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Influence of landscape attributes on Virginia opossum density

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Abstract

The Virginia opossum (*Didelphis virginiana*), North America's only marsupial, has a range extending from southern Ontario, Canada, to the Yucatan Peninsula, Mexico, and from the Atlantic seaboard to the Pacific. Despite the Virginia opossum's taxonomic uniqueness in relation to other mammals in North America and rapidly expanding distribution, its ecology remains relatively understudied. Our poor understanding of the ecology of this important mesopredator is especially pronounced in the rural southeastern United States. Our goal was to estimate effects of habitat on opossum density within an extensive multi-year spatial capture-recapture study. Additionally, we compared the results of this spatial capture-recapture analysis with a simple relative abundance index. Opossum densities in the relatively underdeveloped regions of the southeastern United States were lower compared to the more human-dominated landscapes of the Northeast and Midwest. In the southeastern United States, Virginia opossums occurred at a higher density in bottomland swamp and riparian hardwood forest compared to upland pine (*Pinus* spp.) plantations and isolated wetlands. These results reinforce the notion that the Virginia opossum is commonly associated with land cover types adjacent to permanent water (bottomland swamps, riparian hardwood). The relatively low density of opossums at isolated wetland sites suggests that the large spatial scale of selection demonstrated by opossums gives the species access to preferable cover types within the same landscape.

KEYWORDS

abundance index, *Didelphis virginiana*, landscape ecology, population density, southeast United States, spatial capture-recapture, telemetry, Virginia opossum

The Virginia opossum (*Didelphis virginiana*), North America's only marsupial, has a range extending from southern Ontario, Canada, to the Yucatan Peninsula, Mexico, and from the Atlantic seaboard to the Pacific (Seidensticker et al. 1987, Gardner and Sunquist 2003). Similar to other generalist mesopredators, Virginia opossums (i.e., opossum) have benefited from anthropogenic changes in land use (e.g., urbanization, agriculture; Beatty et al. 2014). Their r-selected life history and opportunistic diets make opossums well-adapted predators and scavengers of natural and anthropogenically provisioned resources (Ryser 1995, Paton 2005, Hill et al. 2018). Because of their expanding populations and close association with developed landscapes, the profile of opossums in wildlife management programs has increased over the last several decades (Jackson 1994, Chicago Animal Care and Control 2019, Stengel et al. 2019, Slate et al. 2020).

Opossums play an important role in the transmission of several important diseases and parasites of humans (e.g., Chagas disease; Bern et al. 2011, Cantey et al. 2012, Manne-Goehler et al. 2016) and livestock (e.g., *Sarcocystis neurona*; Dubey and Lindsay 1998). As members of ecological communities, opossums can affect wildlife disease mitigation efforts, such as oral rabies vaccination efforts targeting raccoons (*Procyon lotor*; Hable et al. 1992, Smyser et al. 2010). The effectiveness of oral rabies vaccination programs depends in part on the proportion of target population(s) immunized. The opossum, a species that is refractory to infection with raccoon rabies, is a non-target species that has been identified as a dominant competitor for vaccine baits in the eastern United States by the United States Department of Agriculture National Rabies Management Program and others (Smyser et al. 2010, Ma et al. 2020, Slate et al. 2020). Given their role as a reservoir of zoonoses and a competitor for management efforts targeting wild carnivores for rabies virus control and elimination, it is important to understand how landscape factors affect spatiotemporal patterns of opossum occurrence and density (McCallum et al. 2001, Begon et al. 2002, Lloyd-Smith et al. 2005).

Previous researchers have revealed considerable fluctuation in densities of opossums across their range, varying from 0.50 to 29.0 opossums/km^2 (Holmes and Sanderson 1965, Seidensticker et al. 1987, Levesque 2001, Gardner and Sunquist 2003). Opossum densities generally are positively associated with riparian corridors, road density, and developed areas (Gardner and Sunquist 2003, Kanda et al. 2009, Beatty et al. 2016), and negatively associated with conifer forests lacking permanent water sources (Weckerly et al. 1987, Kaiser 2017). The most commonly used method for determining opossum population densities has been to divide estimated abundance by some estimate of the effective trapping area (Gardner and Sunquist 2003), ideally derived from telemetry of opossums tracked in concert with trapping efforts (Ryser 1995, Beatty et al. 2016). The development of spatial capture-recapture modeling, however, has facilitated direct estimation of population density (Efford 2004, Royle and Young 2008, Royle et al. 2014) and created a framework for the estimation of the effects of landscape heterogeneity on population processes within a single model (Royle et al. 2018). These models are data intensive and require large numbers of recaptures to ensure model convergence (Dupont et al. 2019). Therefore, these approaches can require lengthy capture sessions, or supplementation with telemetry locations (Ivan et al. 2013, Linden et al. 2018). The cost associated with collecting such data may be too great depending on the project scale or unnecessary because of the scope of the question under study. In such a case, the implementation of a relative abundance index may be warranted. Indices are frequently used to assess opossum relative abundance (Bartelt et al. 2001, Gehrt et al. 2006), and recently the United States Department of Agriculture National Rabies Management Program has developed a validated population indexing method to estimate densities of raccoons that co-occur with opossums in management areas (Slate et al. 2020).

Our objective was to investigate the influence of bottomland swamp, riparian hardwood forest, upland pine (*Pinus* spp.) plantations, and isolated wetlands on the density of opossums. We hypothesized opossum population density would be positively correlated with land cover types associated with water and negatively associated with resource-poor cover types. We predicted opossum densities would be highest in bottomland swamp, riparian hardwood forest, and isolated wetlands and lowest in upland pine plantations. To facilitate future studies in similar landscapes, we compared spatial capture-recapture density estimates to a simple abundance indexing method.

STUDY AREA

We conducted this study on the Savannah River Site (SRS; Figure 1) between late January and May of 2017–2019. We selected the timing of field work to correspond with the peak breeding activity (Feb–Jul) of opossums in the southeastern United States (Gardner and Sunquist 2003), while also avoiding the heat stress of summer. The SRS is a 782-km^2 property managed by the United States Department of Energy in Aiken, Barnwell, and Allendale counties in South Carolina, USA. Historically, the SRS had been mostly cleared for agricultural use. After being acquired by the United States Department of Energy in 1950, pine forests were planted among preexisting deciduous forests. These pine forests mainly consisted of longleaf pine (*P. palustris*), loblolly pine (*P. taeda*), and slash pine (*P. elliottii*) and were managed for timber production by the United States Forest Service. During the study, the SRS was composed of 57% pine forest, 21% hardwood forest, 6% mixed forest, and 16% other (industrial use, roads, shrubs, and lakes). Pine forests were managed with fire and approximately 100,000 m^3 of timber are harvested annually from the SRS. Common megafauna on the SRS included the American alligator (*Alligator mississippiensis*), coyote (*Canis latrans*), raccoon, wild pig (*Sus scrofa*), and wild turkey (*Meleagris gallopavo*). The landscape has an average elevation of 200 m above sea level and is interspersed with 370 Carolina bays (0.027 ± 0.065 km^2[$\bar{x} \pm$ SD]), small periodic water filled depressions. The SRS had a subtropical climate with winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov) temperatures averaging 9°C, 17°C, 26°C, and 18°C, respectively. Annual rainfall on the SRS averaged 120 cm. The Savannah River borders the western side of the property and is characterized by a shallow, wide bathymetric profile (White and Gaines 2000).

METHODS

We delineated 4 natural land cover types common in the rural southeastern United States: bottomland swamp, upland pine plantation, riparian hardwood, and isolated wetlands (Homer et al. 2020). We selected sampling sites within bottomland swamps and upland pine plantations in proportion to percent canopy cover. We also selected

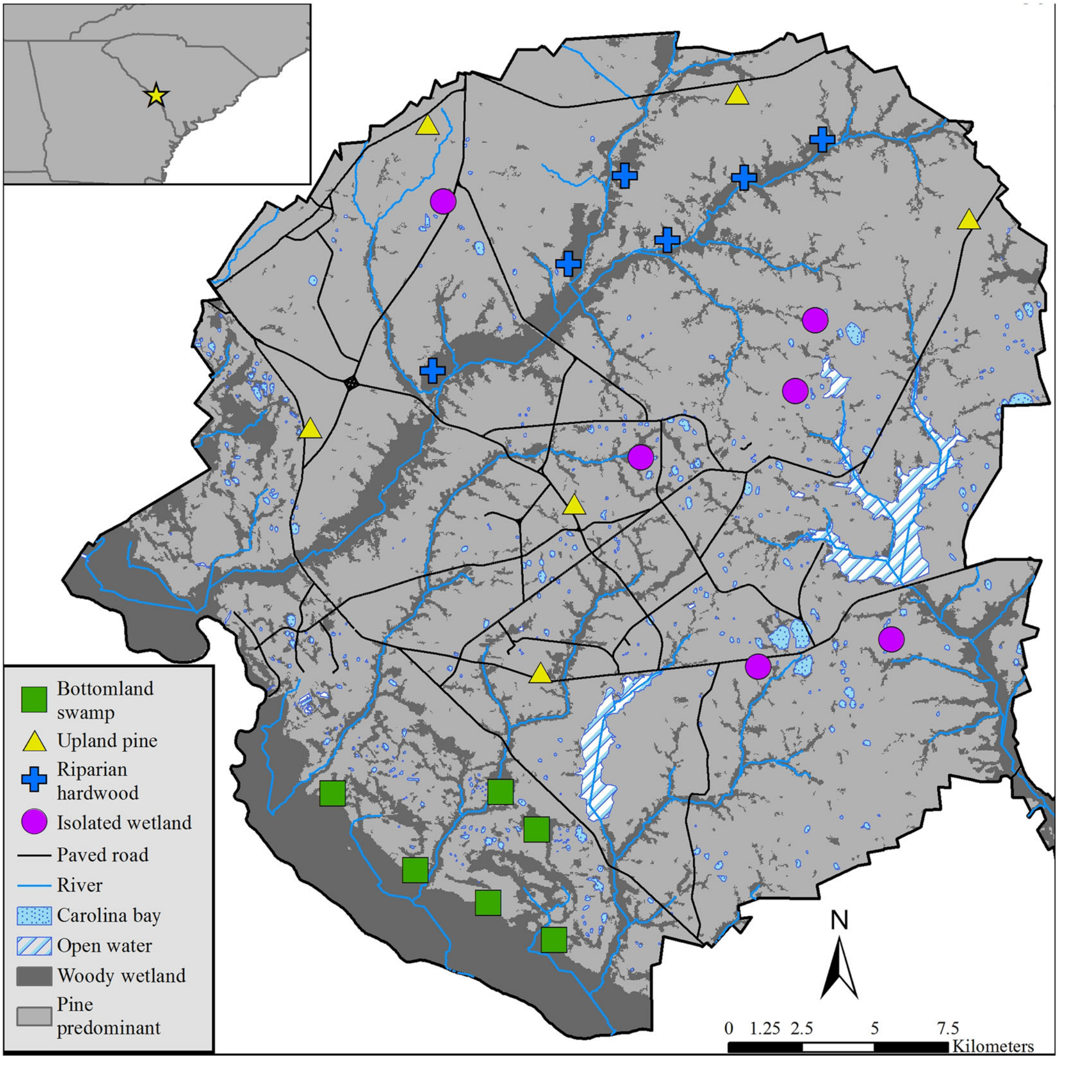

FIGURE 1 Location of Virginia opossum trapping sites within the Savannah River Site in Aiken, South Carolina, USA, January to early May, 2017–2019.

riparian hardwood and isolated wetland sites based on their proximity to permanent creeks and Carolina bays, respectively (Figure S1, available in Supporting Information). We randomly selected 9 sites for each of the 4 land cover types and identified 6 sites that minimized conflict with current and future land management activities (n = 24 sites). In cases of major disturbance in the study area (e.g., clear cutting), we moved sites <100 m from the original location. Except for bottomland swamp sites, which were located linearly along the Middle Savannah River Swamp, we distributed sites throughout the entire SRS during the study.

Animal capture and handling

During January to May, 2017–2019, we trapped all sites for 20 days during 2 distinct 10-day sessions (trapping sessions 1 and 2). Within each site, we placed 25 Tomahawk® live-capture traps (model 108SS; Hazelhurst, WI, USA) in a 5 × 5 or 6 × 4 + 1 rectangular grid pattern with 100-m spacing between traps (Figure S2, available in Supporting Information). We baited traps with whole-kernel corn and plaster tabs soaked in fish oil as lure (Webster and Beasley 2019). We replaced plaster tabs after every capture event, following major rainstorms, or after 5 days of inactivity. We replaced corn when it was consumed by target and non-target species.

Because of the logistic difficulty imposed by the size of the combined study area (782 km^2), we divided the number of actively sampled sites into 3 groups of 8 sites equally represented by land cover types. Following trapping sessions, we relocated traps to the next group of 8 sites. After we trapped all 24 sites for 10 days, we repeated the cycle for a second trapping session. Days between the end of the first trapping session and the start of the second trapping session for a given site ranged 10–50 days ($\bar{x}$ = 35 days).

We conducted all capture and handling methods as outlined in Beasley et al. (2012) and Beatty et al. (2014). We checked traps immediately preceding sunrise to minimize the time that animals spent in traps. Following capture, we injected Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA) intramuscularly at a dosage of 5 mg/kg of estimated body mass to immobilize opossums (Gamble 2004, Kreeger and Arnemo 2018). We recorded morphological data of each unique individual and collected blood (3 cc), whiskers, hair, ticks, and tissue from the ear. We collected blood from opossums using venipuncture of the caudal vein (Williams-Newkirk et al. 2013). We attached matching numerical ear tags (Monel 3; National Band and Tag Company, Newport, KY, USA) to both ears. We collared a subset of adult male and female opossums stratified by land cover type with global positioning system (GPS) telemetry data logging collars (W500-NA, 85 g; Advanced Telemetry Systems, Isanti, MN, USA). We fitted only opossums that were ≥1.7 kg with GPS-collars to ensure the collar mass was <5% of animal mass (Mech and Barber 2002) and we checked fit to minimize chafing.

Spatial capture-recapture density estimation

We directly estimated and compared opossum densities using 9 multi-session spatial capture-recapture (SCR) models (Table 1; Borchers and Efford 2008, Royle and Young 2008, Efford et al. 2009) within the package oSCR (Sutherland et al. 2019) in program R (R Core Team 2020). We randomly subsampled GPS telemetry locations

TABLE 1 Akaike's Information Criterion (AIC) rankings for Virginia opossum spatial capture-recapture models, Savannah River Site, Aiken, South Carolina, USA, 2017–2019. We modeled population density (*D*), individual trap probability of capture (*p*), and spatial scale of detection (σ) using covariates for land cover type (cover), intercept model (1), sex, trap effect (b), and year (yr). Results include Akaike's Information Criterion scores (AIC), relative AIC scores (ΔAIC), number of model parameters (*K*), model weights (w_i), and log-likelihoods (logL).

Model	AIC	ΔAIC	*K*	w_i	logL
D(~cover) *p*(~sex) σ(~sex)	6,929	0.0	9	0.97	3,455
D(~cover) *p*(~1) σ(~sex)	6,936	6.7	8	0.03	3,460
D(~1) *p*(~sex) σ(~sex)	6,946	17.0	6	<0.01	3,467
D(~cover) *p*(~sex) σ(~1)	6,990	61.0	8	<0.01	3,487
D(~cover) *p*(~1) σ(~1)	6,991	62.0	7	<0.01	3,489
D(~cover) *p*(~b) σ(~1)	6,993	64.0	8	<0.01	3,488
D(~cover + yr) *p*(~1) σ(~1)	6,993	64.0	9	<0.01	3,487
D(~1) *p*(~1) σ(~1)	7,008	79.0	4	<0.01	3,500
D(~yr) *p*(~1) σ(~1)	7,009	81.0	6	<0.01	3,499

recorded during trapping sessions without replacement using 1 point/individual/day to match trapping effort and integrated locations into the models for detection probability and space use (Linden et al. 2018).

Modeled SCR sessions within oSCR consisted of the pooled capture histories and telemetry data within each land cover type during a single trapping session. There were 24 modeled sessions during the 3 years of this study (2 trapping sessions in each of the 4 land cover types during 3 years). We used this *post hoc* structuring of model sessions to estimate the effects of land cover type on opossum density given the low numbers of captures in several sites. Pooling capture histories and telemetry data allowed sites with no captures over a given trapping session to be incorporated into models because there is currently no framework within oSCR to include independent sessions without captures (Sutherland et al. 2019). The inclusion of site capture histories without captures is important because it allows the capture process from all sites of the same land cover type to be used to assess the probability of having no captures, and to be considered during density estimation (Royle et al. 2014).

Following the protocol of Sutherland et al. (2019), we defined the model state-space of each session by a 3σ buffer = 740 m around each trapping site with a spatial resolution of 100 × 100-m pixels, where σ is the SCR model parameter that describes the space use and the relationship between detection location and home range centers of individuals. We selected the model buffer to accommodate individual movements in the sampled population and derived the buffer from the average home range size of opossums concurrently tracked using GPS telemetry (Linden et al. 2018). We calculated home ranges using a reference bandwidth kernel density estimator (95% KDE, href; Worton 1995) within the R package adehabitatHR (Calenge 2006). We selected the model spatial resolution of 100 × 100-m pixels to be <0.5σ, which allows for distinguishable space use within home ranges and optimized computational run time, and accounts for inaccuracy of the GPS units ($\bar{x}$ = 10.8 ± 0.7 [SE] m; Royle et al. 2014, Linden et al. 2018).

We tested for the effects of modeled session, land cover type, and study year on estimated density. We also tested for the effects of sex and land cover type on estimated space use (σ) and individual trap detection probability (p_0). We included a null model and tested for trap-specific response to capture affecting recapture. We then predicted response-scale density estimates for the top-ranked model with the lowest Akaike's Information Criterion (AIC) score (Burnham and Anderson 2002).

Opossum abundance index

We used the number of unique opossums caught during a 10-day period from the first opening of traps at a given site as the dependent variable in a generalized linear mixed effects model with a Poisson error distribution as implemented in the R package lme4 (Bates et al. 2015). We included land cover type as an independent variable in this model, with year, site, and trapping session as random effects. We then predicted least square means within the R package emmeans (Lenth et al. 2018) by land cover type and standardized by the global mean, resulting in opossum abundance index (OAI) values for each land cover type.

We compared the predictive capability of the OAI to oSCR-modeled density regarding relative effects of land cover type. For this comparison we used a linear model within the R package stats (R Core Team 2020) in which the 4 standardized predicted oSCR land cover type densities were plotted against the 4 OAI predicted estimates. We tested the congruence in predictions made by the 2 methods by regressing the 2 predictions against each other and assessing the adjusted R^2 value of the linear model (Sewall 1921, Draper and Smith 1998).

RESULTS

Capture and recapture rates of opossums were low across all 3 years of the study. We caught 186 individual opossums, which we recaptured 55 times during 36,000 trap-nights of effort (148.76 trap-nights/opossum capture event). Combined capture events remained consistent throughout the study, with 78 captures during

TABLE 2 The mean number of unique captures and recaptures of Virginia opossum by land cover type on the Savannah River Site, Aiken, South Carolina, USA, 2017–2019. Mean values are averaged across year and trapping session.

	Unique captures			Recapture events		
Site land cover type	$\bar{x}$	**SD**	***n***	$\bar{x}$	**SD**	***n***
Bottomland swamp						
Female	7.7	6.4	23	1.0	0.0	2
Male	14.0	4.2	41	2.0	1.4	4
Riparian hardwood						
Female	7.3	0.6	22	5.3	3.8	16
Male	13.0	2.0	39	4.0	0.0	12
Upland pine						
Female	3.0	2.0	9	3.0	NA[a]	3
Male	8.3	2.1	25	2.3	1.5	7
Isolated wetland						
Female	3.0	0.0	6	1.5	0.7	3
Male	7.0	1.0	21	2.7	0.6	8

[a]Not estimable because recaptures occurred within the same session.

2017 (60 unique captures, 18 recaptures), 83 captures during 2018 (72 unique captures, 11 recaptures), and 80 captures during 2019 (54 unique captures, 26 recaptures). Only 4 opossums were captured between any 2 consecutive years with no individuals being captured in all 3 years of the study. Bottomland swamp and riparian hardwood had the highest number of unique individuals captured and recaptured per year, while upland pine and isolated wetland had the fewest (Table 2). There was a male bias in captures in all land cover types across all years, which was most pronounced in upland pine (9 females, 25 males) and isolated wetlands (6 females, 20 males). This bias was less pronounced in bottomland swamp (23 females, 41 males) and riparian hardwood (22 females, 39 males).

We tracked 37 unique individuals using GPS telemetry during 2018 and 2019. There were more collared opossums in bottomland swamp (10 opossums) and riparian hardwood (11 opossums) compared to isolated wetland (9 opossums) and upland pine (7 opossums). Because modeled SCR detection probability and space use were ultimately pooled across land cover type and year, this imbalance in land cover type representation did not affect density modeling. Subsampled telemetry locations during trapping sessions accounted for 271 relocation events within 16 of 24 modeled sessions. Within each trapping session, we recorded an average of 5.52 ± 2.87 locations/collared individual (Table S1, available in Supporting Information). Home ranges of collared opossums tracked during trapping seasons had an average area of 1.17 km^2 (95% KDE, href).

Spatial capture-recapture density

We analyzed 10 SCR models to describe the variation in capture histories among sessions. Out of the 10 models, we considered only 9 as candidates (Table 1) because a model using the spatial scale parameter as a function of land cover type failed to converge. No competing models were within 2 AIC of the most

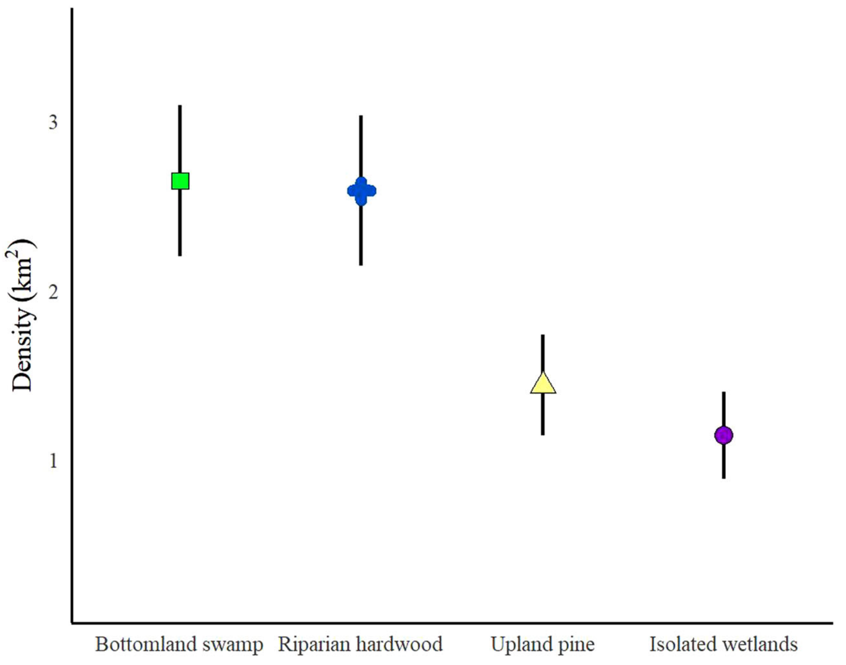

FIGURE 2 Predicted spatial capture-recapture density estimates of Virginia opossums with respective standard errors by land cover type. Spatial capture-recapture models used data collected on the Savannah River Site, Aiken, South Carolina, USA, 2017–2019.

parsimonious model. The top model, which had an AIC weight of 0.97, had land cover type as a predictor of opossum density and sex as a predictor of probability of capture and the spatial scale parameter. The next highest ranked model included land cover type as a predictor of density and sex as a predictor of the spatial scale parameter and had an AIC weight of 0.03 (Table 1).

Parameter estimates of the top model indicated opossum density differed among land cover types. Compared to bottomland swamp ($\text{Intercept}_{\log} = -4.2$, SE = 0.24, $P < 0.001$), both upland pine ($\beta_{\text{Upland log}} = -0.61$, SE = 0.18, $P = 0.004$) and isolated wetland ($\beta_{\text{Wetland log}} = -0.84$, SE = 0.23, $P < 0.001$) had lower density beta coefficients. While the density coefficient for riparian hardwood ($\beta_{\text{Riparian log}} = -0.02$, SE = 0.18, $P = 0.90$) was lower than bottomland swamp, it was not significant in the model. Estimated densities (*D*) of opossums were highest in bottomland swamp ($D = 2.65$ opossums/km^2 ± 0.45 [SE]) and riparian hardwoods ($D = 2.59$ opossums/km^2 ± 0.44), whereas upland pine ($D = 1.44$ opossums/km^2 ± 0.30) and isolated wetlands ($D = 1.14$ opossums/km^2 ± 0.26) had the lowest estimated densities (Figure 2). Globally, the ψ model parameter, which measures the probability that an encountered individual is male, was not significantly different from zero ($\psi_{\log} = 0.20 \pm 0.27$, $P = 0.47$), indicating that the ratio of male to female opossums was equal.

Daily estimated probability of detection per individual trap within a given opossum's activity center (p_0) was generally low for males ($p_0 = 0.014$) and females ($p_0 = 0.006$). The spatial scale parameter (σ), which describes the mean home range use of detected opossums, was 343.02 ± 14.15 m (σ ± SE) for male opossums and 200.53 ± 9.49 m for female opossums. Across all models, a limited number of recapture events within each land cover type prevented us from estimating σ by land cover type. Instead we used σ estimates globally for all land cover types, model sessions, and years (Royle et al. 2014).

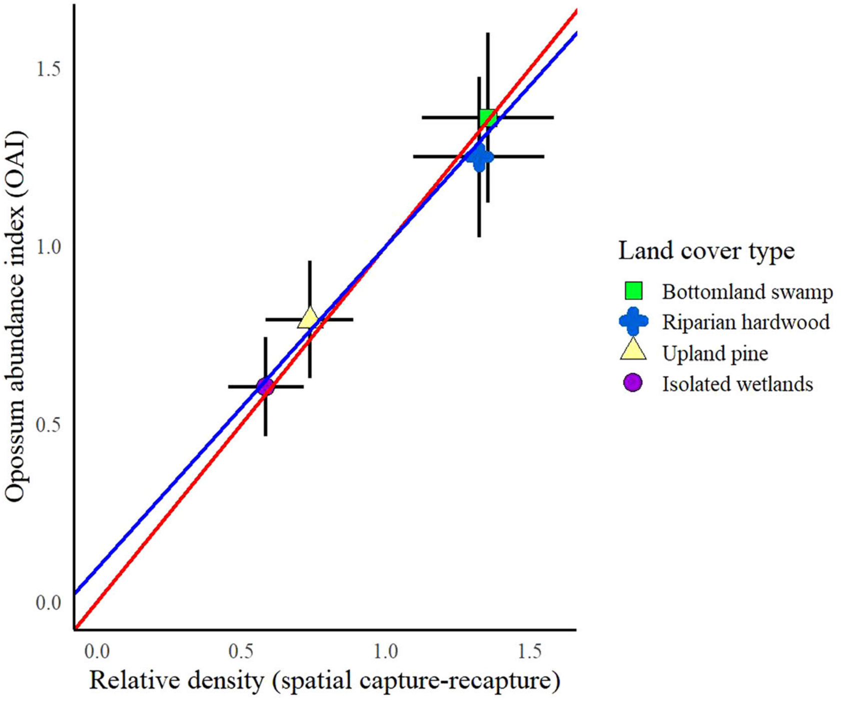

FIGURE 3 A comparison of the relative effects of land cover type on density and indexed abundance of Virginia opossums with respective standardized standard errors, Savannah River Site, Aiken, South Carolina, USA, 2017–2019. We derived standardized density estimates from a spatial capture-recapture model and relative abundance index values from log-likelihood means of generalized linear mixed-effects models.

Opossum abundance index

Indices of abundance followed similar trends to those modeled using SCR. Compared to bottomland swamp ($\text{Intercept}_{\text{log}}$ = 1.2, SE = 0.18, $P < 0.001$), both upland pine ($\beta_{\text{Upland}} = -0.54 \pm 0.27$, $P = 0.048$) and isolated wetlands ($\beta_{\text{Wetland}} = -0.81 \pm 0.29$, $P = 0.005$) had lower relative abundance coefficients. While the coefficient of riparian hardwood ($\beta_{\text{Riparian}} = -0.09 \pm 0.25$, $P = 0.74$) was lower than bottomland swamp, they were not significantly different from one another ($P = 0.737$). Estimated OAI values were highest in sites designated as bottomland swamp (1.4 ± 0.24 [OAI ± SE]) and riparian hardwood (1.3 ± 0.23), and lowest in upland pine (0.79 ± 0.17) and isolated wetlands (0.60 ± 0.14).

Comparison of both population estimation techniques revealed that OAI was nearly as effective as oSCR at predicting the relative effects of the 4 *a priori* designated land cover types on opossum density ($R^2 = 0.98$). Both models predicted the highest densities in bottomland swamp and riparian hardwoods and the lowest densities in upland pine stands and isolated wetlands (Figure 3).

DISCUSSION

We used a spatial capture-recapture study design to model the influence of land cover type on spatiotemporal patterns of opossum density. As expected, we found bottomland swamp and riparian hardwood forests had the highest predicted density of opossums, and that upland pine had significantly lower predicted densities

(Weckerly et al. 1987, Gardner and Sunquist 2003, Kaiser 2017). Contrary to our expectation, isolated wetland sites did not support higher densities of opossums than pine-dominated sites. Considerable variability in opossum densities may exist because of spatial heterogeneity in habitat composition within a given study area. For example, opossums in Chicago, Illinois, USA, were associated with natural water sources in urban areas with high human density, but not in suburban areas with low human density. This suggests that suburban landscapes may contain abundant sources of water associated with human presence, and opossums may not be selecting for landscape-scale water features (Fidino et al. 2016). Similarly, Beatty (2012) and Beatty et al. (2016) reported that fragmented forest patches, within a matrix of intensively managed agricultural land, harbored higher densities of opossums comparable to intact forested landscapes.

Whereas Potkay (1970), Beatty et al. (2016), and Fidino et al. (2016) addressed heterogeneity in opossum densities in fragmented agricultural landscapes and urbanized cities, respectively, the synthesis of these studies suggests that isolated wetlands of the eastern United States may similarly act as high-density population islands for opossums within a matrix of less suitable habitat. In the southeastern United States, isolated wetlands (e.g., Carolina bays; Sharitz 2003) are of particular interest to understanding the population dynamics of this species because they occur separate from the ground water system and often are surrounded by planted pine. It is likely that population density patterns revealed by this study are primarily the product of the scale of resource utilization by opossums as demonstrated by the relatively large home ranges and preferential selection of resources at the second-order (landscape) selection scale (Johnson 1980) as opposed to third-order (home range) selection (Bernasconi 2020). Similar to the sympatric raccoon, which selects for resources primarily at the second order, opossums are likely optimizing the location of home ranges on the landscape and can thus use a greater portion of their respective home range (Beasley et al. 2007).

At the landscape scale of resource selection, isolated wetlands and upland pines are likely functionally similar to opossums. Hennessy et al. (2015) and Beatty et al. (2016) suggested that opossum densities reflect the effects of landscape at a broader scale than is typically sampled and thus local features alone will not be predictive of opossum population parameters. Additionally, isolated wetlands are highly susceptible to variable water periodicity, which can limit amphibian abundance (Snodgrass et al. 2000), a major nutritional source for opossums (Gardner and Sunquist 2003). Depending on the timing of precipitation and resulting amphibian breeding events, it is also possible that this study did not capture the full extent of opossum population dynamics, which often match the phenology of their primary food resources. Research is needed to resolve the effects of wetland size and water periodicity on the densities of local opossum populations they can support.

Our density estimates were lower when compared to opossum densities from other studies. Our trapping seasons coincided with the opossum breeding season, a period that typically corresponds with the highest abundances of opossums on the landscape (Gardner and Sunquist 2003). Opossum density estimates from our study ranged between 1.14 opossums/km^2 in isolated wetlands and 2.65 opossums/km^2 in bottomland swamps. Averaged across studies that used mark-recapture to derive density estimates in non-urban settings, adult opossum populations have a mean density of 7.08 opossums/km^2 ± 5.84 (SD; Gardner and Sunquist 2003, Beatty et al. 2016, Kaiser 2017). Similar to this study, Weckerly et al. (1987) directly compared densities between pine-predominant and riparian hardwood forests in Tennessee, USA, and reported that pine forests (0.9 opossums/km^2) supported substantially lower densities of opossums than riparian hardwood forests (8.40 opossums/km^2). Tsai (2017) used SCR to estimate densities of opossums and reported densities that were much higher (15.0 ± 12.5 opossums/km^2) than those recorded in this study. These differences likely reflect differences in habitat composition and food availability between sites because Tsai (2017) examined opossum densities in a fragmented agricultural setting near major roads in Indiana, USA. Agricultural developments, and the denning resources and predictable food sources they provide, support artificially higher abundances of opossums compared to more forested landscapes (Gardner and Sunquist 2003, Kanda et al. 2009, Beatty et al. 2016). Conversely, the landscape around trapping sites in this study were largely undeveloped, devoid of agricultural food resources, and far from paved roads. Such conditions are common throughout the southeastern United States within large privately owned parcels (Turner et al. 1996, Butler and Leatherberry 2004), public lands, and high security federal lands (Butler and Wear 2013, Vincent et al. 2020).

Daily detection probability for individual traps (p_0) was low in this study. It is likely that p_0 could have been reduced because of multiple factors including the narrow trap spacing, which was roughly a third of the model-estimated spatial scale of space use (σ), and the large number of total occasions per individual trap used in the entirety of the study (Royle et al. 2014, Sun et al. 2014). Using live trapping of opossums, Tsai (2017) predicted p_0 values of 0.01–0.03 while trapping within isolated forest woodlots in a patchy agricultural landscape. In this type of landscape, opossums may concentrate their activity centers within study site grids, increasing the probability of detection compared to our study, which took place in a landscape with greater forest continuity between preferred habitats.

Models that used land cover type as a predictor of the spatial scale parameter (σ) did not converge, probably because of the low number of recapture events within land cover types. Despite this limitation, the global σ estimates are representative for male and female opossums on the SRS, effectively averaging the effects of all the surveyed land cover types (Royle et al. 2014). The global σ estimates that we estimated were larger than the one derived from GPS telemetry home ranges. Larger-than-expected back-transformed σ estimates were similarly described by Burgar et al. (2018) when faced with low recapture and detection rates of fisher (*Pekania pennanti*) within their genetic SCR study. It is also possible the relatively small sampling area relative to home range size inflated estimates of σ (Sollmann et al. 2012). Both SCR-modeled and telemetry-derived σ were larger than those derived by Tsai (2017), who separately estimated male and female opossum σ at 0.16 km and 0.13 km, respectively. This suggests that in a landscape with greater forest continuity, opossums are using more of the landscape than opossums in fragmented agricultural ecosystems.

Population indices have been used in the past to estimate relative abundance of opossums (Bartelt et al. 2001, Gehrt et al. 2006, Kanda et al. 2006). Our results suggest that relative density of opossums can be accurately assessed in undeveloped landscapes using the unique number of individual opossums alone. If this is the case, noninvasive methods that can identify unique individuals (e.g., genetics-based sampling of hair or feces) could be a cost-effective method of estimating relative densities of opossums provided one has access to scat-detection dogs and appropriate genetic equipment (Orkin et al. 2016, Davis et al. 2020, Woodruff et al. 2020). It is unclear, however, to what degree these comparative results are density dependent, given SCR-modeled densities in this study did not fluctuate greatly between land cover types and remained relatively low compared to other opossum density studies. It is possible that at higher population densities the relationship between modeled SCR density estimates and OAI values become inconsistent. As a result, further investigation is needed to test if this method can be implemented in developed landscapes, which can often support artificially high opossum densities (Rodewald and Gehrt 2014).

MANAGEMENT IMPLICATIONS

In undeveloped portions of the southeastern United States, densities of Virginia opossums are likely lower than previously estimated. The densities of opossums are highest in landscapes with permanent water such as bottomland swamp and riparian hardwood forest and lowest in upland pine stands. Isolated wetlands within pine stands are not important influences on opossum density, particularly within landscapes containing easily available permanent water sources and thus should not be considered an important habitat feature when making management decisions. As an additional benefit to management of the species, using the unique number of individual opossums captured appears to be effective at estimating relative densities of opossums when compared to more labor-intensive SCR models.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animal handling protocol were authorized under state collecting permit SC-08-2019 and followed the American Society of Mammalogists guidelines (Sikes 2016). Trapping and handling were conducted in accordance with the University of Georgia Animal Care and Use Guidelines under Animal Care and Use Protocol A2018 06-024-A12.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.14974737, reference number 14974737.

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