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High density and survival of a native small carnivore, the Florida spotted skunk (*Spilogale putorius ambarvalis*), in south-central Florida

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The eastern spotted skunk (*Spilogale putorius*) is a species of conservation concern across much of its range and has experienced a population decline since the 1940s. Little is known about the Florida spotted skunk (*S. p. ambarvalis*), a subspecies endemic to peninsular Florida, but previous studies and the frequency of incidental observations suggest that populations of this subspecies might be more abundant than the two eastern spotted skunk subspecies that occur elsewhere. To better understand the status and demography of the Florida spotted skunk, we assessed the density and survival of a population occurring predominantly in dry prairie habitat in south-central Florida. To obtain density estimates, we trapped spotted skunks on a mark–recapture grid over 11 independent 4-day trapping sessions from 2016 to 2018. To obtain survival estimates, we monitored weekly survival of 38 radiocollared spotted skunks (20 collared initially in 2016 and 18 collared initially in 2017) from February 2016 to August 2017. We captured a minimum of 91 unique spotted skunks on 404 occasions on the mark–recapture grid and our density estimates ranged from 6.52 ± 2.93 skunks/km^2 to 23.29 ± 7.65 skunks/km^2, depending on trapping session, but seasonal differences in density were not significant. The sex ratio of spotted skunks at our site was 1.0M:3.8F. Mean annual survival for all spotted skunks was 0.714 (0.503–0.925, 95% *CI*), and sex, season, and year did not have significant effects on survival. This survival estimate is the highest reported thus far for any skunk species. Collectively, the density and survival estimates from our study are higher than those of many other mephitids and mustelids of similar size, and these findings reinforce the value of studying locally abundant populations of small carnivores to better inform the conservation, management, and potential restoration of these species in the future.

Key words: density, dry prairie, Florida, mark–recapture, *Spilogale putorius*, spotted skunk, survival

Mephitids (skunks and stink-badgers) and mustelids (weasels and allies) are two mammalian families with an almost worldwide distribution whose diverse species occupy a vast array of ecological niches. Some species in this group have large geographical ranges, such as the tayra (*Eira barbara*—Cuarón et al. 2016), striped skunk (*Mephitis mephitis*—Wade-Smith and Verts 1982), and ermine (*Mustela erminea*—King 1983). Likewise, many species in this group generally occur at low densities (< 1 individual/km^2), like the long-tailed weasel (*Mustela frenata*—Sheffield and Thomas 1997) and wolverine (*Gulo gulo*—Banci 1994). Although many of these species are wide-ranging, some are declining or listed as threatened or endangered in all or part of their historic ranges, such as the European mink (*Mustela lutreola*—Maran et al. 2016), black-footed ferret (*Mustela nigripes*—Jachowski and Lockhart 2009), and Everglades mink (*Neovison vison evergladensis*—Florida Natural Areas Inventory [FNAI] 2001). Indeed, as of 2008, approximately 50% of mephitid and 43% of mustelid species occurring in the Americas with known population trends were declining (Belant et al. 2009). Globally, small-bodied carnivores, like many mephitid and mustelid species, have been increasingly listed as threatened or endangered by the International Union for the Conservation of Nature (IUCN) since the 1970s (Di Marco et al. 2014).

The eastern spotted skunk (*Spilogale putorius*) is a small mephitid carnivore native to much of the central and eastern United States and small portions of Canada and Mexico (Kinlaw 1995). The species experienced a range-wide decline in the 20th century, with Gompper and Hackett (2005) noting that harvest rates for eastern spotted skunks (adjusted for harvest effort) declined more than 99% between the 1940s and the 1980s. The eastern spotted skunk's listing by the IUCN recently was changed from Least Concern to Vulnerable (Gompper and Jachowski 2016), and the species has a protected status or is listed as a priority species/species of conservation concern in 21 of the 28 (75%) U.S. states in which it is believed to have occurred historically, and is potentially extirpated in at least three of these states (Eastern Spotted Skunk Cooperative Study Group 2019). The eastern spotted skunk has three recognized subspecies: the Appalachian (*S. p. putorius*), Florida (*S. p. ambarvalis*), and plains (*S. p. interrupta*) spotted skunks, of which the Florida spotted skunk is the least studied (Gompper and Jachowski 2016).

The Florida spotted skunk is the smallest of the eastern spotted skunk subspecies (Van Gelder 1959) and is endemic to peninsular Florida (Kinlaw 1995). The only previously dedicated research on this subspecies occurred during the 1970s and 1980s, when spotted skunks were captured as part of a mammalian mark–recapture trapping grid in Canaveral National Seashore and Merritt Island National Wildlife Refuge (Ehrhart 1974; Kinlaw et al. 1995a, 1995b; Fig. 1). The density of Florida spotted skunks reported at this site was 40 individuals/km^2 (Kinlaw et al. 1995b), over seven times as high as the only other reported density of eastern spotted skunks (5.02 individuals/km^2) in Iowa (Crabb 1948), representing one of the highest reported population density estimates of a mephitid worldwide (Appendix I). A high number of eastern spotted skunk photos captured across multiple game camera sites during a different study at Merritt Island National Wildlife Refuge in 2014 and 2015 (Martin et al. 2017) suggests that densities of Florida spotted skunks may remain high in this part of their range.

While previous research suggested Florida spotted skunks were highly abundant historically, there are no investigations into the factors influencing Florida spotted skunk population dynamics. Only one previous study has investigated survival and cause-specific mortality of eastern spotted skunks, reporting a mean annual survival rate of 35.4% in Arkansas (Lesmeister et al. 2010). This survival rate is lower than previously published rates for the striped skunk (Appendix II), and lower than estimated survival rates of many similarly sized mustelids worldwide (Powell and King 1997; Grenier et al. 2007; Zub et al. 2011; Wereszczuk and Zalewski 2019). Thus, it remains unclear how Florida spotted skunks attain such densities, if these densities are observed in other eastern spotted skunk subspecies, and what factors influence Florida spotted skunk survival. Further, given the reported range-wide decline in this species overall, such knowledge on factors that facilitate the relatively high abundance of the Florida subspecies could be used to inform conservation actions in other portions of its range.

The objective of our study was to provide estimates of Florida spotted skunk density and survival in the dry prairie of south-central Florida. We predicted that the density of spotted skunks at our site would be greatest in autumn, because individuals born during the summer would be independent by this time and available for capture. Given the previously reported high abundance and density of Florida spotted skunks along the Atlantic Coast of Florida (Kinlaw et al. 1995a, 1995b), we predicted that mean annual survival of spotted skunks in our study area would be higher than that reported in Arkansas (35.4%—Lesmeister et al. 2010). We also hypothesized that Florida spotted skunk survival would not differ among seasons, or between sexes, as observed in the only previous study of eastern spotted skunk survival (Lesmeister et al. 2010) as well as findings from other mephitids and mustelids (Greenwood et al. 1997; Gehrt 2005; Zub et al. 2011; Linnell et al. 2017). Our findings represent the first survival estimates of Florida spotted skunks and the first density estimates for the subspecies on mainland Florida, which, when compared to other eastern spotted skunk subspecies and threatened small carnivores, provide important insights into the potential for these species to be conserved.

Materials and Methods

Study area.—We conducted our study from 2016 to 2018 at Three Lakes Wildlife Management Area (hereafter, Three Lakes; Fig. 1) in south-central Florida, near Kenansville, Florida, United States (27.865254, −81.167319). We focused our research on 1,728 ha of dry prairie, a natural community restricted to south-central Florida (U.S. Fish and Wildlife Service 1999), where Florida spotted skunks previously were observed. Typically, vegetation in dry prairie habitats consists mainly of low shrubs and grasses, with early successional stages maintained and hardwood encroachment prevented through frequent fires (every 1–2 years on average) and seasonal flooding (Platt et al. 2006; FNAI 2010). Common plant species at our site 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). Average heights of grasses, woody shrubs, and saw palmettos in our study area were between 50 and 70 cm. Many small, ephemeral depression marshes and patches of wet prairie were distributed throughout this dry prairie landscape. The terrestrial mammal community at Three Lakes included, but was not limited to, Virginia opossums (*Didelphis virginiana*), eastern cottontails (*Sylvilagus floridanus*), hispid cotton rats (*Sigmodon hispidus*), feral hogs (*Sus scrofa*), white-tailed deer (*Odocoileus virginianus*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and nine-banded armadillos (*Dasypus novemcinctus*—U.S. Fish and Wildlife Service 1999). Striped skunks also are known to occur in the region,

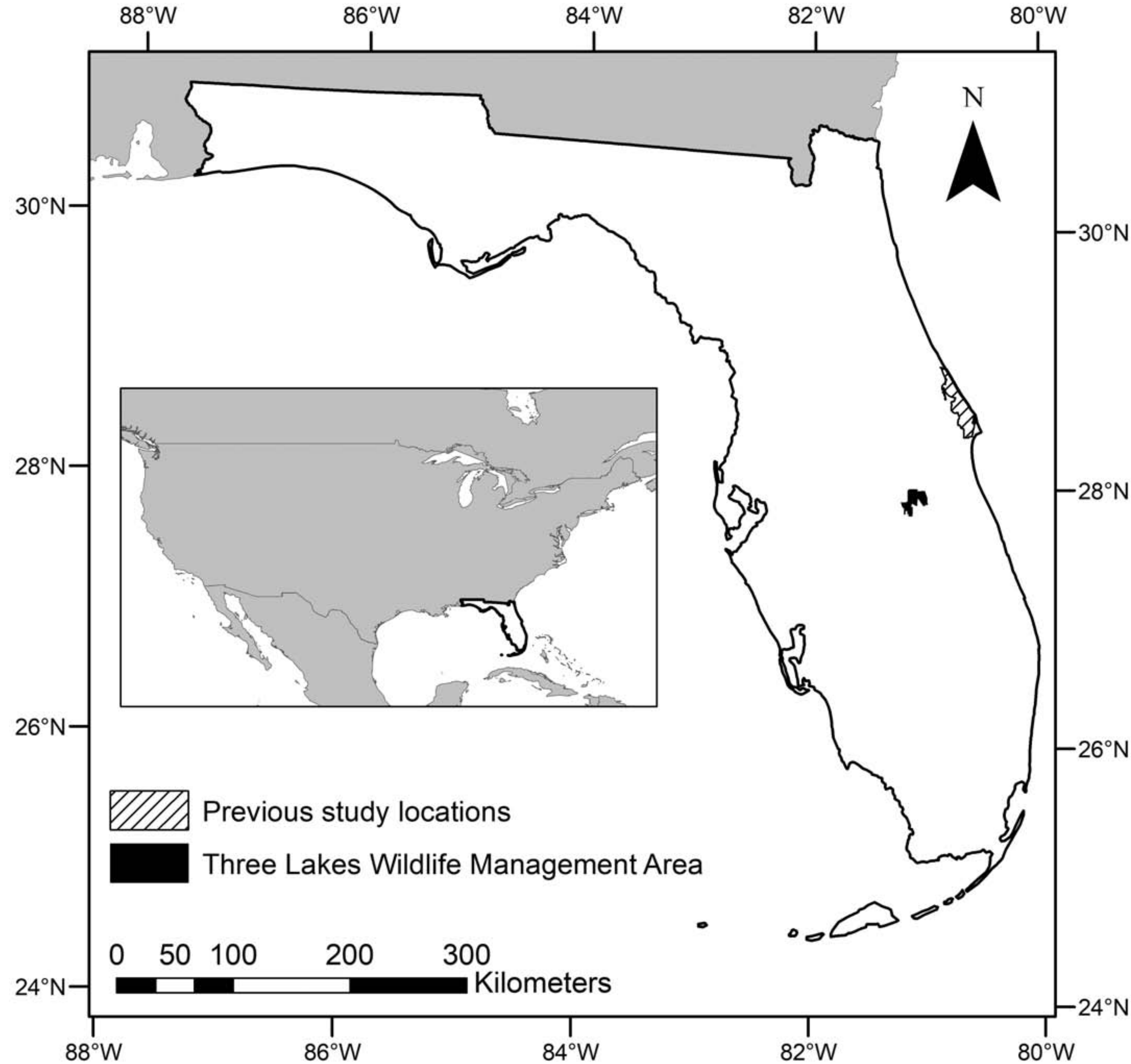

Fig. 1.—Location of mark–recapture and radiotelemetry research on Florida spotted skunks (*Spilogale putorius ambarvalis*) at Three Lakes Wildlife Management Area, Osceola County, Florida, United States, 2016–2018. Previous Florida spotted skunk studies occurred at Merritt Island National Wildlife Refuge and the adjacent Canaveral National Seashore, Florida, United States.

but they do not appear to be a common resident of dry prairie. Resident raptor species occurring in the region that can potentially prey upon spotted skunks included red-tailed hawks (*Buteo jamaicensis*), great horned owls (*Bubo virginianus*), and barred owls (*Strix varia*).

Trapping grid.—In 2016, we set up a trapping grid with 32 trap locations to record mark–recapture data on Florida spotted skunks (Fig. 2), with the ultimate goal of generating estimates of spotted skunk density in dry prairie. Within predominant dry prairie habitat, we placed one live trap (Model #1030-B; Havahart, Lititz, Pennsylvania) at each of these 32 locations such that each trap was ~400 m apart from north to south and ~250 m apart from east to west (Fig. 2). We placed a rectangular section of plywood over each trap to help protect captured animals from intense heat or inclement weather. If an intended trap location was close enough to a depression marsh that flooding was a concern, we moved the location the shortest distance possible (always < 20 m) to avoid inundation. If there was no dry ground within 20 m of the original trap location, we closed the trap for the duration of the trapping session. We carried out our trapping sessions once every 3 months for 11 sessions, starting in May 2016 and ending in November 2018. Each trapping

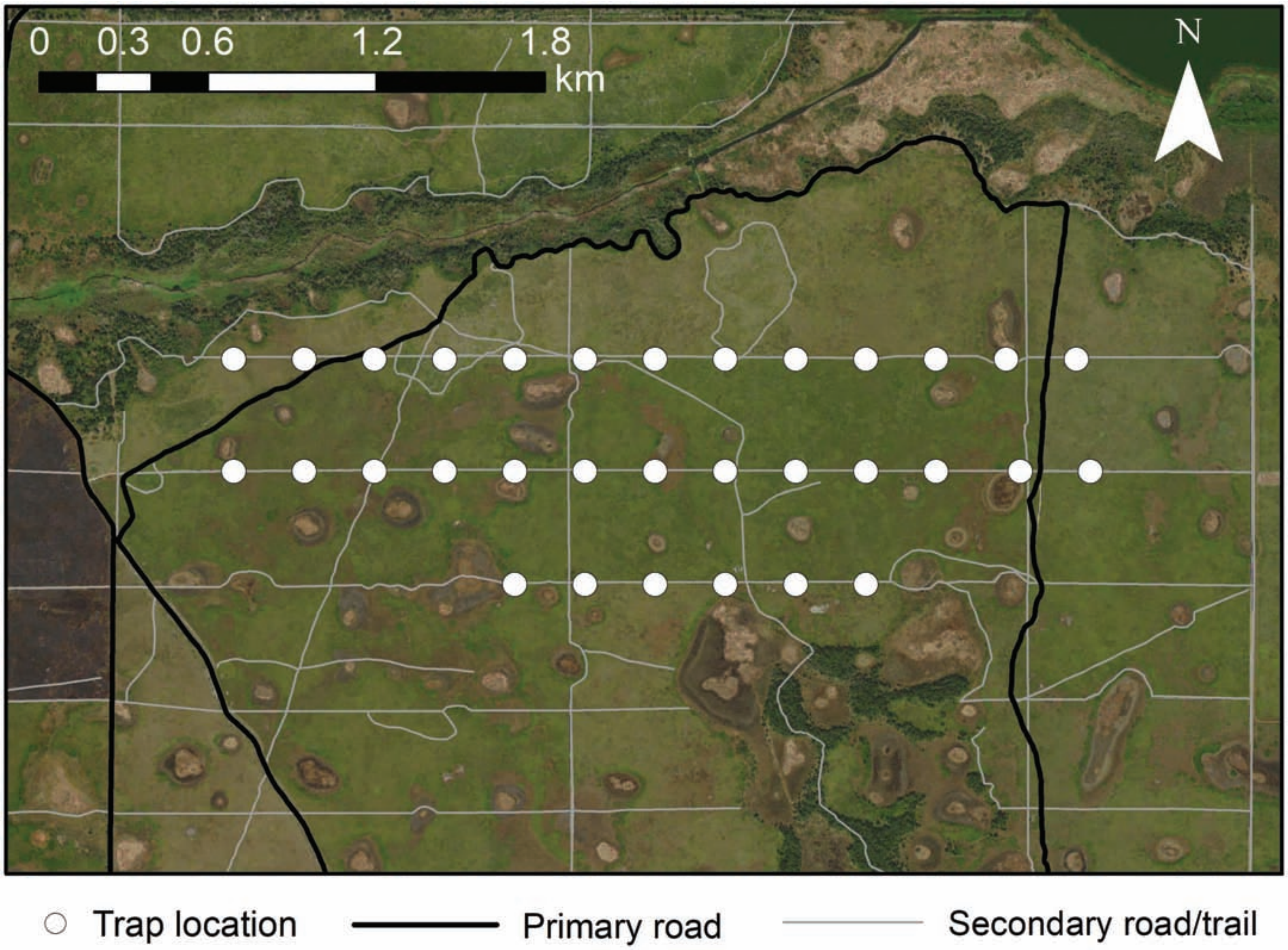

Fig. 2.—Diagram of mark–recapture trapping grid for Florida spotted skunks (*Spilogale putorius ambarvalis*) at Three Lakes Wildlife Management Area, Osceola County, Florida, United States, 2016–2018. Traps were spaced approximately 400 m apart north to south, and approximately 250 m apart east to west.

session was undertaken for four consecutive nights over a 5-day period. We baited the traps each afternoon with canned wet cat food and examined them the following morning, after which we closed the traps until reopening them again in the afternoon. We marked each captured spotted skunk with individually numbered ear tags in both ears (Model #1005-1L1; National Band & Tag Company, Newport, Kentucky) and weighed, identified the sex, and aged each individual as an adult or juvenile (based on body size and tooth wear—Lesmeister 2007) upon each capture. If we subsequently recaptured a skunk and it had lost one ear tag, and the ear was not severely torn from the previous ear tag, we would retag the ear in question. Similarly, if we recaptured a skunk that had lost both ear tags, we would attach new ear tags to any minimally damaged ears, though we were unable to identify these individuals unless they also had on radiocollars with which we could identify them. We followed guidelines from the American Society of Mammalogists (Sikes et al. 2016) and Clemson University Animal Care and Use Committee protocol (permit # AUP2015-042) for all trapping, processing, and collaring in this study.

Radiocollaring and tracking.—We captured spotted skunks for collaring from sites selected across the entire extent of dry prairie habitat in the study area to include individuals that had access to a variety of features on the landscape (e.g., non-dry prairie habitats, different distances from roads and trails, management units with different fire return intervals). We captured these skunks in clusters of 1–5 traps that we placed out opportunistically 1–4 days per week from February to May in 2016 and February to April in 2017. We also collared some skunks that we captured on the trapping grid during these time periods, and we marked, weighed, and identified the sex of all spotted skunks captured for collaring in the manner used on the trapping grid. We considered all spotted skunks captured during these time periods to be adults, as they would have been born some time during the previous year's summer. We fit adult spotted skunks with very high frequency (VHF) radiotransmitter collars (M1525 [~12 g] and M1545 [~18 g]; Advanced Telemetry Systems, Inc., Isanti, Minnesota). We ensured that fitted collars represented < 5.5% of an individual's body mass (Wilson et al. 1996; Sikes et al. 2016).

We attempted to obtain a live signal on all collared spotted skunks at least once per week from February 2016 to August 2017, making sure on each occasion that the collars were not emitting mortality signals. Generally, we first drove around the study area and listened for collar signals using a vehicle-mounted omnidirectional antenna. If we could not hear the signal using this method, we would search extensively on foot for each skunk, starting in the location to which the previously captured skunk last had been tracked. When available, an aircraft equipped with a radiotelemetry antenna was used to search the study area for missing skunks that we were unable to find for > 1 week. If a skunk's collar emitted a mortality signal, we immediately tracked the signal to the collar's location. We then attempted to determine if the collar had slipped off the skunk or if the skunk had died and a carcass was present. If we did find a dead spotted skunk, we surveyed the location where we found the skunk and tried to determine the cause of mortality. Intact carcasses of dead spotted skunks with unconfirmed causes of death were necropsied at the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute laboratory in Gainesville, Florida, United States, to attempt to determine cause of death.

Analysis of mark–recapture data.—We used multi-session spatially explicit capture–recapture (SECR) models in the "secr" package (Efford 2019) in program R (R Development Core Team 2018) to estimate session-specific Florida spotted skunk density in our study area. SECR methods use a state model that estimates density (D) over a state space (i.e., the defined area for which density is estimated) and a spatial detection model fit to individual capture histories. The spatial detection model includes two parameters: g_0 (detection or capture probability at the center of an individual animal's home range) and σ (a function of the scale of an individual animal's mobility; hereafter, spatial scale), that together define detection probability as a function of location (Efford 2004; Efford 2019). We used a half-normal detection function (a circular bivariate normal home range) for the spatial detection model so that detection decreased with increasing distance from an individual skunk's "activity center," which is a stationary point that more or less represents the center of an individual's home range based on capture locations during a trapping session (Efford 2019). We defined the state space by buffering our trapping grid by 337.61 m, based on the average movement of spotted skunks captured during our trapping sessions. Specifically, for each session, we calculated the root pooled spatial variance (RPSV), a measure of the dispersion of locations at which individuals were detected, then used the average RPSV multiplied by four as our buffer width (Efford 2004). We checked that density estimates were stable at this buffer width after running the models by using the "esa.plot" command in the "secr" package (Efford 2019). We set the state space grid spacing to 50 m, a smaller distance than the average RPSV, to specify how often a new activity center could potentially occur.

We created nine a priori models pertaining to all three SECR parameters (D, g_0, σ; Table 1). We included session as a covariate for density (D) in all our a priori models as occurrences of double tag loss (n = 12) between primary trapping sessions prevented any further temporal collapse of this parameter. Covariates we hypothesized to influence g_0 included sex, season, rain, moon illumination, and a learned trap response. Covariates we hypothesized to influence the relevant σ included sex and season. We categorized trapping sessions by season based on the date the sessions occurred: winter (21 December to 19 March), spring (20 March to 19 June), summer (20 June to 21 September), autumn (22 September to 20 December). We treated rain as a binomial covariate with a "1" representing any amount of rainfall within the last 24 h of capture, and a "0" representing no rainfall in the 24 h prior to capture. Our moon illumination covariate was a continuous percentage of moon illumination, which we obtained from the U.S. Naval Observatory moon fraction website (https://aa.usno.navy.mil/data/docs/MoonFraction.php, accessed 14 March 2019). Learned trap response in models accounted for step changes in detection after each individual skunk's first detection (i.e., initial capture).

We hypothesized that the density of Florida spotted skunks at our site would be highest during the autumn (November) trapping sessions, because eastern spotted skunks are born in May and June (Mead 1968) and are weaned at an average of 54 days (Crabb 1944). Some of these juvenile skunks might be independent before the August trapping session, but juveniles appear to reach approximate adult body size by late

Table 1.—A priori model selection results for analysis of Florida spotted skunk density at Three Lakes Wildlife Management Area, Osceola County, Florida, United States, 2016–2018 using spatially explicit capture–recapture. Included for each model are the log-likelihood [log (L)], the number of parameters (K), Akaike's Information Criterion adjusted 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). D = density, g_0 = detection at an individual's activity center, b = learned trap response by individual, σ = spatial scale. A parameter followed by ~ 1 indicates that parameter is held constant in the model.

Model	log(L)	K	AIC_c	ΔAIC_c	w_i
D ~ session, g_0 ~ sex + b, σ ~ 1	−1224.96	16	2484.27	0.00	1.00
D ~ session, g_0 ~ b, σ ~ 1	−1231.64	15	2495.34	11.07	<0.01
D ~ session, g_0 ~ sex, σ ~ sex	−1232.30	16	2498.95	14.68	<0.01
D ~ session, g_0 ~ sex, σ ~ 1	−1234.34	15	2500.74	16.47	<0.01
D ~ session, g_0 ~ moon, σ ~ 1	−1239.26	15	2510.58	26.31	<0.01
D ~ session, g_0 ~ 1, σ ~ 1	−1241.44	14	2512.68	28.41	<0.01
D ~ session, g_0 ~ season, σ ~ season	−1234.95	20	2513.59	29.32	<0.01
D ~ session, g_0 ~ rain, σ ~ 1	−1241.35	15	2514.77	30.50	<0.01
D ~ session, g_0 ~ season, σ ~ 1	−1240.30	17	2517.25	32.98	<0.01

August (Crabb 1944) and would definitely be independent by November, potentially contributing to an influx of individuals captured during the autumn trapping sessions. We also hypothesized that Florida spotted skunk density at our site would be skewed male because natural sex ratios in this species might favor males (Crabb 1948; Van Gelder 1959; Foresman and Mead 1973). Similarly, we predicted that g_0 and σ would be higher for male spotted skunks, because they have been found to have larger home ranges than females (Kinlaw 1995; Lesmeister et al. 2009), but that g_0 and σ would decrease following the breeding season (i.e., in summer) because detection of eastern spotted skunks has been shown to decrease during this period (Kinlaw 1995; Hackett et al. 2007). Likewise, as σ can be treated as an index of home range size, we predicted that σ would increase in spring as eastern spotted skunk home range size has been found to expand during the breeding season (Lesmeister et al. 2009), corresponding to late March–April for the species (Kinlaw 1995). We predicted that g_0 would increase on rainy nights (Kinlaw 1995; Lesmeister et al. 2015) and when there was less moon illumination (Thorne et al. 2017; Benson et al. 2019) because spotted skunks might be more active in these conditions that presumably offer some protection from predators. We predicted that g_0 also would increase on cooler nights (Kinlaw 1995). Lastly, we predicted there would be a positive learned response to trapping on g_0 due to traps being baited (Schlexer 2008).

We compared the fit of our nine a priori models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c—Akaike 1974). We used underlying hybrid mixture models that allowed us to estimate sex-specific detection probabilities and sex ratios in addition to comparing models' AIC_c values (Evans et al. 2017). We considered a top model to be any model contributing to 90% of the AIC_c model weights (w_i). We examined covariates in these resultant top models and considered them important when 95% confidence intervals (*CI*s) of beta estimates did not overlap zero. If sex was included in a top model, we used the proportion of male and female individuals (pmix), accounting for differences in detection probability, estimated in that model to determine sex ratios. We tested whether this sex ratio differed from 1:1 using a likelihood ratio test between the top model and an identical model in which the mixing proportion was fixed to 0.50 (Evans et al. 2017).

Analysis of telemetry data.—We created a known-fate model using the package "RMark" (Laake 2013) in program R (R Development Core Team 2018) to estimate survival probabilities for the radiocollared Florida spotted skunks. Because we collared spotted skunks over several months and across two different years, we used a staggered entry design (Pollock et al. 1989) modification to the Kaplan–Meier procedure (Kaplan and Meier 1958), which allowed us to add new collared skunks into our sample after our study had already started. We consolidated the individual encounter histories (i.e., instances where a skunk was tracked to a den or we detected a live signal from the skunk's collar) of each of our skunks into weekly intervals. For any given week, a "10" represented that a skunk's signal was successfully found during the week, a "00" represented that the skunk's signal was not found, slipped its collar, or disappeared during the week, and a "11" represented that the skunk had died during the week. We assumed that all skunks permanently lost from our study had not emigrated from our study area or died and instead were lost due to radiotransmitter-related issues (e.g., broken antenna, dead battery, slipped collar). We based this assumption on the movement distances of spotted skunks we observed at our site, our extensive searches for missing skunks outside of the core study area, and the apparent nature of any skunk mortalities we had observed.

We developed six a priori models to determine if spotted skunk survival at our site was affected by sex, year, or season (Table 2). We defined seasons in the same manner we did for our SECR models. We included three models to investigate if sex interacted with time since the beginning of the study, year, or season, respectively, to influence spotted skunk survival. In addition to the six a priori models, we included a null model with no covariates and a full model including all of the aforementioned covariates. We used AIC_c to determine relative support for each of the models in our candidate set (Burnham and Anderson 2002). We then compared AIC_c weights (w_i) of our models using evidence ratios to determine how much more likely our top model was in explaining our observed survival rates.

Results

Mark–recapture.—We captured Florida spotted skunks on 404 occasions over 1,404 trap-nights between May 2016 and

Table 2.—Known-fate survival model selection results for Florida spotted skunk (*Spilogale putorius ambarvalis*) survival (S) at Three Lakes Wildlife Management Area, Florida, United States, 2016–2017. Included for each model are the number of parameters in the model (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), the difference in AIC_c score when compared to the model with the lowest AIC_c (ΔAIC_c), the Akaike weight (w_i). S ~ 1 models constant survival and is equivalent to a null model.

Model	*K*	AIC_c	ΔAIC_c	w_i
S ~ 1	1	61.957	0.000	0.271
S ~ sex	2	62.562	0.605	0.200
S ~ time:sex	3	62.912	0.955	0.168
S ~ year	2	63.645	1.688	0.116
S ~ season	4	64.077	2.120	0.094
S ~ sex:year	5	64.736	2.778	0.067
S ~ sex + year + season + time	7	64.854	2.897	0.064
S ~ sex:season	9	67.121	5.164	0.020

November 2018 for an overall trapping success rate of 28.8% (four trap-nights were lost during one session when we had to close a trap location due to flooding). Collectively, we captured between 91 and 103 unique individuals, as 12 individuals we captured we suspected to be recaptures of individuals that had experienced double tag loss.

Our top model for density held ~100% of the AIC_c model weights (Table 1) and included an effect of trapping session on density, an effect of sex and learned response on g_0 (detection at an individual's activity center), and a constant σ (spatial scale; Table 3). Our density estimates ranged from 6.52 ± 2.93 *SE* skunks/km^2 in May 2016 to 23.29 ± 7.65 *SE* skunks/km^2 in August 2017 (Fig. 3). The sex ratio estimated by our top model was female-biased 79:21 ± 0.05 *SE*, and this ratio was significantly different than a 1:1 sex ratio ($\chi^2 = 32.673$, *d.f.* = 1, $P < 0.001$). Naïve detection probability was over 20% higher in males (0.376, 0.163–0.589, 95% *CI*) than females (0.145, 0.036–0.253, 95% *CI*) and a learned response increased naïve detection by about 51% for males (0.731, 0.569–0.894, 95% *CI*) and 33% for females (0.433, 0.336–0.530, 95% *CI*).

Survival.—We collared and tracked 38 individual Florida spotted skunks (16 females, 22 males) during 2016 and 2017 (mean = 111.7 days, range = 1–510 days). We confirmed mortalities for five individuals (1 female, 4 males; 13.2%; Appendix III), while four individuals likely slipped their collars during the study (i.e., we found the collars with no evidence of a mortality event), and two individuals we lost during the study and were never able to locate again. We found high model uncertainty among our candidate set of survival models, with 90% of AIC_c model weight distributed between seven of eight models (Table 2). The top model for survival of Florida spotted skunks was the null model, indicating that sex, year, or season did not have significant effects on spotted skunk survival at our site. Using evidence ratios, the null model was approximately 36% more likely than our second-best model (sex) and ≥ 61% more likely than all other models at explaining mean annual survival of spotted skunks at our site. The annual survival estimate for adult male and female skunks from our top model was 0.714 (0.503–0.925, 95% *CI*).

Discussion

While the eastern spotted skunk generally is believed to be vulnerable to extinction across much of its range due to reported declines over the past several decades (Gompper and Jachowski 2016), the survival and density estimates we observed were greater than we would expect in a declining species. The mean annual survival rate of Florida spotted skunks from our study (71.4%) was approximately twice as high as the only other published estimate from eastern spotted skunks (35.4%), from the Ouachita Mountains of Arkansas, United States (Lesmeister et al. 2010). The density estimates from our study are only the third reported for the species, and while lower than the estimated 40 Florida spotted skunks/km^2 from a barrier island on Florida's Atlantic coast (Kinlaw et al. 1995b), are similar to the range of plains spotted skunk densities reported by Crabb (1948) in the agricultural lands of Iowa prior to or concurrent with the range-wide decline of the species (Gompper and Hackett 2005). These findings suggest that the Florida subspecies occurs at higher densities than eastern spotted skunk subspecies elsewhere, although more estimates of population density from other parts of the eastern spotted skunk's range are needed.

Small carnivore populations sometimes undergo dramatic temporal variations in survival due to a variety of factors including, but not limited to, changes in top-down predation pressure (Powell 1973; Korpimäki and Norrdahl 1989; Jones et al. 2008), food availability (Korpimäki et al. 1991), and disease outbreaks (Greenwood et al. 1997; Matchett et al. 2010). However, multiple lines of evidence from our study suggest Florida spotted skunks in our study area maintained a robust population across seasons and years. First, as we predicted, neither season nor year was a strong predictor of survival in our

Table 3.—Beta (β) parameters of the top model for Florida spotted skunk (*Spilogale putorius ambarvalis*) density at Three Lakes Wildlife Management Area, Florida, United States, 2016–2018. Beta estimates with asterisks (*) had 95% confidence intervals that did not overlap 0. *D* = density, g_0 = detection at individual's activity center, σ = spatial scale, pmix = sex ratio. The reference category for each seasonal trapping session was the first trapping session (spring 2016).

Coefficient	β	*SE*	Lower cl	Upper cl
*D**	−3.0	0.429	−3.571	−1.889
D.summer2016	0.5	0.417	−0.267	1.366
D.autumn2016	0.5	0.422	−0.342	1.311
D.winter2017*	0.9	0.396	0.092	1.643
D.spring2017*	0.8	0.398	0.040	1.602
D.summer2017*	1.3	0.376	0.536	2.010
D.autumn2017*	1.2	0.377	0.503	1.982
D.winter2018*	1.2	0.380	0.433	1.923
D.spring2018	0.8	0.401	−0.014	1.559
D.summer2018*	1.2	0.377	0.503	1.982
D.autumn2018	0.7	0.405	−0.072	1.514
g_0*	−2	0.439	−2.637	−0.919
g_0.male*	1.3	0.417	0.453	2.088
g_0.learned*	1.5	0.435	0.655	2.362
σ*	4.7	0.042	4.626	4.791
pmix.male*	−1	0.288	−1.916	−0.786

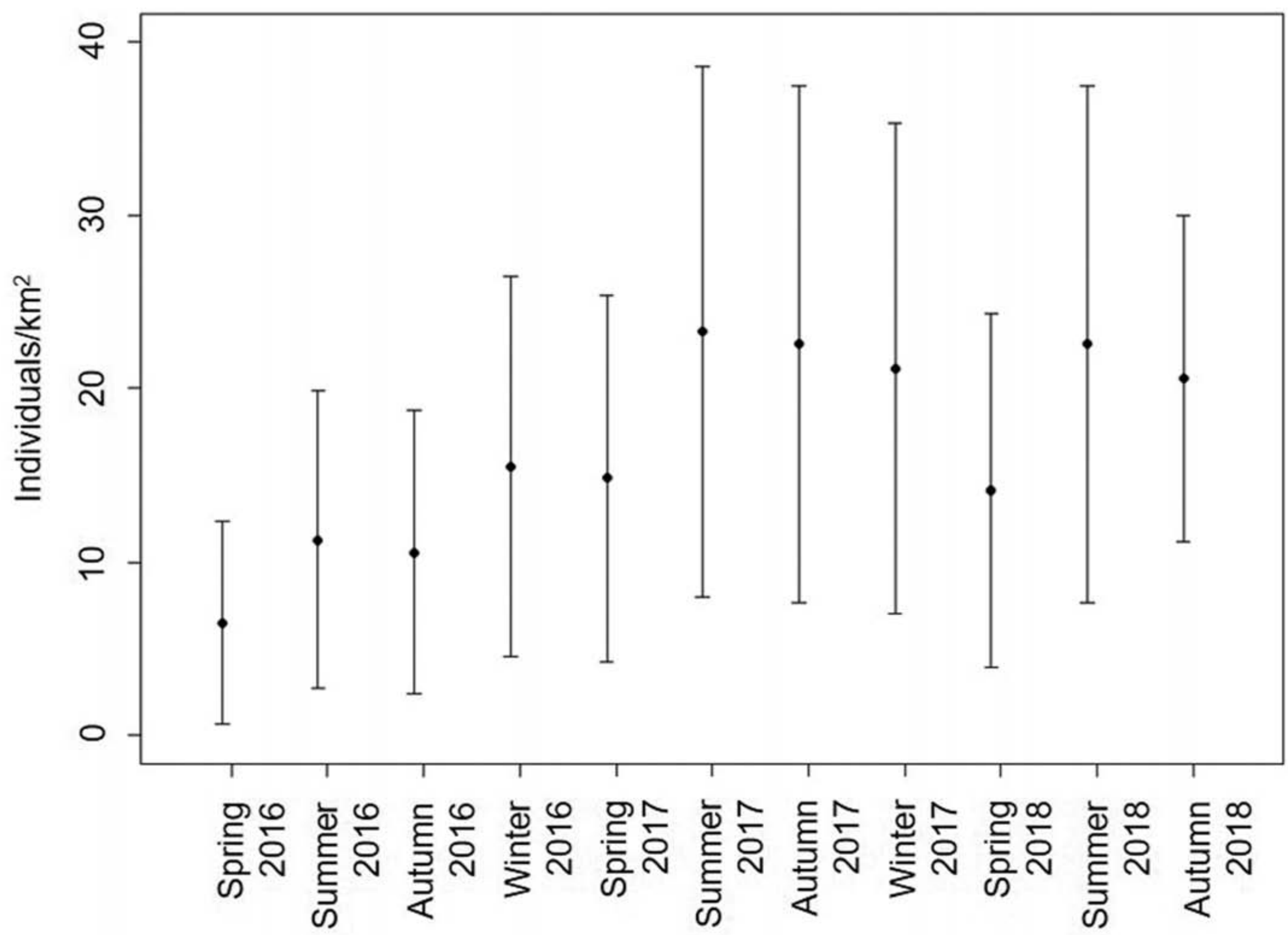

Fig. 3.—Florida spotted skunk (*Spilogale putorius ambarvalis*) density estimate values (individuals/km^2) derived from a mark–recapture grid between May 2016 and November 2018 at Three Lakes Wildlife Management Area, Osceola County, Florida, United States. Error bars represent 2 *SE*.

study. Second, while our density estimates did fluctuate between trapping sessions, we did not observe support for an effect of season on Florida spotted skunk density. Further, in contrast to previous studies of this species (Kinlaw 1995; Hackett et al. 2007), our probability of detecting spotted skunks did not decrease in summer. The consistently high survival and density of individuals we observed in our study area could be due in part to the relatively mild climate in the region, because Florida spotted skunks may not be heavily constrained by limited prey availability, which has been suggested as a potential factor in the eastern spotted skunk's decline elsewhere (Gompper and Hackett 2005), or increased interspecific competition during harsh winters like some mustelids (King 1981; Erlinge 1983; Linnell et al. 2017). However, our study only occurred over a 2-year time period, and longer-term studies are needed to evaluate if there are longer-term temporal variables affecting annual survival rates of skunks in our study area.

Taken together, the high annual survival estimates, high density estimates, and large number of individual Florida spotted skunks captured in our study area lead us to believe that there is a sizable and stable or potentially increasing population of Florida spotted skunks at the site. Including captures on this study's mark–recapture grid, captures from a pilot mark–recapture grid we trapped on in March 2016, and captures for radiocollaring purposes (Harris et al. 2020), a minimum of 215 unique Florida spotted skunks were captured between February 2016 and November 2018 at Three Lakes. This is in contrast to recent studies on other eastern spotted skunk subspecies of a similar length but larger spatial scale that captured between two and 65 confirmed individuals (Sprayberry and Edelman 2018; Benson et al. 2019; Eng and Jachowski 2019; Higdon and Gompper 2020; Thorne 2020). The sex ratio of spotted skunks captured during our study was heavily skewed toward females (1.0M:3.8F), the opposite of previously reported more male-skewed sex ratios of eastern spotted skunks captured in Florida (2.5M:1.0F—Kinlaw et al. 1995b), Iowa (1.8M:1.0F—Crabb 1948), and Arkansas (1.1M:1.0F—Lesmeister et al. 2010). In addition, if we were to look at our second-best model for Florida spotted skunk survival (sex), mean annual survival of females estimated from that model would be 0.856 (0.595–1.117, 95% *CI*), whereas male annual survival would be lower at 0.598 (0.296–0.899, 95% *CI*). While the model including sex was not our top model, it does suggest that annual survival of females at our site might be higher than male survival. Eastern spotted skunks are polygynous breeders (Rosatte and Larivière 2003), suggesting adult female survival and fertility likely are the most sensitive and elastic demographic variables, similar to mustelids and other mammals (Oli and Dobson 2003; Grenier et al. 2007; Wittmer et al. 2007). High annual survival rates (≥ 85%) are known to be important in sustaining populations of low-density carnivore populations (Eberhardt 1990), so a high mean annual survival rate of female spotted skunks at our site in a heavily female-skewed population could be another indication of a population that is increasing or stable.

The survival estimate of Florida spotted skunks from our study is the highest ever reported (Appendix II) for a mephitid, and our density estimates are among the highest recorded for mephitids as well (Appendix I). Compared to the densities both of large and smaller carnivores reported by Carbone and Gittleman (2002), our highest density estimate of 23.29 Florida spotted skunks/km^2 is greater than the range of densities presented for most carnivores, including several mustelids: ermine, pine martens (*Martes martes*), and European badgers (*Meles meles*). Only the least weasel (*Mustela nivalis*) and small Indian mongoose (*Herpestes javanicus*) had potentially higher densities (Carbone and Gittleman 2002), and both of these species are listed as being of Least Concern by the IUCN, whereas the eastern spotted skunk is listed as Vulnerable with a decreasing population trend (Gompper and Jachowski 2016).

However, we caution against the generalization of results from our study to other Florida spotted skunk populations and eastern spotted skunk subspecies. The dry prairie in which we carried out our study is a unique ecosystem that historically covered as much as 1.2 million acres in south-central Florida; much of this land now has been converted to agricultural uses (FNAI 2010) and < 2% of historic dry prairie likely remains (Noss et al. 1995). Dry prairie differs markedly in topography and vegetation composition, structure, and height from the forested landscapes in which eastern spotted skunks primarily have been studied in the past. Even when compared to more similar habitat types (the farmlands and grasslands of South Dakota), our trapping success rate for Florida spotted skunks was considerably higher than that for plains spotted skunks in a recent study (28% versus 1%—Fino et al. 2019), suggesting that there may be factors other than habitat features affecting the density and survival rate we observed in our study. It is possible that spotted skunks in the dry prairie ecosystem have relaxed top-down or bottom-up pressures when compared to other populations of subspecies of eastern spotted skunks. In a study on radiocollared eastern spotted skunks in Arkansas, avian predators (thought to be great horned owls) were the greatest source of mortality to the skunks (Lesmeister et al. 2010). In contrast, we never observed a mortality that could be confidently attributed to avian predators in our grassland system, which was largely devoid of perches for owls (Appendix III), although great horned and barred owls do range throughout Florida. Likewise, a study on den site selection of Florida spotted skunks at our study site showed no support for a predator avoidance hypothesis to explain selection of skunk den sites (Harris et al. 2020).

Reduced interspecific competition also can lead to changes in population demographics. A relevant example can be seen in the island spotted skunk (*S. gracilis amphiala*), a subspecies of the western spotted skunk (*S. gracilis*) endemic to the Channel Islands, California, United States, which increased in density following a likely release from interference competition with its primary competitor, the island fox (*Urocyon littoralis santacruzae*—Jones et al. 2008). Striped skunks and weasels (*Mustela* sp.) are thought to be sympatric food competitors of eastern spotted skunks (Kinlaw 1995), but we never observed or captured them in our study area during any field work or trapping efforts between February 2016 and November 2018. While weasels may not have been attracted to traps containing solely wet cat food, we did capture other mammals of similar or larger size in our traps, including Virginia opossums and small raccoons, and we expected we would have captured some striped skunks, had they occurred in considerable numbers in our study area. Future comparative studies outside of our study area should be conducted to evaluate how variation in food resource availability and predator or competitor communities could influence spotted skunk survival, density, and behavior relative to our findings.

Collectively, our findings provide a key point of comparison from which to guide future research, management, and conservation efforts on behalf of eastern spotted skunks. Many mephitids and mustelids have large geographical ranges and often occur in low densities across these ranges. However, our study adds to a handful of other studies, like those on the island spotted skunk (Jones et al. 2008) and black-footed ferret (Grenier et al. 2007), that suggest that if conditions are favorable, small carnivores otherwise threatened with extinction can establish relatively large and robust populations. These occurrences reinforce the importance of studying locally abundant populations of imperiled carnivores to better understand the conditions where small carnivore populations flourish to provide not only hope, but insights into the conditions necessary for the recovery of threatened populations. To this end, we encourage future research on the population dynamics of other eastern spotted skunk populations, particularly where they are believed to be declining, as this might allow researchers and wildlife managers to comparatively identify potential mechanisms that limit eastern spotted skunk conservation and recovery in other parts of their range.

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Appendix I

Population density estimates of mephitid species worldwide, ordered from highest to lowest. To identify published density estimates, we conducted a search on 8 April 2020 on Web of Science using the search terms: TS=(density OR densities) AND TS=(Conepatus OR Mephitis OR Mydaus OR Spilogale). Additionally, we reviewed mephitid accounts published in *Mammalian Species* and the IUCN's Red List (IUCN 2020, accessed 14 April 2020) and referenced the primary sources cited in them. Finally, we utilized snowball sampling as we reviewed the resultant publications from our prior searches to find more density estimates in the literature.

Species	Density (individuals/km^2)	Region	Reference
Striped skunk (*Mephitis mephitis*)	21.7–43.3	Maine, United States	Dean (1965)
Eastern spotted skunk (*Spilogale putorius*)	40	Florida, United States	Kinlaw et al. (1995b)
Striped skunk	1.0–36.0	Ontario, Canada	Rosatte et al. (1991)
Striped skunk	11.6–25.9	Illinois, United States	Ferris and Andrews (1967)
Striped skunk	23.8	Michigan, United States	Allen (1938)
Eastern spotted skunk	6.5–23.3	Florida, United States	This study
Western spotted skunk (*S. gracilis*)	9.0–19.0	California, United States	Jones et al. (2008)
Striped skunk	0.7–18.7	Eastern United States	Allen and Shapton (1942), Bailey (1971), Bennitt and Nagel (1937), Burt (1946), Jones (1939), Scott and Selko (1939), Stout and Sonenshine (1974), Verts (1967)[a]
Striped hog-nosed skunk (*Conepatus semistriatus*)	0.78–14.8	Oaxaca, Mexico	Hernández-Sánchez et al. (2017)
Striped hog-nosed skunk	13.8	Neotropical forests	Robinson and Redford (1986)
Striped skunk	2.1–6.5	Ontario, Canada	Rosatte et al. (1992)
Striped skunk	2.1–5.9	Illinois, United States	Gehrt (2005)
Striped skunk	5.1	Illinois, United States	Prange and Gehrt (2007)
Eastern spotted skunk	5.02	Iowa, United States	Crabb (1948)
Molina's hog-nosed skunk (*C. chinga*)	5	Chile	Cofré and Marquet (1999)
Molina's hog-nosed skunk	1.1–3.8	Santa Catarina and Piauí, Brazil	Kasper et al. (2012)
Striped skunk	1.9–3.1	North Dakota, United States	Upham (1967)
American hog-nosed skunk (*C. leuconotus*)	2.6	Texas, United States	Brashear et al. (2015)
Striped skunk	0.2–2.2	Ontario, United States	Rosatte et al. (2010)
Hooded skunk (*M. macroura*)	1.2–1.7	Oaxaca, Mexico	Cervantes et al. (2002)
Striped skunk	0.08–1.7	Wisconsin, United States	Bartelt et al. (2001)
Molina's hog-nosed skunk	0.12–1.66	Buenos Aires, Argentina	Castillo et al. (2011)
American hog-nosed skunk	0.6–1.3	Oaxaca, Mexico	Cervantes et al. (2002)
Striped skunk	0.7–1.2	Alberta, Canada	Bjorge et al. (1981)
Striped skunk	0.10–0.71	Texas, United States	Hansen et al. (2004)
Pygmy spotted skunk (*S. pygmaea*)	0.4–0.5	Oaxaca, Mexico	Cervantes et al. (2002)

[a] Summarized by Wade-Smith and Verts (1982).

Appendix II

Highest reported mean annual survival estimates of mephitid species worldwide, ordered from highest to lowest. To identify published survival estimates, we conducted a search on 8 April 2020 on Web of Science using the search terms: TS=("survival rate" or "annual survival") AND TS=(Conepatus OR Mephitis OR Mydaus OR Spilogale). In addition, we reviewed mephitid accounts published in *Mammalian Species* and the IUCN's Red List (IUCN 2020, accessed 14 April 2020) and referenced the primary sources cited in them. Finally, we used snowball sampling as we reviewed the resultant publications from our prior searches to find more survival estimates in the literature. When possible, adult survival rates were used rather than survival rates combined across age classes.

Species	Mean annual survival	Location	Reference
Eastern spotted skunk (*Spilogale putorius*)	0.71	Florida, United States	This study
Striped skunk (*Mephitis mephitis*)	0.29–0.67	Minnesota, United States	Fuller and Kuehn (1985)
Striped skunk	0.46–0.66	Ontario, Canada	Rosatte et al. (1991)
Striped skunk	0.40–0.51	Illinois, United States	Gehrt (2005)
Striped skunk	0.40–0.48	Texas, United States	Hansen et al. (2004)
Eastern spotted skunk	0.35	Arkansas, United States	Lesmeister et al. (2010)

Appendix III

Mortalities of radiocollared Florida spotted skunks (*Spilogale putorius ambarvalis*) between 2016 and 2018 at Three Lakes Wildlife Management Area, Osceola County, Florida, United States.

Date discovered	Sex	Cause of death	Notes
14 February 2016	Male	Burn injuries	Died in a prescribed fire
24 February 2016	Male	Unknown	Severe infestation by parasitic worms (*Spirometra* sp., *Physaloptera maxillaris*, and *Macrocanthorhynchus ingens*)
3 August 2016	Female	Unknown	Found intact but partially decomposed inside a burrow with one of two known kits
13 April 2017	Male	Unknown	Found dead inside of a deceased American alligator (*Alligator mississippiensis*)—unknown if predated or scavenged; see Harris et al. (2019).
25 April 2017	Male	Unknown	Partially decomposed skull only found at entrance of a burrow