Habitat-specific seasonal densities of sympatric raccoons and opossums in the southeastern United States

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Abstract

Raccoon and opossum densities have implications for rabies management, but estimates of seasonal densities of both species are lacking for rural non-agricultural habitats of the Southeastern United States, a core portion of their geographic range. Consequently, it remains unclear whether the densities of 1 species limit the other, which is possible considering their substantial niche overlap. We carried out a mark-recapture study of raccoons and opossums in 4 rural non-agricultural habitats (bottomland hardwood forest, riparian forest, upland pine forest, and isolated wetlands) in South Carolina, USA (2020-2022), and combined this with previous data from the same habitats (2017-2019) to estimate habitat-specific spring and fall densities. Raccoon densities ranged from 5.17 ± 0.96 animals/km^2 (bottomland hardwood fall) to 1.63 ± 0.83 animals/km^2 (upland pine spring) and were on average 19% higher in fall compared to spring. Opossum densities ranged from 10.35 ± 1.98 animals/km^2 (bottomland hardwood fall) to 1.11 ± 1.55 animals/km^2 (upland pine spring) with divergent seasonal patterns among habitats. These low densities across all habitats compared to other studies are likely the result of low resource availability, consistent with other habitats that have minimal anthropogenic influence. We observed a positive association between raccoon and opossum densities across trapping grids, suggesting that raccoons do not suppress opossum densities, but that densities of both species increase with increasing resource availability. Our results can be used to inform oral rabies vaccination efforts such as refining bait densities and timing of bait distribution in these habitats.

Key words: demography, *Didelphis virginiana,* human-wildlife conflict, mark-recapture, mesocarnivore, oral rabies vaccination, population density, *Procyon lotor*

Teaser text: Raccoon and Opossum densities in the Southeast were relatively low but positively correlated. Densities were highest in habitats with highest presumed resource availability.

Densidades estacionales específicas del hábitat de mapaches y zarigüeyas simpátricos en el sureste de los Estados Unidos

Resumen

Las densidades de mapaches y zarigüeyas tienen implicaciones para el manejo de la rabia, pero faltan densidades estacionales de ambas especies para los hábitats rurales no agrícolas del sureste de los Estados Unidos, una parte central de su área de distribución geográfica. En consecuencia, sigue sin estar claro si las densidades de una especie limitan a la otra, lo que es posible considerando su importante superposición de nichos. Llevamos a cabo un estudio de captura y recaptura de mapaches y zarigüeyas en cuatro hábitats rurales no agrícolas (bosque de frondosas de tierras bajas, bosque ripario, bosque de pinos de tierras altas y humedales aislados) en Carolina del Sur, EE. UU. (2020-2022), y lo combinamos con datos anteriores de los mismos hábitats (2017-2019) para estimar las densidades de primavera y otoño específicas del hábitat. Las densidades de mapaches variaron de 5,17 ± 0,96 animales/km2 (otoño de árboles frondosos de tierras bajas) a 1,63 ± 0,83 animales/km2 (primavera de pinos de tierras altas) y fueron en promedio un 19 % más altas en otoño en comparación con la primavera. Las densidades de zarigüeyas variaron de 10,35 ± 1,98 animales/km2 (otoño de árboles frondosos de tierras bajas) a 1,11 ± 1,55 animales/km2 (primavera de pinos de tierras altas) con patrones estacionales divergentes entre hábitats. Estas bajas densidades en todos los hábitats en comparación con otros estudios probablemente sean el resultado de la baja disponibilidad de recursos, en consonancia con otros hábitats que tienen una influencia antropogénica mínima. Observamos una asociación positiva entre las densidades de mapaches y zarigüeyas en las cuadrículas de trampas, lo que sugiere que los mapaches no suprimen las densidades de zarigüeyas, sino que las densidades de ambas especies aumentan con el aumento de la disponibilidad de recursos. Nuestros resultados pueden utilizarse para fundamentar los esfuerzos de vacunación oral contra la rabia, como por ejemplo, para refinar las densidades de cebo y el momento de su distribución en estos hábitats.

Palabras clave: captura y recaptura, conflicto entre humanos y vida silvestre, densidad de población, demografía, *Didelphis virginiana*, mesocarnívoro, *Procyon lotor*, vacunación oral contra la rabia

The Northern Raccoon (*Proyon lotor*) and Virginia Opossum (*Didelphis virginiana*) are generalist mesomammals that overlap extensively in range and thus are often presumed to compete for resources (Kissell Jr and Kennedy 1992; Ginger et al. 2003). As the larger and generally more aggressive species, raccoons are hypothesized to limit the abundance of opossums (Ginger et al. 2003; Troyer et al. 2014). While some studies have suggested a suppressive effect of raccoons on opossum density (Ginger et al. 2003), other studies reported equivocal evidence (Kissell Jr and Kennedy 1992; Kasparian et al. 2002; Kasparian et al. 2004). However, resource availability is known to affect population density of both species, particularly in more natural rural areas where anthropogenic subsidies are less abundant (Leberg and Kennedy 1988). Despite the extensive overlap in geographic distribution and competition potential, there are very few studies that have directly compared the densities of sympatric raccoon and opossum populations (Smyser et al. 2010).

Raccoon densities have important implications for wildlife management because raccoons are a reservoir species for rabies virus in eastern North America (Elmore et al. 2017; Slate et al. 2020). The primary strategy for landscape-level rabies management is oral rabies vaccination (ORV), which consists of landscape level preventive vaccination of wildlife against rabies virus via the coordinated deployment of vaccine-laden baits (Slate et al. 2005; Elmore et al. 2017). The unit cost of bait is the largest factor driving the cost of ORV programs (Slate et al. 2005; Slate et al. 2020), making the appropriate bait densities—which are determined by raccoon densities—an essential component of effective ORV campaigns.

Raccoon densities may fluctuate seasonally due to factors such as changes in movement patterns or demography (Beasley et al. 2007; Troyer et al. 2014). Baiting campaigns are typically carried out in the fall to maximize bait uptake because juvenile raccoons have begun foraging independently during this time (McClure et al. 2020; Schreiner et al. 2020). However, there are few studies of seasonal variation in raccoon densities and there may be an advantage to spring baiting where spring raccoon densities are higher because more raccoons may be targeted by ORV efforts. Survival rates of raccoons are pertinent as well because more rapid population turnover may require greater baiting intensity to achieve target immunity rates.

Opossum densities also have relevance for rabies management because opossums may be the primary competitor of raccoons for ORV baits across much of North America (Smyser et al. 2010; Slate et al. 2020). If raccoon densities have a suppressive effect on opossum densities, the abundance of opossums may increase in areas with lower raccoon densities. Thus, the potential for using lower vaccine bait densities at lower raccoon densities may be negated by the greater non-target consumption of vaccine baits by opossums. Understanding the relationship between population densities for both target and nontarget species across various habitats is, therefore, important for the development and refinement of ORV plans.

Despite the recognized role of raccoon and opossum densities on ORV management, many habitats in major portions of the ORV management zone are understudied regarding seasonal densities of both species, including rural non-agricultural habitats of the Southeastern United States (hereafter Southeast). In urban and agricultural areas, anthropogenic food and denning habitat tend to produce elevated raccoon densities often ranging between 50 and 100 animals/km^2 (Šálek et al. 2015). Opossum densities are also presumed to be higher in urban areas (Hansen et al. 2020), though robust urban opossum density estimates are lacking. By contrast, densities of both species were comparatively low in areas with less human influence. In rural habitats, raccoon densities generally range between 1-20 individuals/km^2 and opossum densities between 1-7 animals/km^2 (Gehrt et al. 1997; Gardner and Sunquist 2003; Šálek et al. 2015; McTigue and DeGregorio 2023).

The abundance and distribution of key resources for raccoons and opossums—mainly water, food, and denning habitat—vary between rural non-agricultural habitats in the Southeast, which in turn results in differing densities of both species (Leberg and Kennedy 1988; Kissell Jr and Kennedy 1992). Bottomland hardwood and riparian forests, for example, are likely to support higher densities because they have permanent water sources that provide foraging opportunities and often contain larger diameter trees for denning (Leberg and Kennedy 1988; Owen et al. 2015), which has been linked to increased abundance and fecundity of raccoons (Beasley et al. 2011). Managed pine forests often have lower densities of both species because there are typically fewer large diameter trees, less favored food resources, and often these habitats do not contain substantial water sources (Leberg and Kennedy 1988; Chamberlain et al. 2003; Byrne and Chamberlain 2011). At isolated wetlands surrounded by pine forests, densities are likely intermediate because the wetland would provide food and water, but the surrounding habitat would offer fewer foraging opportunities (Hill et al. 2023b).

Recent studies have examined the densities of raccoons and opossums in 4 habitats (bottomland hardwood forest, riparian forest, upland pine forest, and isolated wetlands) in South Carolina, USA, during spring based on 3 years (2017-2019) of mark-recapture data (Bernasconi et al. 2022; Hill et al. 2023a). However, density estimates for fall, the season when ORV baiting typically occurs, are currently lacking. There is also a limited understanding of the relationship between densities of both species seasonally in these habitats.

We expanded on previous studies by carrying out a mark-recapture study of raccoons and opossums to estimate seasonal densities of both species, adding new data for 2 fall seasons and for 3 spring seasons during 2020-2022. We tested the hypothesis that variation in raccoon and opossum densities is influenced by competition, habitat, and season. We predicted that opossum densities would be inversely related to raccoon densities due to interspecific competition. We predicted that densities of both species would be lowest in upland pine habitat due to lower resource availability. We also predicted higher densities of both species in fall due to juvenile dispersal. Additionally, we examined survival and age ratio across habitats and seasons due to their relevance for disease management.

Materials and methods

Study site.

We conducted this study from 2020-2022 on the Savannah River Site (SRS), a 780 km^2 site owned by the United States Department of Energy in the upper Coastal Plain region of South Carolina, USA (33°19'N, 81°42'W; Fig. 1). The SRS was established in the 1950s as a nuclear production facility and operations today consist of facilities for nuclear materials processing, tritium extraction, and waste disposal (White and Gaines 2000). Much of the SRS has been managed for timber harvest since 1951—originally Slash Pine (*Pinus elliottii*) and subsequently Loblolly Pine (*P. taeda*) and Longleaf Pine (*P. palustris*)—and pine plantations were harvested on a rotating basis and subject to management practices such as thinning and prescribed burning (White and Gaines 2000). The SRS was mostly covered by the land cover types evergreen forest (54%) and woody wetlands (24%), with other land cover types (e.g., open water, mixed forest, developed) collectively comprising 22% of the land area as classified by the National Land Cover Database (NLCD; (Yang et al. 2018). The average elevation on the site is 200 m above sea level and annual rainfall averaged 120 cm during the study. The climate is subtropical with spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb) temperatures averaging 17°C, 26°C, 18°C, and 9°C, respectively.

We estimated raccoon and opossum densities across 4 prominent habitats on the SRS: upland pine forest, isolated wetland, bottomland hardwood forest, and riparian forest. Upland pine forest (hereafter pine) was characterized by mature stands of Loblolly Pine and Longleaf Pine with land cover classified as evergreen by the NLCD. Isolated wetlands (hereafter wetlands) were natural shallow ovoid or elliptical-shaped depressions that form ephemerally and were usually surrounded by evergreen or mixed forest NLCD classes (White and Gaines 2000). There were 195 such wetlands across the site ranging in size from 0.1–50 ha (White and Gaines 2000). Bottomland hardwood forests (hereafter bottomland) were classified as woody wetlands by the NLCD and were confined to the lower southwest portion of the site along the Savannah River and consist of seasonally flooded cypress-tupelo forests (*Taxodium distichum*-*Nyssa aquatica*), with oak (*Quercus* spp.) and hickory (*Carya* spp.) scattered throughout (White and Gaines 2000). Riparian forest (hereafter riparian) was also classified as woody wetlands, but bottomland is largely 1 contiguous habitat on the SRS. In contrast, riparian was embedded in a matrix of upland habitat such as pine and hardwoods, existing in relatively narrow corridors along smaller rivers and creeks that fed into the Savannah River. This habitat is commonly produced by land conversion where native vegetation along waterways is left intact, resulting in the formation of a riparian zone. Our riparian habitats were located along the upper portions of Tinker Creek and the Upper Three Runs Creek, both of which were relatively undisturbed and never received thermal effluent from nuclear reactors (Thomas IV et al. 2020). Woody wetland land cover on our riparian sites typically spanned about 400 m on either side of the focal water body. The mean distance of grids in each habitat to nearest permanent body of water was 1,273 m in upland pine, 545 m in isolated wetlands, 180 in riparian, and 129 m in bottomlands.

Experimental design.

Animal trapping and handling followed American Society of Mammalogist guidelines (Sikes et al. 2016) and was conducted in accordance with the University of Georgia Animal Care and Use Guidelines under Animal Care and Use Protocol A208 06-024-A12. Field activities were approved by the Site Use Program of the Savannah River Site under Site Use Permit SU-20-42-R. We continued the field methodology described in (Bernasconi et al. 2022) and (Hill et al. 2023b). In each of the 4 habitats, we established 6 trapping grids separated by at least 5 km to maintain spatial independence. At each grid, we placed 25 Tomahawk® model 108SS live-capture box traps (Hazelhurst, WI) at intervals of 100 m in a 5 x 5 square configuration. Whole kernel corn was placed on the ground adjacent to the trap and plaster tabs soaked in fish oil were placed inside the traps as a lure (Webster and Beasley 2019). We replaced the tabs after capture events and halfway through the trapping sessions. Corn was replaced as needed on daily checks of traps.

Each trapping season, the 24 grids were divided into 3 groups of 8 that were randomized with respect to habitat type and trapped consecutively. Eight grids were trapped concurrently during 3 consecutive 10-day sessions and following a minimum of 14 days, they were trapped again in the same order. In previous studies, each of the 24 grids were trapped twice annually during the spring (January-May). Between the previous and current studies, 1 of the pine grids was clearcut and we therefore established a new pine grid. Thus, while 7 pine grids were trapped over the course of the study, only 6 were trapped in each season. For the current study, we split the 2 10-day trapping sessions for each grid between spring (February-March) and fall (October-December) seasons and continued this design until the end of trapping in Spring 2022. For consistency in trapping duration and timing across the dataset, we limited data from the previous studies (2017-2019) to the first 10-day session (January-March).

We immobilized all animals upon capture using intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA) at a dosage of 5 mg/kg of estimated body mass (Kreeger et al. 2002). At initial capture, we marked individual animals with a pair of matching uniquely coded ear tags (1 in each ear; Monel 3, National Band and Tag Company, Newport, KY, USA), then weighed, sexed, and aged individuals based on tooth eruption and wear (Grau et al. 1970).

Statistical analyses.

We combined data from the current study and the first spring sessions of previous work to produce 1 dataset for analysis that spanned 2017-2022, containing 6 spring seasons (2017-2022) and 2 fall seasons (2020-2021). We estimated raccoon and opossum abundance in each grid using the robust design Huggins model (Kendall 2012) with the package "RMark" (Laake 2013). The robust design produces estimates of apparent survival (S) by estimating true survival (i.e., animals not dying) and emigration rates (i.e., animals leaving the study area). The model divides the trapping period into primary and secondary trapping sessions. Primary periods are spaced out temporally such that the population is open, meaning births, deaths, and movement on or off the study area may occur (Kendall et al. 1997), whereas secondary sessions are assumed to be closed to births, deaths, immigration and emigration. We considered each year and season as a primary period and considered each day of trapping within these primary periods as the secondary periods, for a total of 8 primary periods each consisting of 10 secondary periods.

Using this design, we estimated the following population parameters: probability of capture (*p*); probability of recapture (*c*); probability of immigration (1-γ'); probability of emigration (γ"); apparent survival (*S*); and abundance (*N*; (Kendall et al. 1997). Many of our grids had very few captures which made it difficult to accurately estimate population parameters at the grid level. As such, we pooled mark-recapture data from all grids together to obtain robust parameter estimates and then applied these parameters to the mark-recapture data from each grid to estimate grid-specific abundances (White 2005; Beasley et al. 2012).

We chose different candidate model sets for both species by selecting only candidate models that could estimate all population parameters (e.g., opossum model with habitat-varying survival could not properly estimate survival in each habitat). We ranked candidate models by sample size corrected AICc and applied population parameters from the most-supported model (i.e., the model with the lowest AICc) to each of the grids to estimate grid-specific abundances of each sex for each trapping season. For raccoons, we modeled *S* as constant or a function of habitat, session, or sex (4 combinations). We modeled *p* as constant or a function of sex, habitat, session, or session and habitat (5 combinations). We modeled emigration as random (γ" and 1−γ' are time-dependent) or constant (γ" and 1−γ' = 1). Our models were similar for opossums, but without testing *S* as a function of habitat or random emigration. For both species, we set *p* equal to *c* due to sample size considerations. Thus, we compared 40 candidate models for raccoon abundance (4 x 5 x 2 = 40) and 15 candidate models for opossum abundance (3 x 5 x 1= 15). We included sex and habitat as a grouping variable for both species and specified the varying duration of intervals between primary periods.

We divided each of the estimated abundances by the relative effective trapping area of the respective sites to estimate site-specific densities. We calculated the effective trapping area by overlaying a buffer encompassing an area equal to home range size of an animal drawn around the centroid of each trapping grid (Beasley et al. 2012). We used the corresponding mean home range of the sex of the species in the appropriate habitat and season using data from Hill et al. (2023c) for raccoons and Hill et al. (2023a) for opossums (Supplementary Data SD1). We added the estimated male and female densities in each grid to derive a total density per species per season per grid and calculated pooled standard errors using a parametric bootstrap (Bolker 2008).

We assessed correlation between the mean raccoon and opossum density on each grid by calculating the Pearson correlation coefficient using the "cor.test" function in Program R version 4.0.4 (R Core Team 2022). We examined the role of habitat and season on densities of raccoons and opossums using a linear mixed model with the package "lme4" (Bates et al. 2015). Using a separate model for each species, our response variable was the estimated total density of animals (males and females combined) in each grid and the fixed effects were habitat (bottomland, pine, riparian, or wetland) and season (spring or fall). The random effects were year and grid nested in habitat. Secondly, we compared densities of both species as a function of habitat and season with the model structure above, with the addition of species as a fixed effect. Lastly, we compared the age ratio of each species using a generalized linear mixed model with logit link and binomial error distribution. Our response variable was whether the animal was a juvenile (≤ 1 yr old) or adult (> 1 yr old). We included season and habitat as fixed effects with year as a random effect.

We ranked the null and all possible model combinations based on sample-size corrected AIC (AICc), considering the model with lowest AICc to be the most-supported model (Burnham and Anderson 2002). For models with 3 fixed effects, we included the three-way interaction as well as all constituent two-way interactions. We assessed the relative support for the most-supported model by comparing models within 2 AICc units of the most-supported model. We used the odds ratio to test for pairwise comparisons between parameters in the most-supported model with a significance level of 0.05.

Results

Combined with the first spring trapping session of the previous studies, our complete dataset (2017-2022) consisted of 583 captures of 504 unique raccoons and 271 captures of 244 unique opossums. We documented the most unique captures of raccoons in bottomland (*n* = 181 unique individuals, 35.9%), followed by riparian (*n* = 114, 22.6%), pine (*n* = 109, 21.6%), and wetland (*n* = 100, 19.8%). Opossums were captured most frequently in bottomland (*n* = 109, 44.7%), followed by riparian (*n* = 61, 25.0%), wetland (*n* = 36, 14.8%), and pine (*n* = 38, 15.6%). Of the opossums, 221 (91.0%) were caught in a single trapping season, 19 (7.7%) were caught in 2 trapping seasons, and 4 (1.6%) were caught in 3 trapping seasons. Four hundred twenty-six raccoons were caught in a single season (85.4%), 62 were caught in 2 seasons (12.4%), and 11 were caught in 3 seasons (2.2%). The longest period between first and last capture for a raccoon was 5.1 years and for an opossum was 1.2 years.

The most-supported model for raccoon abundance included survival varying as a function of sex, random emigration, and capture probability as a function of both session and habitat (Supplementary Data SD2). Estimated survival was 0.858 ± 0.037 for females and 0.776 ± 0.031 for males. For opossums, the most-supported abundance model included constant survival (estimated survival = 0.476 ± 0.080) and capture probability varying as a function of session (Supplementary Data SD2).

There was a significant positive correlation between the mean raccoon and opossum density on each grid (*r* (23) = 0.677, $P < 0.001$; Fig. 2). Raccoon densities varied by habitat and season (Supplementary Data SD3; Fig. 3) and ranged from 5.17 ± 0.96 animals/km^2 (bottomland fall) to 1.63 ± 0.83 animals/km^2 (pine spring; Table 1). Raccoon densities were on average 19% higher in fall compared to spring and higher in bottomland compared to pine ($P = 0.06$), but no other pairwise habitat differences were significant. Opossum densities varied by habitat differently based on seasons (Supplementary Data SD3; Fig. 3) with densities ranging from 10.35 ± 1.98 animals/km^2 (bottomland fall) to 1.11 ± 1.55 animals/km^2 (pine spring; Table 1). During fall, opossum densities were higher in bottomlands than all other habitats, with no other significant pairwise differences. These patterns changed for some habitats during spring, with spring opossum densities greater in riparian compared to pine ($P = 0.03$) and no difference between riparian and bottomland ($P = 0.75$).

Across habitats, opossum densities were only higher than raccoon densities in bottomlands ($P <0.01$). Opossum densities overall were higher than raccoon densities in spring ($P <0.01$), with no difference during fall ($P =0.28$; Supplementary Data SD4). Adults comprised a greater proportion of our captured raccoons in spring compared to fall (estimated proportion of adults = 0.83 ± 0.08 and 0.63 ± 0.04, respectively; Supplementary Data SD5). The same pattern was also documented for opossums (estimated proportion of adults = 0.53 ± 0.05 in spring and 0.31 ± 0.06 in fall; Supplementary Data SD5).

Discussion

We found that rural non-agricultural habitats of the Southeast generally support relatively low densities of raccoons and opossums, consistent with other habitats that have minimal human influence (Leberg and Kennedy 1988; Šálek et al. 2015). In contrast to our predictions, raccoon and opossum densities were positively correlated. Densities of both species were comparatively high in habitats that have the highest presumed resource availability (bottomland and riparian). Raccoon and opossum densities across these habitats appear to be more influenced by resource availability than raccoon presence, which was also documented in Tennessee (Kissell Jr and Kennedy 1992) and Michigan (Stuewer 1943). These studies suggest that temporal or dietary niche partitioning prevents raccoons from suppressing opossum densities, despite considerable ecological overlap between the species (Ginger et al. 2003).

We found support for our prediction of lowest densities in upland pine. Densities in these habitats were ≤ 3 animals/km^2, among the lowest recorded for both species in the United States (Gehrt et al. 1997; Šálek et al. 2015; McTigue and DeGregorio 2023). Water is an important resource for raccoons and opossums (Leberg and Kennedy 1988; Gehrt et al. 1997) and upland pine grids were on average more than 1 km away from the nearest permanent water source. Timber harvest in pine forests also results in trees with smaller diameters that are less suitable for denning (Owen et al. 2015). Additionally, pine forests at the SRS are subject to management practices such as thinning and burning that can reduce the availability of understory vegetation, an important food source for both species (Chamberlain et al. 2002). The lower densities in pine are consistent with opossum avoidance of evergreen land cover at the SRS (Hill et al. 2023a).

By contrast, densities of both species tended to be highest in bottomland hardwoods. Leberg and Kennedy (1988) found the presence of water and large deciduous trees to be primary factors influencing raccoon densities in natural habitats of Tennessee. Similarly, in Indiana, Beasley et al. (2011) found that raccoon densities were positively associated with density of tree cavities. Both water and denning resources are abundant in bottomland habitat, likely contributing to the higher raccoon and opossum densities compared to pine and wetland. Large deciduous trees provide denning sites as well as food such as hard mast, an important resource for raccoons (Leberg and Kennedy 1988; Chamberlain et al. 2003). These habitats are also defined by presence of permanent water, providing both drinking water and food such as crustaceans and amphibians (Byrne and Chamberlain 2011). However, riparian densities were sometimes lower than bottomland densities and not distinguished from those in pine or wetland during some seasons. Whereas bottomland habitat is mostly contiguous, riparian habitat exists in relatively narrow patches within upland habitat. As a result, riparian animals likely move beyond the small riparian habitat patches to meet resource requirements, leading to densities that are sometimes lower than those in bottomlands (Hill et al. 2023c). Similarly, Algeo et al. (2017) suggested that the low resource availability in pine forests may extend to adjacent riparian areas resulting in lower riparian raccoon densities than expected.

Although raccoon densities were low in bottomland habitats compared to other studies, opossum densities were relatively high in bottomland hardwoods, especially during fall (Gehrt et al. 1997; McTigue and DeGregorio 2023). At the SRS, opossums consistently select for woody wetland land cover throughout the year (Hill et al. 2023a). In addition to abundant resources, the dense vegetation in bottomland hardwoods may offer protection from predators such as coyotes, which primarily select for early successional habitat on the SRS (Schrecengost et al. 2009). Furthermore, vehicle collisions are a major mortality source for opossums (Hill et al. 2019), but most of our bottomland trapping grids were more than 1.5 km from the nearest paved road and opossums were unlikely to encounter these roads based on their mean home range sizes (Hill et al. 2023a). This may also account for the higher opossum survival rates that we reported compared to other studies (Gipson and Kamler 2001; Kasparian et al. 2004). Bottomland hardwood habitat may offer a unique combination of abundant resources combined with lower mortality risk that produces higher opossum densities compared to many other habitats.

Similarly, raccoons had relatively high survival rates compared to other studies. In addition to minimal vehicle mortality, raccoons likely also benefit from the lack of harvest on our study site, which tends to be the primary raccoon mortality source where regulated harvest occurs (Mankin et al. 1999; Urbanek et al. 2009). The lower survival of male raccoons compared to females may result from increased mobility (Hill et al. 2023c), which is often correlated with greater mortality risk (Hasbrouck et al. 1992). Relatively high raccoon survival rates could be beneficial for ORV operations in these habitats because reduced population turnover may decrease the frequency and intensity of baiting required to achieve target immunity thresholds (Johnson et al. 2021).

In the Southeast, raccoons and opossums tend to breed during the spring with juveniles typically dispersing during fall (Gardner and Sunquist 2003), which is reflected in the higher ratios of juveniles in fall compared to spring for both species. This seasonal variation in age structure supports the timing of vaccination campaigns in the fall to target a greater number of juvenile raccoons (McClure et al. 2020). Vaccination of juveniles is important to population level rabies reduction because juveniles are highly mobile and variability in home range size is linked to a greater chance of disease transmission (McClure et al. 2020). Additionally, targeting a younger age class is beneficial because these animals likely have more years remaining in their lives, giving them a cumulatively greater lifetime chance of contracting and transmitting rabies. There were also no increases in density for raccoons during spring in any habitat, negating the potential to vaccinate more individuals during spring due to higher densities. In addition, opossum densities overall were higher than raccoon densities during spring, which could potentially lead to increased nontarget bait consumption during spring baiting.

We also found support for our prediction of higher raccoon densities in fall, whereas opossum densities varied by habitat seasonally. Opossums inhabiting the resource-poor pine forests may move into riparian forests to satisfy increased nutritional needs during spring, which coincides with the breeding season, resulting in greater riparian compared to pine densities in spring but not in fall. Additionally, juvenile survival is greater in weaning dens that are in habitat with more vegetative cover, so this pattern may be linked to female selection of more suitable weaning dens (Hossler et al. 1994). Indeed, opossums at the SRS show a greater selection preference for woody wetlands while avoiding evergreen cover during the breeding season compared to the non-breeding season (Hill et al. 2023a), and female opossums captured in spring in riparian are on average about 20% more likely to be carrying pouched young compared to those in pine or wetland (J. Hill,). Dispersal distance of juvenile opossums is typically larger than the width of our riparian zones (Doerr 2002). As a result, juvenile opossums born in riparian habitat are likely to leave the riparian habitat when they disperse, whereas those originating in bottomland are more likely to remain in the more expansive blocks of bottomland habitat. This difference may account for the opposite seasonal density patterns in these habitats and for the increased densities in bottomland compared to riparian densities during fall despite similar spring densities.

The raccoon densities we recorded can be used to inform ORV management in these habitats. Each year, 8-10 million ORV baits are cooperatively distributed in the United States, predominantly in rural areas, and a key decision in the implementation of ORV is the appropriate density of baits to distribute (Elmore et al. 2017). The National Rabies Management Program

(NRMP) uses a standard bait density of 75 baits/km^2 in rural areas, although higher bait densities (150 baits/km^2) may be required where raccoon densities are higher, particularly in urban settings (Slate et al. 2020; Bastille-Rousseau et al. 2024; Davis et al. 2024). Conversely, some studies have suggested that densities as low as 37 baits/km^2 may be adequate in areas where raccoon densities are low (Slate et al. 2020). Based on the low raccoon densities we recorded, such bait densities lower than the standard may be effective in rural non-agricultural habitats of the Southeast. The positive association between raccoon and opossum densities suggests minimal potential for greater ORV bait consumption by opossums as raccoon densities decline. This conclusion is supported by previous work in these habitats indicating minimal nontarget ORV bait consumption by opossums (Dixon et al. 2023; Helton et al. 2023; Hill et al. 2024). Additional bait uptake research in these habitats is needed to ensure that lower bait densities do not compromise the effectiveness of ORV campaigns in the Southeast.

Supplementary Data

Supplementary Data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Raccoon and opossum home ranges.

Supplementary Data SD2. Model comparisons for raccoon and opossum abundance estimates.

Supplementary Data SD3. Model comparisons for estimated raccoon and opossum densities.

Supplementary Data SD4. Model comparisons for estimated opossum and raccoon densities together

Supplementary Data SD5. Model comparisons for estimated proportions of adult and juvenile raccoons and opossums

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Conflict of Interest

None declared

Author contributions

All authors contributed to study design and conception. JEH and MLM performed data collection. JEH and GD performed analysis. JEH wrote the first draft of the manuscript and all authors commented on the drafts. The final manuscript was read and approved by all authors.

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Data availability

Data required to replicate these results available at https://github.com/jehill01/Raccoon-Opposum-Density

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Fig 1. Map showing locations of 25 grids where raccoons and opossums were trapped on the Savannah River Site, Aiken, South Carolina, USA (2017-2022) to estimate densities.

Fig 2. Correlation between mean raccoon and opossum densities on 25 trapping grids across 4 habitats at the Savannah River Site, Aiken, South Carolina, USA, 2017-2022. Each data point represents the overall densities at one trapping grid. Dotted lines represent the 95% confidence interval for regression line.

Fig 3. Estimated densities of raccoons and opossums in fall and spring across 4 habitats at the Savannah River Site, Aiken, South Carolina, USA, 2017-2022.

Table 1. Estimated densities of raccoons and opossums during spring and fall across four habitats at the Savannah River Site, Aiken SC (2017-2022).

Species	Habitat	Season	Estimated density (animals/km^2)	Standard Error
Raccoon	Bottomland	Fall	5.17	0.96
		Spring	4.32	0.84
	Upland Pine	Fall	2.48	0.94
		Spring	1.63	0.83
	Riparian	Fall	3.30	0.96
		Spring	2.44	0.84
	Wetland	Fall	2.73	0.96
		Spring	1.88	0.84
Opossum	Bottomland	Fall	10.35	1.98
		Spring	7.06	1.56
	Upland Pine	Fall	2.60	1.97
		Spring	1.11	1.55
	Riparian	Fall	2.58	1.98
		Spring	5.58	1.56
	Wetland	Fall	2.02	1.98
		Spring	1.78	1.56