number of occasions in which a used site was correctly predicted to determine the probability of our model correctly predicting selection of a used site. If the proportion of used sites correctly predicted from our pooled test sets was >0.5, we determined that our model was a better fit for our data than what would be expected at random.

RESULTS

Den Site Habitat Characterization

We tracked 19 male and 17 female Florida spotted skunks to 757 used den sites at Three Lakes WMA in 2016 and 2017 (Table 3). There were 250 den sites located for breeding females and 507 den sites for males and nonbreeding females (Table 3). The mean number of used den sites identified per individual skunk was 21 (range = 1–51). The mean number of non-consecutive den sites (i.e., when a skunk was not tracked to the same den site twice in a row) we tracked skunks to was 18.1 ± 1.87 (SE) over 97.0 ± 7.64 days. We observed skunks denning in mammal burrows

Table 2. *A priori* models developed for hypotheses of Florida spotted skunk den site selection at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016 and 2017. I represents a random effect for individual skunks included in all models.

Hypothesis	Model
Cover	
Positive effect of visual obstruction index (VOI), % palmetto leaves, % forb, % grass, % oak, % woody shrub, time since fire (time); negative effect of % palmetto trunk, % bare soil	VOI + leaves + forb + grass + oak + shrub + time + trunk + bare + I
Positive effect of % leaves, % grass, % forb, % oak, % woody shrub	Leaves + grass + forb + oak + shrub + I
Positive effect of VOI	VOI + I
Negative effect of trunk %	Trunk + I
Negative effect of bare soil %	Bare + I
Positive effect of time since fire	Time + I
Burrow	
Positive effect of den type (reference: gopher tortoise burrow)	Type + I
Positive effect of number of burrows	Burrows + I
Positive effect of den type (reference: gopher tortoise burrow), positive effect of number of burrows	Type + burrows + I
Predator avoidance	
Positive effect of relative vegetation height (perch; reference: low), distance to forest edge (forest dist), distance to nearest shrub clump or tree (clump dist); negative effect of number of trees, number of shrub clumps	Perch + forest dist + clump dist + tree + clump + I
Positive effect of relative vegetation height (reference: low)	Perch + I
Positive effect of relative vegetation height (reference: low), distance to nearest forest edge	Perch + forest dist + I
Positive effect of distance to forest edge, positive effect of distance to nearest shrub clump or tree	Forest dist + clump dist + I
Positive effect of distance to nearest shrub clump or tree; negative effect of number of trees, number of woody shrub clumps	Clump dist + tree + clump + I
Water avoidance	
Positive effect of distance to wetland (water dist); positive effect of elevation (elev)	Water dist + elev + I
Road avoidance	
Positive effect of distance to primary road (road dist); negative effect of distance to secondary road, trail or firebreak (trail dist)	Road dist + trail dist + I
Global model	
All covariates collected	VOI + leaves + forb + grass + oak + shrub + trunk + bare + type + burrows + perch + forest dist + tree + clump + clump dist + water dist + elev + time + road dist + trail dist + I
Subglobal models	
Covariates collected ≤5 m from the den site	VOI + leaves + forb + grass + oak + shrub + trunk + bare + + type + burrows + I
Covariates generally collected >5 m from the den site	Perch + forest dist + tree + clump + clump dist + water dist + elev + time + road dist + trail dist + I

(61.6%), above-ground sites (35.5%), gopher tortoise burrows (1.5%), depressions (1.2%), and hollow saw palmetto trunks (<0.3%; Table 3). Four of the sites we classified as above-ground were large, bell-shaped mound-type structures that were primarily comprised of small fragments of saw palmetto leaves. Fifteen other above-ground sites resembled the side-entrance nests of ground-nesting birds and were primarily composed of grasses but did not contain a lining typical of birds' nests. All other above-ground sites ($n = 250$) had no discernible structures, and skunks using these locations appeared to simply be resting on the ground surface amongst vegetation. Den sites were reused on 114 occasions (15.1%), sometimes by different individuals. Communal denning was rare, but we did observe 2 females in an above-ground mound on 1 occasion, and 1 male and 1 female in the same mammal burrow on another.

For male and nonbreeding female skunks, our cover and burrow hypotheses had partial support, whereas our

Table 3. Counts of used and available den types examined for discrete choice analysis of male and nonbreeding female ($n = 34$) and breeding female ($n = 17$) Florida spotted skunk den site selection at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016 and 2017.

	Used			Available		
Den type	Male and non-breeding female	Breeding female	Total	Male and non-breeding female	Breeding female	Total
Above-ground	230	39	269	276	89	365
Depression	3	6	9	16	7	23
Gopher tortoise burrow	9	2	11	36	26	62
Hollow trunk	2	0	2	2	0	2
Mammal burrow	263	203	466	177	128	305
Total	507	250	757	507	250	757

Table 4. Output of top 5 discrete choice models for hypotheses of den site selection for male and nonbreeding female and breeding female Florida spotted skunks at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016 and 2017. The related hypothesis or model set is listed in parentheses following each model. Included for each model are the log-likelihood [log ($\mathscr{L}$)], the number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AIC$_c$), the difference in AIC$_c$ score when compared to the model with the lowest AIC$_c$ (ΔAIC$_c$), and the Akaike weight (w_i).

Model[a]	log($\mathscr{L}$)	K	AIC$_c$	ΔAIC$_c$	w_i
Male and nonbreeding females					
VOI + leaves + forb + grass + oak + shrub + trunk + bare + type + burrows + I (subglobal)	−236.69	14	501.94	0.00	0.999
VOI + leaves + forb + grass + oak + shrub + trunk + bare + type + burrows + perch + forest dist + tree + clump + clump dist + wat dist + elev + time + road dist + trail dist + I (global)	−233.38	24	516.39	14.45	0.001
VOI + bare + trunk + leaves + grass + forb + oak + shrub + I (cover)	−283.12	10	586.53	100.55	<0.001
VOI + I (cover)	−299.24	2	602.50	106.03	<0.001
Leaves + grass + forb + oak + shrub + I (cover)	−297.93	6	607.97	106.69	<0.001
Breeding females					
Type + burrows + I (burrow)	−116.71	5	243.50	0.00	0.979
VOI + leaves + forb + grass + oak + shrub + trunk + bare + type + burrows + I (subglobal)	−112.34	13	251.17	7.67	0.021
VOI + leaves + forb + grass + oak + shrub + trunk + bare + type + burrows + perch + forest dist + tree + clump + clump dist + wat dist + elev + time + road dist + trail dist + I (global)	−108.63	23	264.76	21.26	<0.001
Type + I (burrow)	−136.54	4	281.13	37.63	<0.001
Burrows + I (burrow)	−141.49	2	287.00	43.50	<0.001

[a] VOI = visual obstruction index; leaves = % palmetto leaves; forb = % non-woody, herbaceous plants; grass = % graminoids; oak = % oak species; shrub = % non-oak woody shrub plants; trunk = % palmetto trunk; bare = % bare soil; type = classification of den site; burrows = number of burrows ≤5 m from site; perch = relative vegetation height of reclassified natural community; forest dist = distance to nearest forest edge; tree = number of trees ≥3 m tall within 100 m; clump = number of woody shrub clumps ≥1.5 m tall within 50 m; clump dist = distance to the nearest woody shrub clump; water dist = distance to nearest wetland; elev = elevation; time = time since most recent prescribed fire; road dist = distance to nearest primary road; trail dist = distance to nearest secondary road, trail, or firebreak; I = random effect for individual skunks.

predator avoidance, water avoidance, and road avoidance hypotheses had no support. For these skunks, we observed the most support for our subglobal model including all covariates measured ≤5 m from the used or available den site ($w_i = 0.999$; Table 4). Supporting our cover hypothesis, the amount of visual obstruction measured at a den site had a small positive effect on male and nonbreeding females' odds of selecting a den site; the odds of a skunk selecting a den site increased by about 3% for every 10-cm increase in the visual obstruction index (Table 5). All other cover covariates in this top model had odds ratio 95% confidence intervals that overlapped 1.0, so we were unable to determine if the effects from these covariates had a positive or negative influence on male and nonbreeding female spotted skunk den site selection. Male and nonbreeding female skunk den site selection at Three Lakes WMA was positively associated with den sites that were mammal burrows (Table 5; Fig. 2), running contrary to the positive association with gopher tortoise burrows we expected in our burrow hypothesis. Relative to gopher tortoise burrows, the odds of a male or nonbreeding female skunk selecting a mammal burrow were approximately 5-fold greater. The odds of male and nonbreeding female skunks selecting a site were approximately 34% greater with every 1-burrow increase in the number of

Table 5. Parameter estimates for each covariate in the top models for den site selection of male and nonbreeding female and breeding female Florida spotted skunks at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016 and 2017. We present the odds ratio (OR) with 95% confidence intervals for each parameter. Selection of den types is relative to the reference category, gopher tortoise burrows. An asterisk denotes a covariate with an OR confidence interval that does not overlap 1.0.

Parameter	Estimate	SE	OR	OR lower CI	OR upper CI
Male and nonbreeding females					
Type: above-ground	−0.422	0.522	0.656	0.236	1.826
Type: depression	−0.853	0.890	0.426	0.074	2.438
Type: mammal burrow	1.662	0.441	5.268*	2.217	12.514
Type: hollow trunk	0.532	1.223	1.702	0.155	18.691
Number of burrows within 5 m	0.393	0.096	1.481*	1.228	1.787
Visual obstruction index	0.034	0.006	1.034*	1.022	1.047
% bare soil	0.002	0.008	1.002	0.988	1.018
% palmetto trunk	0.011	0.014	1.011	0.984	1.039
% palmetto leaves	0.013	0.007	1.013	0.999	1.028
% grass	0.005	0.007	1.005	0.992	1.018
% forb	−0.003	0.010	0.997	0.977	1.017
% oak	0.004	0.010	1.004	0.984	1.024
% shrub	0.008	0.010	1.008	0.988	1.028
Breeding females					
Type: above-ground	0.859	0.864	2.361	0.434	12.839
Type: depression	2.572	1.022	13.097*	1.766	97.161
Type: mammal burrow	2.771	0.764	15.975*	3.575	71.389
Number of burrows within 5 m	0.560	0.121	1.750*	1.380	2.219

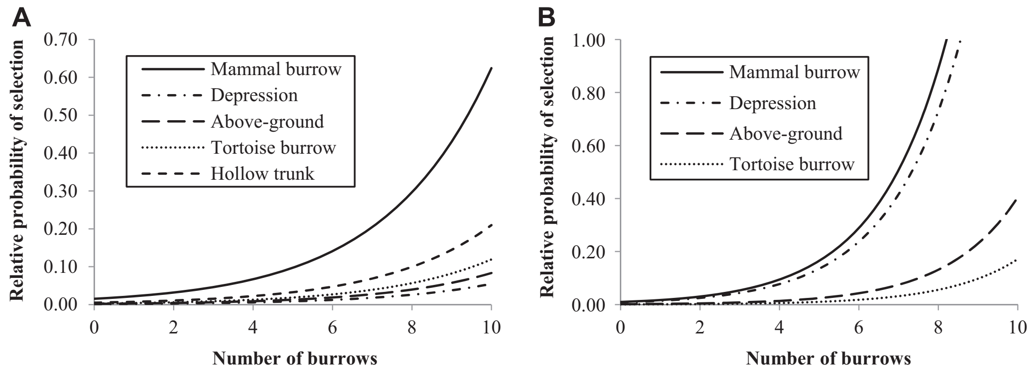

Figure 2. Relative probability of male and nonbreeding female (A) and breeding female (B) Florida spotted skunks at Three Lakes Wildlife Management Area, Osceola County, Florida, USA, 2016–2017, selecting a den site as the number of burrows of any type (≤5 m from the den site) increases, based on the top models for each of these groups. We set all other covariates included in the top model for male and nonbreeding female skunks to their respective mean values. Hollow trunk is not included as a den site type in (B) because breeding females never used this den type in our study.

burrows ≤5 m from the site (Fig. 2), which lends support to our burrow hypothesis.

For breeding females, we observed strong support for our burrow hypothesis, and no support for our cover, predator avoidance, water avoidance, and road avoidance hypotheses. The top model for breeding females included den type and number of nearby burrows; ($w_i = 0.979$; Table 4). In support of our burrow hypothesis, breeding female skunks' odds of selecting a site increased approximately 75% for every 1-burrow increase in the number of burrows ≤5 m from the site (Fig. 2). In contrast, breeding female spotted skunks at Three Lakes WMA did not select gopher tortoise burrows over other den types, as we had predicted in our burrow hypothesis. Instead, the odds of breeding females selecting mammal burrows relative to gopher tortoise burrows were approximately 16-fold greater (Table 5; Fig. 2). Breeding female skunks also had 13-fold greater odds of selecting depressions as den sites over gopher tortoise burrows.

Our model validation suggested that our top model for male and nonbreeding female skunks accurately predicted den site use by this group approximately 70% of the time. Our top model for breeding females performed slightly better, predicting den site use correctly on approximately 74% of occasions.

DISCUSSION

Den type and burrow presence (i.e., number of burrows ≤5 m from a site), the 2 covariates relating to our burrow hypothesis, were the most important factors affecting den site selection of male and female Florida spotted skunks at our site. Contrary to what we hypothesized and what has been observed elsewhere in Florida (Manaro 1961, Toland 1991), skunks did not select for gopher tortoise burrows over the other den types observed at the study site. These results suggest that den type and prevalence of nearby burrows might be more important in skunk den site selection at our site than other covariates collected ≤5 m from a used den site (i.e., microhabitat characteristics) or those covariates collected >5 m from a used den site (i.e., coarser-scale habitat characteristics). Mammal burrows were the most selected den type at our site, echoing findings by Lesmeister et al. (2008) and Sprayberry and Edelman (2018), who observed that eastern spotted skunks in the Ouachita Mountains of Arkansas, USA and the Appalachian Mountains of Alabama, USA, respectively, selected mammal-derived burrows most often. The mammal burrows at our site met Crabb's (1948) 3 den site requirements, and these burrows intrinsically provided much more protection than above-ground den sites, which were the second most commonly used den type at our site.

Our study suggests that den site selection differs to some degree between breeding female spotted skunks and male and nonbreeding female spotted skunks at our site. Although burrow type and nearby burrow prevalence were important for both groups of skunks, our top model for female skunks during the breeding season only included these covariates. This outcome suggests that den site selection by these female skunks during parturition and care of young might be influenced by finding den sites suitable for raising young. Although breeding female spotted skunks at our site most often used mammal-excavated burrows, they also appeared to select for depressions. The greater odds of selection for mammal burrows and depressions by breeding females than for tortoise burrows available on the landscape could be explained in a few ways. First, tortoise burrows might be more likely to be inhabited or explored by other animals, including potential spotted skunk predators, than den sites with smaller entrances (Jackson and Milstrey 1989, Lips 1991, Lesmeister et al. 2008). Second, breeding females might simply prefer those dens they excavate themselves, though the origins of each mammal burrow or depression in our study could not be confirmed. Most burrows and depressions at our study site were likely excavated by nine-banded armadillos (*Dasypus novemcinctus*), rodents, or Florida spotted skunks themselves (Seton 1929). Other mammal burrows were likely abandoned, collapsed gopher tortoise burrows that were repurposed by mammals.

The positive effect of the visual obstruction index, which appeared in our top model for male and nonbreeding female den site selection, provided some support for our cover hypothesis for Florida spotted skunk resource selection.

Increased vegetative cover also influenced eastern spotted skunk den site selection in other parts of the species' range (Lesmeister et al. 2008, Sprayberry and Edelman 2018), though the positive effect at our site was very small, and all other vegetative covariates we included in our study had undiscernible effects on spotted skunk den site selection. This suggests that spotted skunks at our site might be generalists, different in their ecology from eastern spotted skunks in other regions. Specifically, we suggest that 2 factors are influencing this generalist behavior. First, eastern spotted skunks are omnivorous (Crabb 1941, Kinlaw 1995, Sprayberry and Edelman 2016, Thorne and Waggy 2017) and food within our study area was widely available (Harris 2018), suggesting that Florida spotted skunks at our site might be able to find adequate food resources without needing to forage in specific areas (e.g., certain natural communities, locations near wetland features). Second, spotted skunks in the Route 60 unit likely did not have to cope with the food competitors or predators present in other regions. In particular, Kinlaw (1995) lists striped skunks (*Mephitis mephitis*) and weasel species (Mustelidae) as sympatric food competitors, but we did not observe any of these species during our 2 years of field work at the study site. Great horned owls are major predators of the eastern spotted skunk elsewhere (Lesmeister et al. 2010), but this species was never heard or seen at our site. Barred owls (*Strix varia*) are common in the forests surrounding the Route 60 unit but are rarely seen in the prairie. The lack of these avian predators might also provide some explanation as to why our predator avoidance hypothesis was unsupported. Of 7 known mortalities of skunks in the Route 60 unit in 2016 and 2017, only 2 were likely due to predation and neither were due to an avian predation; 1 skunk was killed by a mammalian predator and the other was consumed, and possibly killed, by an American alligator (*Alligator mississippiensis*; Harris et al. 2019). Thus, skunks might be more willing to use areas with less cover because of the lack of predators in the Route 60 unit. Future research on the Florida spotted skunk should be conducted at sites where intraguild competitors and owls occur in adequate numbers to assess how predators and competitors might influence spotted skunk den site selection.

Further supporting our view that Florida spotted skunks are landscape generalists within dry prairie, we failed to find support for our water avoidance and road avoidance hypotheses. Though it happened on too few occasions ($n = 19$) to likely influence support for our water avoidance hypothesis, the use, and possible construction, of aboveground structures by spotted skunks might have been a response to occasional flooding at our study site. Dry prairie can flood seasonally (FNAI 2010), which did occur at our study site during the 2 years of our study, but it was difficult to determine how long portions of our study site and the burrows in these areas were affected by high water levels. Additionally, though the roads at Three Lakes WMA were open to public travel, and multiple roads run through the Route 60 unit, the remote location of our site meant that vehicle travel was low.

Time since fire was not retained as a covariate in the top den site selection models for either male and nonbreeding female or breeding female spotted skunks. This lack of support suggests that differing fire return intervals do not have a discernible effect on spotted skunk den site selection at our site, contrasting with findings by Sprayberry and Edelman (2018) that more frequent fires may negatively affect eastern spotted skunks in Alabama. The tracking methodology we used in our study (locating skunks every 1–3 days) prevented us from studying how spotted skunks handle recent prescribed fires in the hours and days immediately following these events (e.g., the average time it likely took for a skunk to recolonize a burned subunit after a fire). Additionally, the relatively small prescribed fire management subunits at our study site (generally 400 m wide) might have dampened any effects of different fire return intervals because skunks would not have had to move far to escape a subunit being burned and to take refuge in an adjacent unburned unit. Further research on the fine-scale movements of this species, such as that possible with GPS-enabled collars, might be informative in this regard.

Our research provides novel information on resource selection of the little-known Florida spotted skunk subspecies and, more broadly, highlights the variability in landscapes in which eastern spotted skunks persist. Our study, conducted in a non-forested grassland, reveals some stark differences in the resource selection of the Florida spotted skunk compared to results from other studies on the species in mountainous, forested areas (Lesmeister et al. 2008, Eng and Jachowski 2019, Sprayberry and Edelman 2018). Further, the abundance of spotted skunks at our site (>100 unique individuals caught over a 2-yr period; S. N. Harris, unpublished data), coupled with high densities reported in coastal Florida (40 skunks/km^2; Kinlaw et al. 1995*b*) raise questions about whether spotted skunks in peninsular Florida could have been insulated from or have recovered from the range-wide decline documented for the species in the early to mid-1900s (Gompper and Hackett 2005). To improve our understanding of why this subspecies persists while others are in decline, more research is needed to determine if similar distribution, density and resource selection patterns exist for this subspecies throughout the remainder of its range in Florida. Further studies leading to improvements in our understanding of eastern spotted skunk population dynamics (e.g., fecundity, recruitment, survival) range-wide might elucidate what mechanisms are affecting these demographic parameters and how we might begin to counteract the species' observed decline.

MANAGEMENT IMPLICATIONS

The few associations we found regarding Florida spotted skunk den site selection can inform biologists tasked with conserving the Florida grasshopper sparrow and managing its habitat. Because mammal burrows were clearly important den site locations for spotted skunks at our study site, removing these burrows in a specific area could be a potential management strategy for reducing predation of Florida grasshopper sparrows. Additionally, our study's conclusion that vegetative cover (e.g., visual obstruction) is at least marginally important to male and nonbreeding female skunk den site selection suggests that reduction of vegetation heights in a particular section of the Route 60 unit, perhaps below the 40-cm average observed for used den sites, might reduce the odds that a spotted skunk would select a den site in that section. Though the amount of time since a prescribed fire treatment was not itself an important covariate in our study, prescribed fire as a management technique could still be used as a means to reduce vegetative cover in priority sparrow breeding habitat. The presence and prevalence of vegetative cover might be important to Florida grasshopper sparrow resource selection at the site as well, so any decisions to reduce cover at a site inhabited by the Florida grasshopper sparrow would have to be carefully weighed.

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