Demography of the Appalachian Spotted Skunk (*Spilogale putorius putorius*)

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Abstract - *Spilogale putorius* (Eastern Spotted Skunk) is a small, secretive carnivore that has substantially declined throughout the eastern United States since the mid-1900s. To better understand the current status of Eastern Spotted Skunks, we studied survival and reproduction of the *S. p. putorius* (Appalachian Spotted Skunk) subspecies across 4 states in the central and southern Appalachian Mountains from 2014 to 2020. Using encounter histories from 99 radio-collared Appalachian Spotted Skunks in a Kaplan–Meier known-fate survival analysis, we calculated a mean annual adult survival rate of 0.58. We did not find support for this survival rate varying by sex, predator cover (canopy cover and topographic ruggedness), or climate. Compared to estimates of survival from previous research, our data suggest that Appalachian Spotted Skunk survival is intermediate to the *S. p. interrupta* (Plains Spotted Skunk) and *S. p. ambarvalis* (Florida Spotted Skunk) subspecies of Eastern Spotted Skunk. We located 11 Appalachian Spotted Skunk natal dens and estimated mean litter size to be 2.8 juveniles per female. We used a Lefkovitch matrix to identify the most important demographic rates and found that adult survivorship had the largest impact on the population growth rate. These results provide important demographic information for future Eastern Spotted Skunk population viability analyses and can serve as a baseline for future comparative assessments of the effects of management interventions on the species.

Introduction

Spilogale putorius (L.) (Eastern Spotted Skunk) is a species of conservation concern over much of its range. Once common from Pennsylvania south through the Appalachian Mountains and into Florida, and west of the Mississippi River to the Continental Divide (Kinlaw 1995), Eastern Spotted Skunks have experienced a >90% decline due to unknown causes since the mid-1900s as determined based on trapping records (Gompper and Hackett 2005). There are currently 3 recognized subspecies based on morphology (Van Gelder 1959) and genetics (Shaffer et al. 2018): *S. p. ambarvalis* Bangs (Florida Spotted Skunk), *S. p. interrupta* (Rafinesque) (Plains Spotted Skunk), and *S. p. putorius* (L.) (Appalachian Spotted Skunk). The Florida Spotted Skunk is classified as a species of greatest conservation need in Florida (Florida Fish and Wildlife Conservation Commission 2019),

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although it has been documented as extremely abundant within portions of its range (Harris et al., in press). The Plains Spotted Skunk is believed to be in greatest conservation need and has been petitioned for listing under the US Endangered Species Act (US Fish and Wildlife Service 2012). There are increasing concerns about the reduction in the range and abundance of the Appalachian subspecies due to the limited number of confirmed sightings over the past several decades (Eastern Spotted Skunk Cooperative Study Group 2020).

Despite evidence of a range-wide decline and concern for the future persistence of the species, only 2 studies across the entire range have examined the survivorship of the Eastern Spotted Skunk. Lesmeister et al. (2010) radio-tracked 33 Plains Spotted Skunks over 2 years at a single study site in Arkansas, finding that adult Plains Spotted Skunks had a relatively low annual survival rate (0.34; sexes and years pooled). The largest sources of mortality were avian predators, likely *Bubo virginianus* (Gmelin) (Great Horned Owl), and mammalian predators. Additionally, most mortalities occurred in mature *Pinus echinata* Miller (Shortleaf Pine), the most avoided habitat type in the study area but also the most abundant habitat type locally (Lesmeister et al. 2009). In contrast, Harris et al. (in press), radio-tracked 38 Florida Spotted Skunks for 2 years at a single study site in Florida and found that the annual survival rate of adult Florida Spotted Skunks was 0.71 in a sub-tropical dry prairie ecosystem. This result was potentially attributable to low variation in seasonal food availability and few avian or terrestrial predators occurring in that system. Prior to our work, there had been no demographic studies of the Appalachian subspecies of Eastern Spotted Skunk.

The Appalachian Spotted Skunk historically ranged across 13 states and a variety of habitats from the Coastal Plain, through the Piedmont and into the highest elevations of the Appalachian Mountains (Diggins et al. 2015, Shaffer et al. 2018). Recent sightings and studies of the subspecies have been restricted largely to the Appalachian Mountains, where they inhabit forests across a gradient of age/condition classes and elevations, though usually with a commonality of dense understory and midstory cover (Eng and Jachowski 2019b, Sprayberry and Edelman 2018, Thorne 2020). These habitats are thought to provide Appalachian Spotted Skunks with both thermal cover and protection from avian predators (Eng and Jachowski 2019b). Collectively, it appears that Appalachian Spotted Skunks persist in localized mountainous, forested areas but infrequently occur in valley bottoms with mixed agriculture–forest mosaics (Perry et al. 2021 [this issue]). Further, recent evidence suggests these populations are genetically isolated from one another (Thorne 2020). It remains unknown if populations of Appalachian Spotted Skunks are increasing or decreasing, and by association, if conservation intervention is warranted.

Several factors are hypothesized to influence Appalachian Spotted Skunk survival. First, Eastern Spotted Skunk survival may be influenced by the sex of an individual, as males are predicted to have a higher survival rate than females due to lower reproductive demands (Lesmeister et al. 2010). Alternatively, males may experience reduced survival as they travel more during the breeding season to seek out mates, which may increase their predation risk (Lesmeister et al. 2009).

Second, Eastern Spotted Skunk survival could be positively influenced by vegetative cover, because higher levels of tree canopy closure may provide increased cover from predators (Lesmeister et al. 2008). In addition, terrain ruggedness has been predicted to have a positive influence on survival because ravines and drainages can have greater ericaceous and other understory woody cover that decreases predation risk from avian predators more than surrounding hillsides (Eng and Jachowski 2019b). Moreover, survival may decrease with decreasing elevation due to increases in younger forests, fragmentation, and human modification (Eng and Jachowski 2019a, Thorne et al. 2017) Third, similar to that of other small to mid-sized carnivores occurring in temperate ecosystems, survival of Eastern Spotted Skunks may be influenced by climate, where individuals that live at higher elevations and latitudes have lower survival because colder areas may increase energetic demands, especially in winter when prey abundance is lower (Bartoń and Zalewski 2007, Fuller et al. 1995).

To better understand the demography of Appalachian Spotted Skunks, we synthesized data collected from 4 independent studies from the central and southern Appalachian Mountains across 4 states (Alabama, North Carolina, South Carolina, and Virginia) to address 5 objectives: (1) estimate adult survival, (2) evaluate support for several hypotheses regarding survival, (3) estimate average litter size, (4) construct a basic demographic model to estimate population growth rate and conduct a demographic elasticity analysis, and (5) provide recommendations for future survival research.

Field-site Description

We studied Appalachian Spotted Skunks from 2014 to 2020 on national, state, nonprofit, and corporate properties across predominantly forested areas of the central and southern Appalachian Mountains (Fig. 1; Fenneman 1938). Elevation of the study sites varied from 200 to 650 m in Alabama, 300 to 800 m South Carolina, 350 to 1100 m in North Carolina, and 350 to 1450 m in Virginia. The forests vary in their composition based on elevation, aspect, slope, and latitude but *Quercus* spp. (oak) and *Carya* spp. (hickory) predominate throughout with *Pinus* spp. (pine) occurring on more xeric sites and mesophytic species such as *Liriodendron tulipifera* L. (Yellow-poplar) and *Acer* spp. (maple) occurring on mesic sites. Understories are dominated by *Kalmia latifolia* L. (Mountain Laurel) on xeric sites or *Rhododendron maximum* L. (Rosebay Rhododendron) on mesic sites, particularly along riparian areas (Ford et al. 2006). In Alabama, *Vaccinium arboreum* Marshall (Sparkleberry) also is common in the understory. One study site on the border of Virginia and North Carolina is a high-elevation northern hardwood–*Picea rubens* Sarg. (Red Spruce) community (Diggins et al. 2015).

Methods

We utilized radio-tracking data from 4 independent field studies designed to better understand resource selection patterns of adult Appalachian Spotted Skunks

(Cornelison 2018; Eng and Jachowski 2019b; S.N. Harris, unpubl. data; Spraybery and Edelman 2018; Thorne 2020). In all studies, we identified areas of recent sightings, placed trail cameras to confirm presence, then set traps to attempt capture

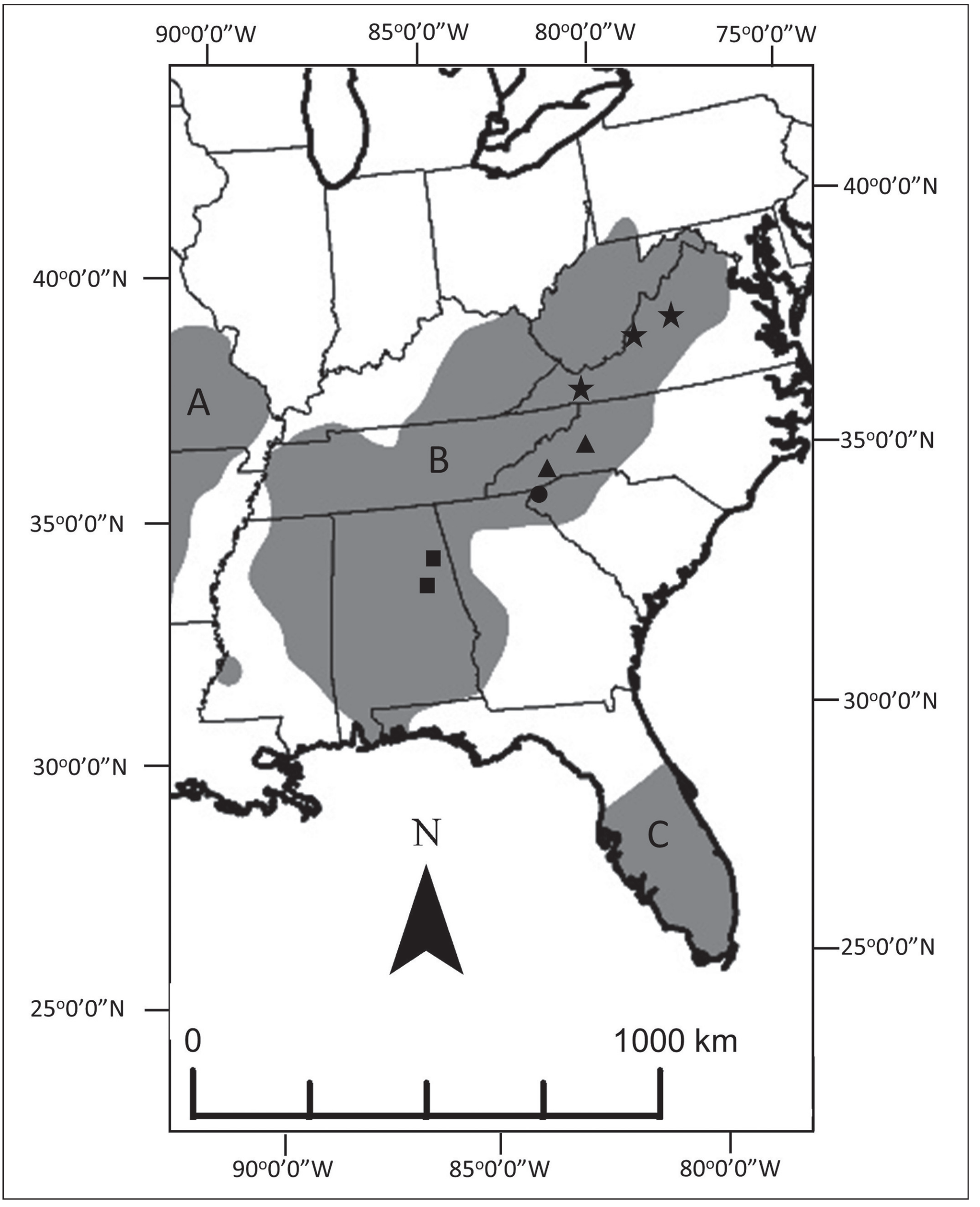

Figure 1. The current known range of the (A) Plains Spotted Skunk, (B) Appalachian Spotted Skunk (including isolated population in Alabama), and (C) Florida Spotted Skunk (adapted from Jachowski et al. [in press]). Symbols indicate where Appalachian Spotted Skunk survival was studied from 2014 to 2020, and correspond to each study in Table 1 (squares = Alabama, circle = South Carolina, triangles = North Carolina, and stars = Virginia).

between January and April. We baited cage traps with canned sardines, canned wet cat food, or a mixture of rolled oats, bacon grease, and peanut butter. We set traps and checked them the following morning. We then transferred captured skunks to a denim or canvas handling cone, or pillowcase for processing. We weighed and determined the sex of each skunk prior to fitting with a very high frequency (VHF) radio-transmitter collar that weighed <5% of their body weight. Collar brand and trapping methods varied among sites; additional details can be found in Cornelison (2018) and Sprayberry and Edelman (2018) for Alabama, Eng and Jachowski (2019b) for South Carolina, and Thorne (2020) for Virginia. Our study in North Carolina (S.N. Harris, unpubl. data) used Pro Series 103SS cage traps (48 cm x 15 cm x 15 cm; Tomahawk Live Trap, Hazelhurst, WI) and M1740 collars (Advanced Telemetry Systems, Isanti, MN) that weighed 16 g. All handling protocols were approved by the Institutional Animal Care and Use Committees at Clemson University (#2015-042 and 2017-065), University of West Georgia (#1003), and Virginia Polytechnic Institute and State University (#13-119-FIW).

Across all sites, we attempted to locate Appalachian Spotted Skunks weekly by triangulation and homing methods. When we detected a mortality signal or lack of movement over several days, we attempted to locate the mortality site and examine the remains to determine the cause of mortality. We classified mortalities as avian predation, mammalian predation, disease, collar-related, or unknown. We attributed mortalities to avian predation based on the presence of feathers, owl pellets, bird guano, and location relative to perch trees. We identified mammalian predation by damage to the skull and collar, canine puncture marks, fur matted down by saliva, and the absence of signs of avian predation. We sent Appalachian Spotted Skunks that were suspected to have died from disease to the Southeastern Cooperative Wildlife Disease Study at the University of Georgia for diagnostic confirmation. Collar-related mortalities occurred when an Appalachian Spotted Skunk immobilized its paw in the collar or the collar was caught on vegetation.

We estimated litter size by tracking females to natal dens in late spring and placing motion-sensitive camera traps at the sites. Cameras were positioned ~3–4 m away from a den entrance and set to high sensitivity to capture images or videos of juveniles emerging from the den. We did not reposition the camera monitoring a den until the female Appalachian Spotted Skunk was known to have moved to another den location, in which case we moved the camera to this new location. We removed cameras once juveniles appeared to be independent of their mother. We recorded a female's litter size as the maximum number of juveniles seen with her on camera at one time.

We estimated monthly survival using the Kaplan–Meier method (Kaplan and Meier 1958) with staggered entry in program R (Version 4.0.2; R Core Team 2018) using the package 'RMark' (Laake and Rexstad 2008). In each study, we summarized telemetry locations into weekly encounter histories where we assigned a "10" if a Appalachian Spotted Skunk was located during the weekly interval, a "00" if the Appalachian Spotted Skunk was not located during the weekly interval, or a "11" if the Appalachian Spotted Skunk had died during that weekly interval (Laake and Rexstad 2008). Kaplan–Meier survival estimation allows for staggered entry of marked individuals and for individuals to be "lost" during a study, allowing us to include data from individuals that were collared at different points during the study and animals that left the study area or slipped their collars. In this way, animals were censured from survival estimation until the individual's fate was confirmed (Kaplan and Meier 1958). Due to occasional gaps in tracking certain individuals weekly across datasets, we consolidated all weekly encounter histories into monthly encounter histories, using the same entry notation. Lastly, during months when no Appalachian Spotted Skunks were located or monitored, we censored all individuals.

We developed 13 a priori models based on the hypothesized influence of sex, predator cover, and climate on Appalachian Spotted Skunk survival (Table 1). To approximate aspects of predator cover, we used estimates of percent tree canopy cover by deciduous and coniferous species from the 2016 National Land Cover Database (Coulston et al. 2013, Homer et al. 2020), which contains estimates as a 30-m raster grid across all land-cover types, with values varying from 0 (no canopy cover) to 100 (full canopy cover). We also estimated terrain ruggedness by calculating the terrain ruggedness index (Riley et al. 1999) across the study area, with 0 representing level terrain and larger values representing more rugged terrain. To approximate aspects of climate, we determined latitude using the Universal Transverse Mercator (UTM) northing value from trap locations. For latitude, we divided the northing value by 100,000 to be equal in magnitude with the other variables. For temperature, we used the average (1981–2010) annual minimum temperature PRISM raster data (https://prism.oregonstate.edu). In addition, we incorporated values of elevation using 30-m digital elevation model (DEM) rasters. Multicollinearity analysis indicated that elevation and minimum temperature were highly negatively correlated (-0.79) and UTM northing and

Table 1. Hypotheses and model structure for the 13 a priori models developed to evaluate survival of Appalachian Spotted Skunks in the central and southern Appalachian Mountains of Alabama, North Carolina, South Carolina, and Virginia, 2014–2020. Null = intercept only, TRI = terrain ruggedness index, cover = forest canopy cover, northing = Universal Transverse Mercator northing coordinate.

Hypothesis	Model
Null	Null
Sex	Sex
Predator cover	TRI Cover Cover + TRI Cover + elevation Cover + elevation + TRI
Climate	Elevation Northing Northing + elevation
Sex + climate	Sex + northing + elevation
Sex + Predator cover	Sex + cover + elevation + TRI
Global	Sex + cover + elevation + TRI + northing

minimum temperature were highly negatively correlated (-0.73). Therefore, average annual minimum temperature was not retained for the model-selection process. We did not have sufficient relocation information across all individuals at each study site to estimate home ranges. Therefore, we used the average home-range size from the 95% fixed kernel density estimator of males and females in Virginia (5.72 km^2 and 3.61 km^2, respectively; Thorne 2020) to buffer initial trap locations from which to estimate the average values of environmental covariates for each individual. In addition, to test the effect of these covariates individually, we developed 2 sub-global models: one that evaluated the influence of sex and climate, and another that evaluated sex and predator cover (Table 1). Finally, we evaluated a global model that included all variables.

We evaluated support for each a priori monthly survival model in an information-theoretic model selection framework using Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We selected a top model by first considering all models within 2 AIC_c values and then comparing relative support of remaining models by model weights (Burnham and Anderson 2002). Model variables were considered informative if their 95% confidence intervals did not overlap 0. We then estimated survival based on the top-ranked model and extrapolated monthly values to annual survival estimates by raising the monthly survival estimate to the twelfth power.

To collectively determine which vital rates had the largest impact on population growth of Appalachian Spotted Skunks, we created a pre-birth-pulse, female-based Lefkovitch matrix consisting of juvenile (<7 months old) and adult (≥7 months old) stages. As there are no published estimates of Appalachian Spotted Skunk density or population size, our intent was not to provide specific estimates of population size over time for the region; rather, we primarily wanted to determine which vital rates had the largest impact on population growth and secondarily, if the population was increasing or decreasing, and by how much each year (λ). Therefore, we started with an initial abundance vector of 100 juvenile and 100 adult Appalachian Spotted Skunks. We used our estimate of annual adult survival and the annual survival rate of radio-collared juvenile female Plains Spotted Skunks from Arkansas (0.313; averaged across 2 years), from Lesmeister et al. (2010), which, to our knowledge, is the only available estimate of juvenile spotted skunk survival. To estimate fecundity, we assumed a 1:1 sex ratio of juveniles and divided the average litter size in half. To incorporate demographic stochasticity into the model, we varied survival and fecundity values based on the normal distribution between the low and high 95% confidence intervals, similar to other models of carnivore population growth (Bales et al. 2005, Butler et al. 2021, Miller et al. 2002, Wielgus et al. 2013). We estimated the population growth rate and elasticity values based on 1000 simulations using the package 'popbio' (Stubben and Milligan 2007) in program R (R Core Team 2018).

Results

We captured and radio-collared 99 adult Appalachian Spotted Skunks (76 males, 23 females) between December 2014 and May 2020 (Table 2), and gathered 439 detection events. Across all studies, we monitored at least 1 Appalachian Spotted Skunk during each month except for October 2017 to January 2018 and September to December 2018, totaling 58 months of monitoring. During the course of each study, we monitored Appalachian Spotted Skunks for an average of 6 months (min–max = 1–28), with the majority of detection events collected from February to August. There were 25 occasions when Appalachian Spotted Skunks shed their collars or collars malfunctioned (i.e., antenna breakage), and we lost contact with 46 Appalachian Spotted Skunks before the end of the study, likely due to individuals leaving the study areas (undetermined fate) (Table 2).

We documented 23 mortalities: 10 avian mortalities (43%), 4 canine distemper virus (CDV) mortalities (17%), 4 unknown mortalities (17%), 3 mammalian mortalities (13%), and 2 collar-related mortalities (9%) (Table 2). Six of the avian mortalities occurred in Virginia, and 2 each occurred in both Alabama and North Carolina, all of which were attributed to owls (likely Great Horned Owl or *Strix varia* Barton [Barred Owl]). All 4 cases of CDV occurred in North Carolina over a 4-week period in April and May of 2020 and resulted in 57% mortality of the 7 Appalachian Spotted Skunks monitored at the site at the time (Harris et al. 2021 [this issue]). Two mammalian mortalities occurred in Alabama and 1 in North Carolina. The 2 collar-related mortalities occurred in North Carolina due to collar entanglement. We censored the encounter histories of skunks after collar-related mortality events because they were non-typical sources of mortality. In South Carolina, we documented 7 additional collars emitting a mortality signal, but were not able to retrieve collars due to denial of property access. We highlight this situation because it would have lowered the survival estimate if we had been able to classify these events as mortalities rather than undetermined fate.

Table 2. Summary of Appalachian Spotted Skunk monitoring in the central and southern Appalachian Mountains of Alabama, North Carolina, South Carolina, and Virginia, 2014–2020. *n* = number of individuals tracked during the study; monitoring length = mean number of months that individual skunks were monitored during the studies; mortalities = the total number of mortalities documented during the study and in 5 categories (avian = avian predator, mam. = mammalian predator, dis.= disease; collar = collar entanglement); slipped/malf. collars = the number of collars that slipped off skunks or had a known problem, such as a broken antenna, during the study; und.= the number of skunks that were otherwise lost during the study and their fate was undetermined.

Study area	Study timeline	*n*	Monitoring length (months)	Mortalities						Slipped/ malf. collars	Und.
				Total	Avian	Mam.	Dis.	Collar	Unk.		
Alabama[A]	12/2014–10/2016	12	6	4	2	2	0	0	0	0	8
Virginia[B]	12/2015–09/2017	16	8	6	6	0	0	0	0	2	6
South Carolina[C]	03/2016–09/2017	28	4	2	0	0	0	0	2	10	16
North Carolina[D]	02/2018–05/2020	43	6	11	2	1	4	2	2	13	16
Total		99		23	10	3	4	2	4	25	46

[A]Cornelison (2018) and Sprayberry and Edelman (2018), [B]Thorne (2020), [C]Eng and Jachowski (2019*b*), [D]This study.

Our model-selection analysis showed a high amount of model uncertainty (Table 3), with all univariate models within 2 ΔAIC_c values of the top model, the null model. The 95% confidence intervals of all covariate estimates from the univariate models overlapped 0: terrain ruggedness index (-0.11, 0.52), sex (-0.39, 1.5), elevation (-0.002, 0.001), UTM northing (-0.393, 0.256), and forest canopy cover (-0.05, 0.07). These results suggest that none of these covariates were strong predictors of survival, and therefore, we used the null model to estimate a monthly survival rate of 0.96 (95% CI = 0.93, 0.97), and an annual survival rate of 0.58 (95% CI = 0.44, 0.72).

We monitored 11 natal dens over the course of the study with 5 in Virginia, 3 in South Carolina, and 3 in North Carolina. We observed litters for an average of 39 days after we started monitoring dens (min–max = 1–50; North Carolina mean = 15 days, South Carolina mean = 47 days, Virginia mean = 47 days). We also opportunistically observed 2 litters associated with different adult Appalachian Spotted Skunks in Alabama, both with 2 kits, but did not include these observations in our analysis because of their opportunistic nature. Litter counts averaged 2.82 (min–max = 1–5) kits per female (Virginia mean = 2.4 [min–max = 1–4], South Carolina mean = 2.3 [min–max = 1–3], North Carolina mean = 4.0 [min–max = 3–5]).

We parameterized our matrix using the estimated 95% confidence intervals from the null model of annual adult survival (0.44, 0.72), the average annual juvenile female survival (0.26, 0.36; Lesmeister et al. 2010), and our estimated 95% confidence intervals of female fecundity (1.05, 1.77). The mean estimated population growth rate was 0.997 (95% CI = 0.99, 1.00). Adult survival was more elastic (0.40) than adult fecundity (0.30) and juvenile survival (0.30), indicating that a proportional change in adult survivorship had a larger influence on population growth than fecundity or juvenile survival.

Table 3. Model-selection results for Appalachian Spotted Skunk (n = 99) survival in the central and southern Appalachian Mountains of Alabama, North Carolina, South Carolina, and Virginia, 2014–2020. k = number of parameters, AIC_c = Akaike's information criterion adjusted for small sample size values for each model, ΔAIC_c = difference in AIC_c value between top model and other model, w_i = Akaike weights, TRI = terrain ruggedness index, northing = Universal Transverse Mercator northing coordinate.

Model	k	AICc	ΔAICc	w_i
Null	1	164.73	0.00	0.21
TRI	2	165.01	0.28	0.18
Sex	2	165.50	0.77	0.14
Elevation	2	166.51	1.79	0.09
Northing	2	166.57	1.85	0.08
Cover	2	166.63	1.90	0.08
Cover + TRI	3	166.98	2.25	0.07
Northing + elevation	3	168.48	3.75	0.03
Cover + elevation + TRI	4	168.49	3.76	0.03
Cover + elevation	3	168.53	3.80	0.03
Sex + cover + elevation + TRI	5	168.73	4.01	0.03
Sex + northing + elevation	4	169.26	4.53	0.02
Sex + cover + elevation + TRI + northing	6	170.69	5.96	0.01

Discussion

Our study is the first to estimate the survival rate of Appalachian Spotted Skunks, and we found that on average adult survival rate for this subspecies (0.58) was intermediate between estimates of the locally abundant Florida Spotted Skunk (0.71; Harris et al., in press) and the imperiled Plains Spotted Skunk (0.35; Lesmeister et al. 2010). Similar to Lesmeister et al. (2010), we found that inter-specific predation was the largest source of mortality to Appalachian Spotted Skunks across all study populations, with most of the predation events caused by avian predators. However, the dominant causes of mortality varied among studied populations. For example, disease was the largest source of mortality in North Carolina. Therefore, wildlife managers will likely need to adopt differing, adaptive management approaches to conserving local populations of Appalachian Spotted Skunks that account for a variety of mortality sources.

The lack of support for environmental covariates influencing survival could be due to several methodological aspects of our study. First, all study sites were located within relatively intact forested lands with minimal recent human disturbance and modification, so there was less variability in covariates than exists across the entire Eastern Spotted Skunk range. Nonetheless, there have been sightings of Appalachian Spotted Skunks in more developed areas (ESSCSG 2020), and studying survival in more human-dominated landscapes should provide a wider range in covariate values to calibrate survival models. Second, due to difficulties in monitoring animals, we were unable to collect enough locations to develop fine-scale estimates of space use for all individuals. Future research should prioritize collecting enough locational data to create individual home ranges from which to extract covariates so that survival data are linked to individual-specific covariates. Lastly, Lesmeister et al. (2009) observed that understory cover associated with distinct forest-management conditions likely was responsible for observed differences in Plains Spotted Skunk mortality due to avian predators. In our study system, where a diversity of forest conditions existed, the remotely sensed land-cover variables we used may not accurately represent understory conditions. Therefore, future research assessing how understory characteristics at the home-range scale potentially influence avian predation and overall survival is warranted.

Very little is known about the reproductive rates of Eastern Spotted Skunks, and our estimate of average litter size across the central and southern Appalachians (2.82) was lower than those reported for harvested and captive Prairie and Florida Spotted Skunks (5.5 kits; Mead 1968a) and *Spilogale gracilis* Merriam (Western Spotted Skunk; 3.9 kits; Mead 1968b). In addition, the estimated average litter size was much lower than that of *Mephitis mephitis* (Schreber) (Striped Skunk; 5.4–7.2 kits; Greenwood and Sargeant 1994, Patton 1974). Our litter sizes may be lower than previous estimates because our estimates are from when kits emerged from dens, and it is possible that kits may have died beforehand in the dens. We documented litter sizes of 1–5 kits, similar to that of *Conepatus leuconotus* (Lichtenstein) (American Hog-nosed Skunk; 1–5 kits; Dragoo and Sheffield 2009), but less than *Mephitis macroura* Lichtenstein (Hooded Skunk; 3–8; Hwang and

Lariviere 2001). Unfortunately, we were unable to monitor a sufficient number of litters to conduct an analysis on what variables might influence Appalachian Spotted Skunk litter size. Moreover, to date there have not been any successful studies of juvenile Appalachian Spotted Skunk survival or movements after independence. Additional studies of the factors influencing litter size and juvenile survival would enhance our understanding of long-term Appalachian Spotted Skunk population viability given that our elasticity analysis indicated that reproduction and juvenile survival were fairly influential to the population growth rate.

During the course of our study, we encountered 2 primary difficulties related to studying the demography of Appalachian Spotted Skunks. First, was the difficulty of catching individuals. In order to capture enough Appalachian Spotted Skunks to address individual studies' objectives, we focused research efforts in areas that generally had contained the majority of recent sightings (Perry et al. 2021 [this issue]) and that had sufficient access. We then deployed baited motion-sensitive camera traps in areas of recent sightings followed by cage traps at camera sites where Appalachian Spotted Skunks were detected. Despite this targeted approach, our trapping success was very low, varying from 0.04 captures per trap night in Alabama to 0.12 captures per trap night in North Carolina in 2018. For many of the study sites, trapping was constrained to occur during the winter months when *Ursus americanus* Pallas (American Black Bear) were less active. In Virginia, these seasonal restrictions resulted in trap sites that often were inaccessible due to snow cover. The second-most common problem was loss of contact with study animals. We "lost" many Appalachian Spotted Skunks due to a combination of the limited radio signal range of the small VHF radio-collars used and rugged terrain that further reduced VHF transmission distance and line of sight. Therefore, we suggest future researchers incorporate telemetry flights or novel techniques that can be paired with traditional VHF tracking such as drones (Muller et al. 2019), automated antennae arrays (Kays et al. 2011), or genetic mark–recapture through hair snares (Kéry et al. 2011, Mowat and Paetkau 2002) to reduce occurrences of "lost' individuals. Moreover, checking collar status more frequently and using predator DNA from saliva (Wengert et al. 2013, Williams et al. 2003) may lead to improved identification of causes of mortality. Using these and other alternative methods will be particularly important in studying the demography of this species outside of the areas we studied where the chance of encountering Eastern Spotted Skunks is likely lower (Eng and Jachowski 2019a, Thorne et al. 2017).

Overall, we estimated that the Appalachian Spotted Skunk population is, on average, declining at an annual rate of 0.3% within what is likely the core of its range in the central and southern Appalachian Mountains. Combined with recent genetic evidence that suggests Appalachian Spotted Skunk populations are relatively isolated from one another (Thorne 2020), our estimated population growth rate indicates that these remnant populations are likely not producing enough recruits to allow recolonization of historically occupied areas necessary for functional population connectivity. If populations are small and show low growth rate, they are particularly vulnerable to stochastic events such as the disease outbreak we observed in North Carolina. Finally, although some Appalachian Spotted Skunks persist outside of large, intact forested areas where our fieldwork was conducted, these habitats support many of the highest densities of remaining Appalachian Spotted Skunks (Perry et al. 2021 [this issue]). Thus, if current conditions in these areas are not producing a growing or stable population, based on our small number of sites, there is an urgent need to formulate management actions to improve Appalachian Spotted Skunk population growth. As a first step, we suggest expanded long-term demographic monitoring to assess the trends over time across a wider land-use gradient, particularly at the edge of the range where landscape heterogeneity is likely higher than in core areas. In addition, to better inform specific management efforts, we suggest the implementation of direct experimental studies involving monitoring of Appalachian Spotted Skunks on replicated sites and/or before and after habitat manipulations such as forest harvesting/regeneration and prescribed burning. Further, given the impact of predation and disease we observed on adult survival, studies involving disease immunization and habitat modification to increase understory cover may also help identify particular drivers of Appalachian Spotted Skunk survival and indicate management alternatives where populations are deemed particularly vulnerable.

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