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Home Range and Resource Selection of Virginia Opossums in the Rural Southeastern United States

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ORIGINAL PAPER

Home range and resource selection of Virginia opossums in the rural southeastern United States

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Abstract

The Virginia opossum (*Didelphis virginiana*) has a rapidly expanding distribution in North America, but many aspects of its ecology remain relatively understudied, particularly in rural areas of its core range. We collected GPS telemetry data from 93 opossums in a rural, non-agricultural landscape in South Carolina, USA (2018–2019) to examine factors influencing space use and resource selection. Estimated male home ranges (99% utilization distributions) were on average 50% larger than those of females (mean home range 115.9 ± 103.7 ha vs 76.7 ± 75.0 ha). The home range size decreased on average by 20% with each 20% increase in deciduous land cover but was not affected by season or other landscape factors. Core area sizes (65% utilization distributions) were not influenced by sex (mean core area size 29.1 ± 23.7 ha and 22.4 ha ± 13.8 for males and females, respectively) or season, but the core area size decreased by 14% with each 400 m increase in distance from a permanent water source. Resource selection by opossums primarily occurred at the landscape level. Both males and females generally selected for wetlands while avoiding pine forests and developed/open areas, likely the result of differences in resource availability and predation risk between habitats. Opossums also tended to select for linear features such as unpaved roads and edge habitat, which may facilitate movement across the landscape. The home ranges we documented are among the largest recorded for opossums in the USA, likely the result of the relatively low resource abundance throughout our study area due to comparatively minimal anthropogenic influence.

Keywords Home range · Mesomammal · Marsupial · Spatial ecology · Telemetry

Introduction

The Virginia opossum (*Didelphis virginiana*, hereafter opossum) possesses a high degree of diet and habitat flexibility, which is credited in part for its wide geographic distribution (McManus 1974). The geographic range of opossums has expanded over the past century and today extends over much of the area from southern Ontario to the Yucatan Peninsula and from the Atlantic seaboard to the Pacific (Beatty et al. 2014; Walsh and Tucker 2018). Concurrent with a growing geographic range has been an increase in reports of opossums as a source of human-wildlife conflict. Potential conflicts involving opossums include foraging in trash, denning in manmade structures, and nest predation of ground-nesting

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birds (Clark 1994; Staller et al. 2005). Additionally, opossums may be vectors for diseases such as Chagas disease (Bern et al. 2011; Bernasconi et al. 2023), murine typhus (Civen and Ngo 2008), and bovine tuberculosis (Walter et al. 2013). Opossums are also the definitive hosts to the parasite that causes equine myeloencephalitis, a disease that costs the horse industry millions of dollars annually (Dubey et al. 2001; Dubey and Lindsay 1999). Although opossums are refractory to rabies virus infection, they may consume oral rabies vaccine baits meant to target raccoons (*Procyon lotor*) and other mesocarnivore reservoirs, potentially limiting the effectiveness of rabies management efforts in some areas of the eastern United States (US) (Slate et al. 2020; Smyser et al. 2010).

Despite an expanding geographic range and potential to cause conflict with humans, many aspects of opossum ecology remain poorly understood, such as their spatial ecology and resource selection. Given their role as a reservoir of zoonoses and potential nontarget competition with raccoons in certain rabies management areas, it is important to understand how landscape factors affect spatiotemporal patterns of opossum occurrence and density (Begon et al. 2002; Lloyd-Smith et al. 2005; McCallum et al. 2001), which is pertinent to predicting and mitigating human-wildlife conflicts (Walter et al. 2013).

Early research regarding opossum space use suggested the species was nomadic without stable home ranges (Fitch and Sandidge 1953; Lay 1942; Reynolds 1945; Verts 1963), but distinct home ranges were later identified with the use of radio telemetry (Gillette 1980; Gipson and Kamler 2001; Ryser 1995), although some evidence of long-distance movements of adults are still reported for some populations (Beasley et al. 2010). Important resources for opossums include food, free water, and denning habitat (Gardner and Sunquist 2003; Sandidge 1953; Seidensticker et al. 1987). In rural habitats, opossums typically select for land cover where these resources are more plentiful, such as forests, and avoid relatively resource-poor land cover types, such as open grasslands (Beatty et al. 2014) or open agricultural fields (Llewellyn and Dale 1964; Nixon et al. 1994), where they may also be exposed to higher predation risk (Levesque 2001). Similarly, opossums often reach higher densities in deciduous compared to evergreen forest as the former tends to have larger diameter trees for denning, greater understory cover, and increased foraging opportunities (Bernasconi et al. 2022). Landscape features that facilitate travel such as habitat edges and roads are often selected by opossums (Dijak and Thompson III 2000; Greenspan et al. 2018), while roads may serve an additional benefit by provisioning food (Beatty et al. 2014; Beatty et al. 2016; Hill et al. 2020).

Opossum home ranges can vary by season, sex, and landscape complexity, with average estimates of 3–318 ha for males and 3–160 ha for females reported among studies (Beatty et al. 2014; Gardner and Sunquist 2003; Kanda et al. 2009). The large home ranges maintained by adult males may allow them to overlap with the home ranges of multiple females during breeding seasons (Ryser 1992). The breeding behavior also impacts temporal shifts in space use by both sexes, especially in temperate regions where nightly movements and home ranges are typically largest during the breeding and post-breeding seasons and smallest during winter (Allen et al. 1985; Beatty 2012; Gillette 1980). Home range sizes may also be larger in habitats with fewer resources because individuals must travel farther to satisfy resource requirements (Ryser 1995). Most studies of opossum spatial ecology and habitat selection have focused on agricultural and urban habitats, whereas relatively few have been conducted in rural, non-agricultural habitats, especially in the southeastern US. Furthermore, few studies have employed resource selection functions to examine habitat selection in rural areas.

We used GPS telemetry data to examine opossum spatial ecology and resource selection in rural, non-agricultural habitats of SC, USA. We examined home range and core area sizes as a function of landscape composition, sex, and season. We also examined temporal shifts in home range locations as well as seasonal and sex-specific differences in opossum resource selection. We predicted that males would have larger home ranges than females (Gardner and Sunquist 2003; Walter et al. 2013) and that the home range size would decrease as non-evergreen forest cover increased (Beatty 2012; Harestad and Bunnel 1979). We also predicted that the home ranges of males would be the largest during the breeding season to overlap multiple female home ranges (Ryser 1995). We predicted that opossums would select for non-evergreen forests, water, and roads, and avoid pine forests and open areas (Beatty et al. 2014; Ginger et al. 2003; Walter et al. 2013). Lastly, we predicted that male and female resource selection patterns would overlap the most during breeding seasons while males are actively searching for females.

Method

Study area

We conducted this study at the Savannah River Site (SRS), a 78,000-ha property managed by the U.S. Department of Energy on the coastal plain of South Carolina (Figure S1). Historically, the SRS had been mostly cleared for agricultural use but was acquired by the U.S. Department of Energy in the 1950s and established as a nuclear production facility. Operations today consist of facilities for nuclear materials processing, tritium extraction, and waste disposal (White and Gaines 2000). Since 1951, much of the SRS has been managed by the US Department of Agriculture (USDA) for timber harvest (originally slash pine [*Pinus elliottii*] and subsequently loblolly pine [*Pinus taeda*] and longleaf pine [*Pinus palustris*]), and pine plantations are harvested on a rotating basis and subject to management practices such as thinning and prescribed burning (White and Gaines 2000). Today, the SRS is covered mostly by evergreen forest (54%) and woody wetlands (24%), with other land cover types (e.g., developed, open water, mixed forest) collectively comprising 22% of the land area (Yang et al. 2018).

We trapped and collared opossums in four prominent habitats on the SRS: upland pine, isolated wetland, bottomland hardwoods, and riparian forest. Upland pine is characterized by mature stands of loblolly and longleaf pine with land cover classified as evergreen by the National Land Cover Database (NLCD). Isolated wetlands are natural shallow ovoid or elliptical-shaped depressions that form ephemerally and are usually surrounded by evergreen or mixed forest NLCD classes (White and Gaines 2000; Workman and McLeod 1990). There are 195 such wetlands across the site ranging in size 0.1–50 ha (White and Gaines 2000). Bottomland hardwoods are classified as woody wetlands by the NLCD and are 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 is also classified as woody wetlands but is more fragmented and embedded in a matrix of upland habitat such as pine and hardwoods, existing in relatively narrow corridors along smaller rivers and creeks that feed 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 (Stutter et al. 2021). Our riparian habitats were located along the upper portions of Tinker Creek and the Upper Three Runs Creek, both of which are relatively undisturbed and never received thermal effluent from nuclear reactors (Layman 1993; Thomas IV et al. 2020).

Animal capture and handling

Prior to deployment, we quantified the accuracy of GPS transmitters by deploying collars in open and closed canopy land cover types within the SRS. To calculate transmitter error, we took the average distance from all points to the known GPS coordinates (determined by waypoint averaging) and ran an analysis of variance (ANOVA) to test for differences between land cover types. We also calculated the average proportion of successful fixes for each stationary GPS unit to compare between open- and closed-canopy land cover types. Following recovery from collared opossums, we filtered points that did not meet the criteria of having ≥4 satellites at the time of location (Cain III et al. 2005).

Opossums were captured January 2018–November 2019 as part of a concurrent study to estimate the densities of opossums across the focal habitats (Bernasconi et al. 2022). To trap opossums, we established six trapping grids consisting of 25 Tomahawk® model 108SS live-capture box traps (Hazelhurst, WI, USA) at intervals of 100 m in a 5 × 5 square configuration within each of the four focal habitat types (total of 24 trapping grids). Each grid was trapped in both years for 2 sessions consisting of 10 consecutive days between January and May. We also trapped animals outside these annual trapping seasons by placing trap lines along secondary roads with traps spaced 100 m apart. We placed whole-kernel corn on the ground adjacent to the trap and paster tabs soaked in fish oil inside the trap as a scent lure (Webster and Beasley 2019). Plaster tabs were replaced after every capture event, following major rainstorms, or after 5 days of inactivity, and corn was replaced as needed. To process animals, we anesthetized them upon capture using intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA) at a dosage of 5 mg/kg of estimated body mass (Beasley and Rhodes Jr 2008; Gehrt et al. 2001; Smyser et al. 2010). We attached matching unique ear tags (Monel #3, National Band and Tag Company, Newport, KY) to both ears prior to release at the capture site.

We fit adult opossums ≥1.7 kg with data logging GPS telemetry collars (W500-NA, 85 g, Advanced Telemetry Systems, Isanti, MN) to ensure the collar weight was less than 5% of the total animal weight (Mech and Barber 2002). We downloaded collar data via UHF antenna every 2 weeks during daylight hours while opossums were denning. Originally (January 17, 2018, to May 10, 2018) we programed collars to collect GPS locations every 3 h starting at midnight for a total of eight points per day. However, based on location failure patterns due to opossums denning underground, we subsequently scheduled collars to collect GPS locations every 2 h during peak active hours (1800–0600, determined by previously collared individuals) and once at 1200 for a total of eight points a day during the remainder of the study (Figure S2). Collars had a minimum battery life of 168 days with many exceeding 200 days.

Home range estimation

We calculated home ranges (99% utilization distribution [UD]) and core areas (65% UD) using the adaptive local convex hull (a-LoCoH) with the package ADEHABITATHR (Calenge 2006) in Program R (R Core Team 2020). We selected 99% and 65% a-LoCoH UDs instead of 95% and 50% UD's, which are typically used in home range estimators, to compensate for the conservative nature of a-LoCoH as a home range estimator (Getz et al. 2007; Stark et al.

2017). However, we include the 95% and 50% estimates, in addition to minimum convex polygon and reference bandwidth kernel density estimator calculations in Table 1 to provide a comparison to previous studies.

The adaptive local convex hull is conservative when constructing estimated home range sizes but robust at accounting for linear use of the landscape due to edge selection or impermeable landscape features (Getz et al. 2007). This non-parametric method calculates a convex hull for every telemetry point in the data set, based on its nearest neighboring points, before combining the hulls into a set of nonparametric kernels based on the density of points. The nearest neighboring points for each GPS fix are the sets of points whose cumulative distance to the root fix is less than or equal to a defined threshold *a* (Getz et al. 2007). This ultimately results in areas of higher use having smaller convex hulls. We selected the *a* value based on the two-step method described by Getz et al. (2007). This method uses (i) the maximum distance between any two points for a given individual as the starting value for *a* followed by (ii) visual inspection and refinement of *a* utilizing the "minimum spurious hole covering" technique, which is meant to ensure unusable landscape features such as open bodies of water do not form portions of the estimated home range area.

Home range analysis

Based on observed patterns of pouched young captured throughout the year and breeding patterns described in other opossum studies throughout the southeastern US (Gardner and Sunquist 2003), we *a posteriori* classified the year into two periods: breeding (January 15th – August 15th) and non-breeding (August 16th – January 14th). We analyzed a seasonal (breeding and non-breeding) home range from at least three unique male and three unique female opossums within each of the four focal habitats. More than one home range could be included from the same individual for analysis, provided it represented a different season of the same year (relative to initial inclusion in the dataset) or the same season of a different year. Home ranges were not calculated for individuals within a season that had less than 90 relocations within 30 days of movement.

We used the 2016 NLCD (Jin et al. 2019) to delineate land cover types on the SRS for the home range analysis. Based on predominant land cover types on the study site and presumed ecological relevance for opossums, we binned the 15 original land cover types of the NLCD into 5 categories: open water, wetland, pine, upland deciduous, and open/developed (Table S1). The wetlands category consisted mostly of woody wetlands but also included herbaceous wetlands. Forest or shrubland accounts for greater than 20% of vegetative cover in this habitat, and the soil is periodically saturated with water. Upland deciduous included deciduous forest (greater than 75% deciduous tree species) and mixed forest (neither deciduous nor evergreen account for more than 75% of tree species) but without seasonal flooding. Both wetlands and upland deciduous featured primarily deciduous tree species, but the former experienced seasonal flooding whereas the latter did not. Developed and open land cover types were binned together since they typically occur together on the SRS due to industrial activity. We used spatial data for roads (both paved and unpaved) as well as stream vector layers provided by the USDA Forest Service for the SRS and surrounding area (USDA Forest Service, Savannah River).

For each opossum GPS point, we calculated distances (meter) to permanent water sources (streams, ponds, and lakes) in ArcMAP 10.6 (ESRI, Redlands, California, USA) using the Euclidean Distance tool. We used this metric to examine the use of water sources and we excluded open water land cover (NLCD class 11) from all analyses. We also calculated the density for paved and unpaved roads separately in a 1 km radius surrounding each point using the Line Density tool in ArcMAP. We also quantified edge habitat by calculating the land cover edge (meter/hectare) within a 100-m window of each point in FragStats (McGarigal et al. 2002).

We z-transformed all continuous covariates prior to analyses and examined pairwise correlations between covariates using Pearson's correlation coefficients with a cutoff of $r = 0.60$ implemented in the package HMISC (Harrell 2019). We

Table 1 Home range and core area estimates (in hectares) as calculated by minimum convex polygon (MCP), reference bandwidth kernel density estimator (KDE_{href}), and adaptive local convex hull (a-LoCoH) for male and female Virginia opossums on the Savannah River Site in Aiken, SC, USA, between January 2018 and December 2019

Sex	MCP		KDE_{href}		a-LoCoH			
	95%	50%	95%	50%	99%	95%	65%	50%*
Female	49.8 ± 24.2	16.3 ± 13.9	90.9 ± 48.5	21.8 ± 13.9	76.7 ± 75.0	58.2 ± 43.2	22.4 ± 13.8	11.7 ± 5.8
Male	176.5 ± 186.5	40.9 ± 47.2	304.2 ± 314.2	66.3 ± 72.9	115.9 ± 103.7	85.5 ± 71.4	29.1 ± 23.7	21.4 ± 15.6
Both	116.7 ± 149.9	29.2 ± 37.5	203.5 ± 253.1	45.3 ± 57.9	97.4 ± 92.8	72.7 ± 60.9	26.0 ± 19.8	17.2 ± 13.2

*50% UD a-LoCoH estimates only calculated for a subset of opossum home ranges further tested for multicollinearity using variance inflation factors, using a cutoff of 4.0 and the package CAR (Fox et al. 2019). Following preliminary analysis of home range and core area covariates, we found pine land cover (%) was negatively correlated with wetland land cover (%). As a result, we removed pine land cover (%) to retain an independent set of predictors for subsequent home range and core area modeling.

We used a linear model to analyze log-transformed home range and core area sizes separately as a function of season (breeding or non-breeding), sex, and the following landscape covariates: proportion of each land cover type present (deciduous, open/developed, or wetland), paved road density, unpaved road density, and distance to permanent water. We also included an interaction between season and sex. We ranked null and all model combinations based on sample size corrected Akaike's Information Criterion (AIC_c) values, choosing that with the lowest AIC_c as the best-supported model and making inferences from this top model (Burnham and Anderson 2002).

Temporal shifts in home range

We described fidelity in home ranges and core areas between breeding and non-breeding seasons by conducting a spatial-temporal analysis of moving polygons (STAMP) (Robertson et al. 2007). STAMP is a geographic tool that is used to describe related polygons that are spatially distinct and experience discrete changes through time. This technique has been used to describe aspects of home range change such as expansions, contractions, and displacement (Smulders et al. 2012). We used a subset of individuals pooled across all years that had contiguous GPS location data in consecutive non-breeding and breeding seasons (10 F, 6 M). We used the R package STAMPR (Long et al. 2018) to measure changes in the horizontal displacement of individual home range centroids and home range overlap between seasons.

Resource selection

We quantified resource selection at the population (second order) and home range (third order) levels (Johnson 1980) by implementing a type III used-available study design to create resource selection functions (RSF) (Manly et al. 2002) using a modified all subsets approach. We defined availability for second-order resource selection as the combined 99% a-LoCoH estimated home ranges of all opossums plus an added buffer equal to the mean maximum displacement of any two points within an individual opossum's home range. We generated random points equal to the number of used points throughout the available landscape. We defined availability at the third-order resource selection level as all areas contained within an individual's 99% a-LoCoH estimated home range. We generated random points equal to the number of used points contained within a given opossum's available home range.

We used the package LME4 to construct generalized linear mixed-effects models with a binary response variable, presence (i.e., an opossum GPS location) or absence (i.e., random generated point) of an opossum. We constructed models separately for each sex and spatial scale combination, resulting in 4 sets of models (i.e., male second order, female second order, male third order, female third order). Our continuous fixed effects included distance to an unpaved road, distance to the paved road, distance to permanent water, and a proportional amount of edge habitat. We also included land cover as a categorical variable (evergreen, wetland, deciduous, or open/developed) and assessed all two-way interactions between pairs of fixed effects. We included individual nested within the habitat type of capture location as the random intercept to account for spatial autocorrelation (Gillies et al. 2006).

We ranked null and all possible model combinations based on AIC_c, choosing that with the lowest AIC_c as the top model. We used the package EMMEANS to predict least-square means (LSMs) and standard errors for each fixed covariate in each season. The LSMs were calculated separately for each sex-specific model, and these LSMs were used for data visualization and interpretation of the resource selection functions.

Results

Location quality and sample size

Between January 2018 and January 2019, we recorded 31,265 locations from 93 (51 males, 42 females) adult opossums. After filtering collars with insufficient data, we obtained 72 seasonal home ranges from 55 unique opossums (32 males, 23 females; Table 2). Collars recorded on average 4.0 ± 0.9 ($\overline{X} \pm$ SD) locations per day with peak location frequency between 2000 and 0200 h (Figure S2). Stationary collar testing revealed a significant difference in the predicted horizontal collar error between open (4.7 m, SE = 0.6) and closed (10.8 m, SE = 0.7) canopy conditions (F (1,136) = 43.8; $P < 0.001$). This difference in horizontal error was acceptable for this study, given that it was likely smaller than our ability to measure using point-averaged commercial GPS units. The analysis of variance of GPS fix rates based on canopy conditions showed a significant difference (F (1,46) = 7.7; $P = 0.008$) between open (100% fix rate) and closed canopies (91.7% fix rate), averaging 8.3% (SE = 3.0%) fewer points in closed canopies. The difference in fix rate was acceptable for this study context, as collared opossums rarely used open-canopy habitats.

Table 2 Sample sizes by habitat, sex, and season of 55 Virginia opossums (*Didelphis virginiana*) collared and monitored using GPS fix locations on the Savannah River Site Aiken, SC, USA (2018–2019)

Habitat Type	Sex	Unique opossums	Season	Number of home ranges	$\overline{X}$ GPS locations
Bottomland hardwood	F	5	Breeding	3	112.7
			Non-breeding	4	153.3
	M	8	Breeding	7	126.1
			Non-breeding	5	161.0
Upland pine	F	7	Breeding	7	134.7
			Non-breeding	4	130.5
	M	9	Breeding	3	110.3
			Non-breeding	7	119.7
Riparian hardwood	F	6	Breeding	5	128.2
			Non-breeding	4	134.3
	M	8	Breeding	4	128.3
			Non-breeding	4	150.0
Isolated wetland	F	5	Breeding	4	131.0
			Non-breeding	3	141.0
	M	7	Breeding	4	144.8
			Non-breeding	4	148.5

Home range sizes

The number of GPS locations per home range was negatively correlated with a-LoCoH home range (99% UD) ($P = 0.03$, $t = -2.25$, $R^2 = 0.05$) and core area (65% UD) ($P < 0.01$, $t = -2.69$, $R^2 = 0.008$) sizes, but the low R^2 values indicate that these effects may have little biological significance. The mean back-transformed a-LoCoH home range size for both sexes combined was 97.4 ± 92.8 ha ($\overline{x}$ ± SD), range 15.1–404.07 ha (Table 1). The mean male home range size was 115.9 ± 103.7 ha, range 15.1–393.7 ha, and the mean female home range size was 76.7 ± 75.0 ha, range 20.12–404.7 ha. Our top model included only sex and deciduous land cover, estimating that males had home ranges on average 50% larger than females and that home range sizes decreased on average by 20% with each additional 20% increase in upland deciduous land cover (Table S2). The season was not included in any of the competitive models.

The mean a-LoCoH core area size for both sexes averaged 26.0 ±19.8 ha, range 5.0–119.3 ha. The mean core area size for males was 29.1 ± 23.7 ha, range 5.0–119.3 ha, and the mean core area size of females was 22.4 ha ± 13.8, range 5.0–60.5 ha. Across all estimator types (a-LoCoH, MCP, KDE_{href}), a-LoCoH provided the most conservative estimates (Table 1). The top model estimated a 14% reduction in core area size with every 400 m increase in distance from water (Table S3) and did not include any other predictors. In contrast to home range sizes, there was no difference in core area size between males and females.

Temporal shifts in home range

The STAMP analyses revealed patterns of both stability (i.e., maintaining some portion of their original home range) and displacement (i.e., shifting to a home range that did not overlap with the original home range) from breeding to non-breeding seasons (Fig. 1). Between breeding and non-breeding seasons, 12 (4 M, 8 F) of the 16 (6 M, 10 F) surveyed opossums maintained stable home ranges, with males shifting their home range centroids an average (±SE) of 836.6 ± 275.7 m and females shifting centroids an average of 323.0 ± 154.5 m. The home range displacement was observed in 4 (2 M, 2 F) opossums, with males averaging a 1397.5 ± 377.4 m shift in the centroid location and females averaging a 769.4 ± 205.5 m shift. Stable core areas occurred in 6 (1 M, 5 F) of the surveyed opossums, with a single male shifting its core area centroid 349.0 m and females averaging 331.8 ± 143.13 m. The core area displacement occurred in 10 (5 M, 5 F) of the surveyed opossums, with males and females averaging 1149.0 ± 511.9 m and 640.1 ± 204.8 m shifts in core centroid locations, respectively.

Resource selection

The top model for analysis of resource selection at the second-order scale was the full model for both sexes (Table S4). Individuals of both sexes were more likely to be located closer to unpaved roads and in wetland land cover than random points throughout the year, whereas they were less likely to be located in open or pine land cover (Table S5,

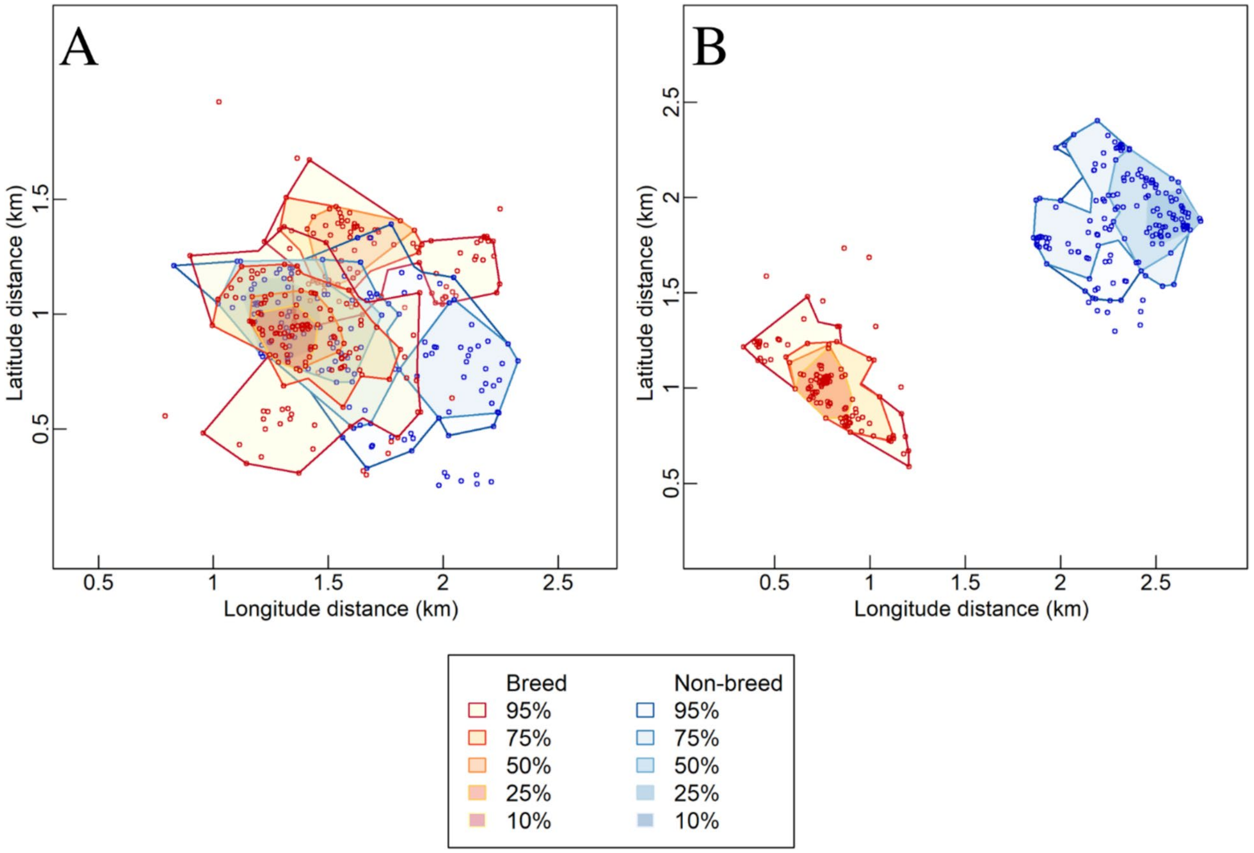
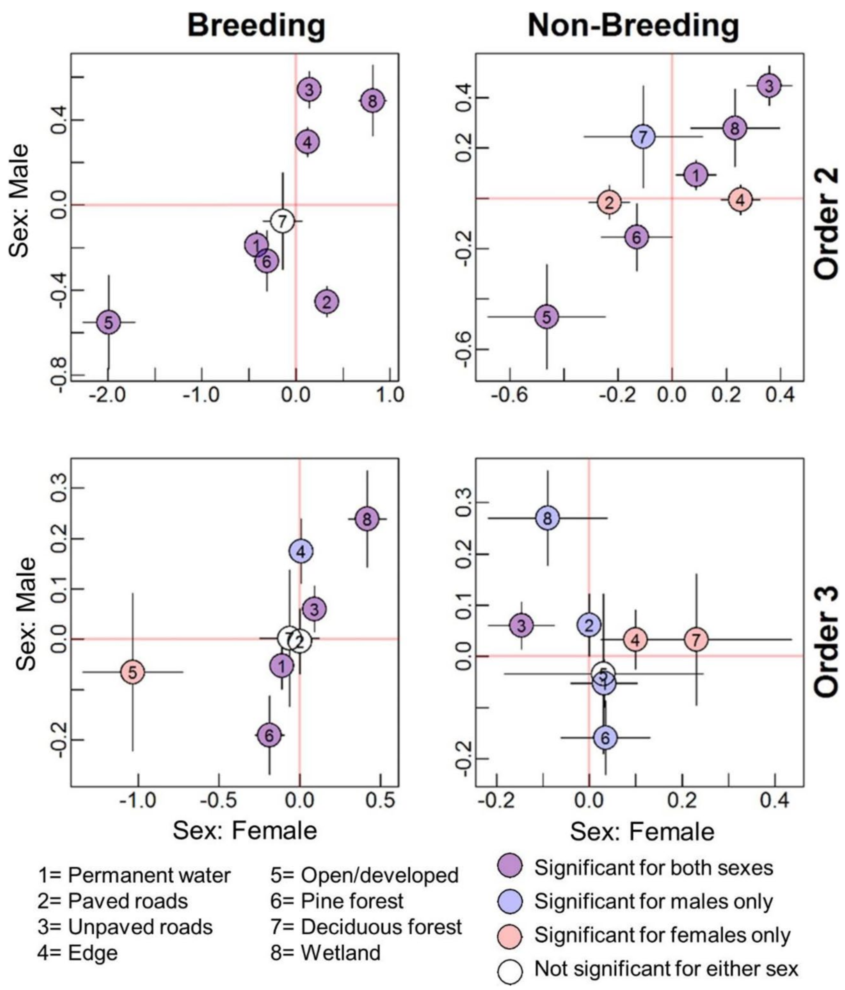


Fig. 1 Example of varying patterns of home range and core fidelity between female and male opossums on the Savannah River Site in Aiken, SC between January 2018 and December 2019. **A** Female opossum OP396 core remained largely stable from non-breeding to breeding seasons while **B** male OP346 displaced entire home range and core area between non-breeding and breeding season. Percentages indicate different isopleths

Fig. 2). During the breeding season, both sexes selected for greater edge habitat and against proximity to permanent water bodies, but neither showed a response to deciduous land cover. Females selected wetlands and avoided open/developed and pine land cover types to a greater extent than males during the breeding season (Table S5, Fig. 2). During the breeding season, females selected for paved roads whereas males selected against them. In contrast to the breeding season, both sexes selected for permanent water bodies during the non-breeding season (Table S5, Fig. 2). Female opossums selected for greater edge habitat and avoided paved roads during the non-breeding season, whereas males showed no response to either landscape feature. Male opossums selected for upland deciduous land cover during the non-breeding season, whereas females showed no response to this land cover type (Table S5, Fig. 2).

There were six competitive models for the third-order resource selection of males (Table S6). All competitive models for males included distance to unpaved roads, distance to permanent water, edge habitat, land cover, season, and the land cover × season interaction. For females, there were three competitive models which each included distance to unpaved roads, distance to permanent water, edge habitat, land cover, and season (Table S6). These competitive models also included the following interactions: land cover × season, unpaved road × season, permanent water × season, and edge × season. During the breeding season, both sexes selected for wetland land cover and unpaved roads, while selecting against permanent water and pine land cover (Table S7, Fig. 2). Males selected for edge habitat whereas females showed no response, and females avoided open habitats while males showed no response. Neither sex showed a response to paved roads or deciduous habitat during the breeding season. During the non-breeding season at the third order, males selected for wetland land cover and paved roads while selecting against permanent water and pine land cover; females showed no response to any of these landscape features during the non-breeding season. Whereas females selected for edge habitat and deciduous cover, males showed no response

Fig. 2 Parameter estimates and 95% confidence intervals for habitat selection variable effects at the second- (population level) and third-order (individual level) scale in a sample of 72 home ranges from 55 GPS-tracked Virginia opossums (*Didelphis virginiana*) during January 2018 to December 2019 on the Savannah River Site in Aiken, SC. Parameter estimates are displayed in separate subpanels for the breeding season and non-breeding season, for male and female opossums. Covariates represented numerically as (1) distance to any permanent water source; (2) distance to paved road; (3) distance to unpaved road; (4) edge density within a 100 m window; (5) open and developed land cover; (6) pine; (7) deciduous land cover; and (8) wetland land cover. For distance-based covariates, positive values indicate positive selection



to these features. Neither sex showed a response to open habitats at the third order during the non-breeding season.

Discussion

Using a robust opossum telemetry dataset, we documented sex- and season-specific patterns in opossum home range ecology and resource selection across typical rural habitats of the southeastern US. Direct comparisons between our findings and previous studies are complicated by the sparse data, as well as inconsistent techniques and methodologies over time, but the home range and core area sizes we report are among the largest for opossums. These home range sizes suggest reduced resource availability or greater resource dispersion for opossums in the rural habitats we examined, which is reinforced by the comparatively low opossum densities in these same habitats (Bernasconi et al. 2022).

Compared to urban areas, the mean annual MCP of opossums in our study is ~5 times greater and ~6 times greater for males and females, respectively (Harmon et al. 2005; Kanda et al. 2009; Meier 1983; Wright et al. 2012). Even within other rural habitats, the home ranges we documented were relatively large, especially for males. In rural areas, agricultural habitat often provides food for opossums (Walsh and Tucker 2023), but the SRS features no agricultural habitat and the resulting lower food abundance may contribute to the large home ranges we observed. In urban areas, opossums benefit from manmade structures for denning and ample anthropogenic food such as garbage, bird feeders, and pet food (Bateman and Fleming 2012; Clark 1994). Previous research has been ambiguous as to whether opossums have smaller home ranges in urban areas (Bateman and Fleming 2012), but the large home ranges across a rural landscape we documented support this hypothesis.

In accordance with our predictions, the home ranges of males were larger than females, although there was no difference in core area sizes between the sexes. The greater body mass of males compared to females in our study (mean mass 2.79 vs 1.88 kg, respectively) likely leads to greater space use as males seek to meet their increased resource requirements (Tucker et al. 2014). Larger home range sizes of males also likely result from reproductive behavior because greater space use allows them to overlap their home ranges with more individual females, leading to increased mating opportunities (Ryser 1992). However, we did not find support for our prediction that males would expand their home ranges during the breeding season. Considering the relatively large home ranges of males at our study site, further increases in space use during the breeding season may not be energetically feasible, especially with opossums' high energetic cost of locomotion (Fournier and Weber 1994). Additionally, the large home ranges of males likely allow them to overlap with several females throughout the year, and marginal increases in mating opportunities may not justify the energetic cost of expanding home ranges during the breeding season. These movement patterns, however, may not hold for more northern latitudes where colder climates place greater foraging pressures on opossums (Kanda 2005a; Kanda 2005b).

Instead of increasing the size of their home ranges, our results indicate that males may shift the locations of their home ranges to overlap more with females during the breeding season. Compared to females, males exhibited a greater frequency of home range displacement between the non-breeding and breeding season and a greater distance between relocated home ranges as indicated by the STAMP analyses. Resource selection trends for males overlapped more with females during the breeding season than the non-breeding season at both spatial scales, indicating males may be maximizing overlap with female home ranges during the breeding season. Altering the location of the home range may be a reproductive strategy to increase mating opportunities while avoiding the energetic costs associated with large increases in the area of space use.

Upland deciduous cover was the only landscape factor that influenced home range size. Contractions in home range size with greater amounts of upland deciduous cover suggest that this habitat provided relatively higher concentrations of resources for opossums. Deciduous forests likely provision ample food for opossums including invertebrates, hard mast, and soft mast (Sandidge 1953). While many of these food items are also available in wetlands, deciduous forests do not experience seasonal flooding. Because opossums often den underground (Lay 1942; Shirer and Fitch 1970), flooding can reduce denning habitat by making ground level dens unusable (Klimas et al. 1981). In mixed deciduous forests, exposed tree roots along stream banks also form common denning sites (Sandidge 1953). Thus, opossums using upland deciduous land cover may have smaller home ranges resulting from the proximity of food resources and denning habitat.

Resource selection by opossums primarily occurred at the landscape level as indicated by the difference in magnitude of selection coefficients between second and third-order analyses. This suggests that opossums optimize the location of home ranges across the landscape so they can maximize resource availability within home ranges (Beasley et al. 2007). Females generally appear to be more selective than males, a trend most pronounced in second-order breeding season selection, which may maximize caloric uptake and minimize distances traveled while carrying young. In contrast, males may mimic the resource selection patterns of females during the breeding season to increase access to mates. Conversely, non-breeding season patterns at the landscape scale were generally weaker and more divergent between the sexes. During this season, females are likely less constrained by the energetic demands and risks of raising pouched young.

In agreement with our predictions, opossums were generally consistent throughout the year at both spatial scales in their selection for wetland land cover. Woody wetlands, which primarily comprised the wetland classification, consist of bottomland hardwood swamp and riparian hardwood forest on the SRS. Opossums prefer such habitat due to the cover they provide as well as the abundance of prey such as amphibians, reptiles, and invertebrates (Gardner and Sunquist 2003; Paton 2005; Ryser 1995). Compared to upland pine, trees in these habitats are also generally larger in diameter and thus more suitable for denning (Byrne and Chamberlain 2011; Owen et al. 2015). The use of woody wetlands may also explain the lack of support for our prediction that opossums would select for permanent water bodies; seasonal flooding, especially in bottomland hardwoods, results in ephemeral water sources that are likely available to opossums but not accounted for in our analyses. This may also account for the unexpected decrease in core area size with greater distance to water as the permanent water bodies used in our analysis may not accurately reflect all of the water sources available to opossums. Furthermore, frequent flooding of bottomland hardwood forest may preclude opossums from selecting home ranges adjacent to rivers due to their underground denning habits.

Consistent with our predictions, pine land cover was generally avoided by opossums at the SRS. Water is an important resource for opossums, but mature pine stands feature sparse water availability on our site. Pine stands across the SRS are routinely managed with fire, which reduces understory vegetation including soft mast (Stratman and Pelton 2007), an important food source for opossums (Kasparian et al. 2002). Lack of vegetative cover may also reduce denning habitat as opossums often choose dens with entrances covered by vegetation (Sandidge 1953). Reduced understory vegetation may also expose opossums to increased risk from predators such as great horned owls (*Bubo virginianus*) or coyotes (*Canis latrans*) (Wright 1989). Opossums often mitigate predation risk by avoiding coyotes (Crooks and Soulé 1999) and on the SRS, coyotes select for mature pine stands over hardwoods (Schrecengost et al. 2009). Thus, the inverse habitat selection by opossums compared to coyotes may be influenced in part by predator avoidance. These trends in habitat selection are supported by the relatively high densities of opossums in bottomland hardwoods and riparian forest compared to pine forest on our study site (Bernasconi et al. 2022).

Across rural landscapes, opossums selected for features that may facilitate movement such as edge habitat and unpaved roads. These features are likely important to opossums due to their propensity for long-distance dispersal (Beasley et al. 2010; Beatty et al. 2014; Ryser 1995). They may be especially relevant for opossums in our study considering their preference for wetlands which are characterized by dense understories that can be difficult to navigate. The juxtaposition of different habitats along edges can also increase foraging opportunities for opossums (Beatty et al. 2014). Although opossums tended to select for unpaved roads, they generally avoided paved roads. Previous studies have suggested that paved roads are important for scavenging opossums due to availability of road kill (Beatty et al. 2014), but the SRS is a restricted access site with limited vehicular traffic and road kill (Hill et al. 2018). At the SRS, opossums scavenge equally between forest interior sites and paved roads, suggesting scavenging by opossums is opportunistic and they do not focus activities along paved roads (Hill et al. 2018).

We documented expansive home ranges by opossums on a site with minimal anthropogenic influence. The much smaller home ranges recorded by other studies in urban and suburban areas suggest that opossums respond to increased resource availability by decreasing the area of space use, a trend documented for many other mesomammals including raccoons, striped skunks (*Mephitis mephitis*), and red foxes (*Vulpes vulpes*) (Bateman and Fleming 2012). Our work can serve as an important baseline study for future work examining opossum responses to urbanization in the southeastern US, which is currently lacking. Such research will have increasing relevance to wildlife management as the expanding geographic range of opossums across North America precipitates increased conflicts with humans and domestic animals.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

Ethics approval All legal guidelines for the care and use of animals were followed. Trapping and handling activities were conducted in accordance with the University of Georgia Animal Care and Use Guidelines under Animal Care and Use protocol A2018 06-024-A12.

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