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Resource selection of deer hunters in Georgia's Appalachian Mountains

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Abstract

White-tailed deer (*Odocoileus virginianus*) and hunters on 2 Wildlife Management Areas (WMAs) within the Chattahoochee National Forest of northern Georgia, USA, significantly declined in number from the 1980s to 2018. Managers were interested in understanding how they could manipulate hunter distribution according to deer management goals. To understand the spatial distribution of hunting pressure and factors driving hunter resource selection, we analyzed GPS tracking data from 58 deer hunters over the 2018–2019 and 2019–2020 hunting seasons. We evaluated hunter selection on 3 spatial scales relative to elevation, slope, and distance from roads, trails, wildlife openings, deciduous forest, mixed forest, and evergreen forest. We incorporated covariates into 6 binary logistic regression models, plus a null model, within a used versus available framework. First, we compared hunter locations to available locations generated within the 2 WMAs. Elevation and distance to deciduous forest had the greatest effect on hunter selection, where hunters selected for lower elevations and closer proximity to deciduous forest. Second, we compared individual hunting bout locations to available locations generated within a buffer around the hunter's starting location with a buffer radius equal to the maximum distance they travelled from their starting location. At the bout scale, distance to wildlife openings and elevation were the most important drivers of hunter selection; hunters selected areas closer to wildlife openings and higher elevations. Third, we compared individual hunter stand locations (used) to randomly selected locations along the hunter's travel path (available). Only distance to roads and deciduous forest were significant in explaining hunter selection of stands. Hunters chose locations farther from roads and closer to deciduous forest relative to their travel paths. Mapping our WMA-scale results revealed that only 5% of the total WMA area contained a greater relative probability of hunter selection compared to the probability of non-selection. Our results suggest that vast refuge areas for deer likely existed on the WMAs during our study period. Manipulating hunter distribution is not necessary to aid in sustaining deer on either WMA at this time.

KEYWORDS

Global Positioning System, hunter distribution, hunting, management, national forest, public land, resource selection, spatial ecology, tracking, white-tailed deer

Spatial distribution of hunting pressure has implications for management of game species, such as white-tailed deer (*Odocoileus virginianus*). Hunting seasons and bag limits are commonly manipulated by managers to influence deer harvest, however, these strategies may prove ineffective when hunting pressure is unevenly distributed across the landscape (Diefenbach et al. 2005, Keenan 2010). In addition to harvest, behavioral responses of deer and other wild ungulates are influenced by the spatial characteristics of hunting pressure (Root et al. 1988, VerCauteren and Hygnstrom 1998, Kilpatrick and Lima 1999, Simoneaux et al. 2016, Ranglack et al. 2017). Hunters may act as predators on the landscape, inducing periods of risk for deer (Proffitt et al. 2009, Spitz et al. 2019, Brown et al. 2020) and perceived risk can cause deer to shift their activity away from key foraging areas to those associated with lower risk (Hernández and Laundré 2005, Benhaiem et al. 2008, Lone et al. 2015, Spitz et al. 2019). Infrequent periods of high risk may also cause deer to devote less energy to activities related to reproduction (Lima and Bednekoff 1999) or alter normal activity related to breeding (Marantz et al. 2016, Little et al. 2016*a*). For example, female white-tailed deer in low-density populations have been observed to adopt a mate-searching strategy by increasing movements during the rut (i.e., breeding season; Labisky and Fritzen 1998, D'Angelo et al. 2004). However, hunting pressure may cause deer to decrease movements, potentially disrupting their normal approach to connecting with mates (Little et al. 2016*a*). Impacts of hunting pressure on deer movements that hinder normal activities, such as procurement of food resources or breeding, may have negative population effects (Spitz et al. 2019, Brown et al. 2020).

An accurate understanding of hunter distribution across the landscape can help managers better manipulate hunting pressure to achieve deer management goals. Previous studies that have tracked hunters with GPS units or measured hunter distribution through aerial surveys revealed an inverse relationship between hunter use of the landscape and 2 variables: slope and distance from roads (Thomas et al. 1976, Fuller 1988, Lyon and Burcham 1998, Diefenbach et al. 2005, Gross et al. 2015). Diefenbach et al. (2005) found that 87% of deer hunters in the mountains of northcentral Pennsylvania, USA, were within 0.5 km of a road. In addition, hunters were 1.5 times less likely to hunt for every 5 degree increase in slope (Diefenbach et al. 2005). On Anticosti Island in Quebec, Canada, 80% of white-tailed deer hunter locations were ≤100 m from a road or trail (Lebel et al. 2012). Forty percent of all turkey (*Meleagris gallopavo* spp.) hunter locations on a 10,483-ha Wildlife Management Area (WMA) complex in South Carolina, USA, were <25 m from roads open to vehicle or foot traffic (Gerrits et al. 2020). Millspaugh et al. (2000) suggested that limiting hunter access to roads, especially in areas with low levels of cover, would limit disturbance to elk (*Cervus elaphus*). Otherwise, animals with home ranges near roads may experience more disturbance and pressure than those with home ranges farther from access points (Gross et al. 2015), resulting in *de facto* refugia, which are areas open to hunting but serve as refuges for game due to their physical characteristics (Diefenbach et al. 2005). Rowland et al. (2021) suggested that closing roads on their study site in northeastern Oregon, USA, would lessen hunting pressure and alleviate concerns with overharvest of the declining mule deer (*Odocoileus hemionus*) population. If managers seek to decrease deer harvest, increasing refugia may be more effective than reducing bag limits or shortening the length of hunting seasons (Keenan 2010).

To evaluate space use, resource selection functions (RSFs; Manly et al. 2002) have been applied in animal movement studies but have not been regularly applied in hunter movement studies. Within a use versus availability framework, RSFs measure the importance of environmental covariates in animal space use (Manly et al. 2002). Binary logistic regression predicts presence or absence and generates coefficients that determine selection or avoidance of environmental characteristics (Manly et al. 2002). Incorporating multiple orders or spatial scales (i.e., multiple spatial extents within which available locations are randomly generated) is important to minimize biases in interpreting RSF model output (Boyce 2006). Currently, only 2 studies have utilized an RSF to assess hunter selection and to predict hunter distribution across a landscape (Stedman et al. 2004, Diefenbach et al. 2005). Both studies incorporated only one spatial scale into an RSF and used hunter locations from an aerial survey, which was limited in temporal resolution, to provide a snapshot of hunter locations at a given time (Stedman et al. 2004, Diefenbach et al. 2005). Using GPS data in an RSF analysis would likely provide unique insights into fine-scale hunter selection and improve the modelling of hunting pressure across a landscape.

We used 3 orders of selection to evaluate the space use of deer hunters. Our goal was to determine if hunters would demonstrate altered preferences for slope and proximity to roads, in order to potentially increase their chances at harvesting a deer, in a landscape with low deer density, low hunter density, and low hunter success. Our study focused on white-tailed deer hunters on 2 WMAs within the Chattahoochee National Forest of northern Georgia, USA. Historically, the WMAs provided a mountain hunting experience with abundant deer populations. However, deer density estimates dropped from 7.7 deer/km^2 on Coopers Creek WMA and 8.9 deer/km^2 on Blue Ridge WMA in 1992 (GDNR–WRD–GMS 1993) to 1.9–3.9 deer/km^2 on each WMA in 2018 (Little et al. 2018). Concurrently, the number of hunters on the WMAs decreased 74% and harvest success rates (i.e., antlered deer harvested/hunter/day) declined 35% (C. Killmaster, Georgia Department of Natural Resources, unpublished data). Our main objectives were to map predicted hunting pressure across the WMAs and to evaluate hunter selection in terms of slope, distance from roads, and other landscape-specific covariates across 3 spatial extents: WMAs, individual hunter use areas, and stands of individual hunters relative to their corresponding travel paths. The research questions associated with each objective (i.e., spatial scale) were: 1) Where is hunting pressure concentrated across the WMAs from a deer's standpoint? 2) What explains hunter selection relative to what is available to them across the WMAs? 3) If hunters have a propensity for a particular area on the WMAs, why did they select a certain path from their starting location relative to other available paths/directions from the starting location? and 4) Why did hunters select a particular stand location relative to other locations available along their travel path? Understanding the spatial distribution of hunting pressure and, in turn, harvest vulnerability of deer is necessary for managers to determine if and how hunter distribution should be manipulated.

STUDY POPULATION AND AREA

We recruited deer hunters (≥18 years of age) on Blue Ridge and Coopers Creek WMAs, which collectively comprise 212 km^2 within the Chattahoochee National Forest in northern Georgia, USA (Figure 1). Through a cooperative agreement, Georgia Department of Natural Resources maintains wildlife openings (i.e., food plots),

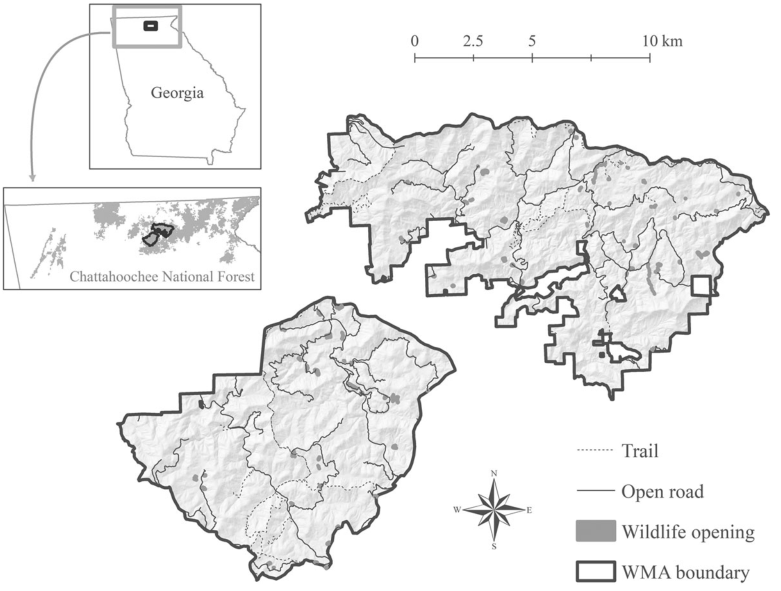

FIGURE 1 The study area for tracking locations of white-tailed deer hunters during the 2018–2019 and 2019–2020 hunting seasons was Blue Ridge (bottom left) and Coopers Creek (top right) Wildlife Management Areas which collectively comprise 212 km^2 (GDNR–WRDNC 2018). Wildlife Management Areas are located in the northern region of Georgia, USA, within the Chattahoochee National Forest (USDC and USCB 2008, GDNR–WRDNC 2017). Wildlife openings (i.e., food plots), roads open to vehicular traffic during hunts, and trails are shown (E. Mavity, USFS, unpublished data; USFS 2012, and 2020).

sets hunting regulations, and conducts hunts on the WMAs, while the U.S. Department of Agriculture–Forest Service conducts the remaining management activities, including timber harvest and prescribed fire (S. Frazier, Georgia Department of Natural Resources, personal communication). The Chattahoochee National Forest is within the Blue Ridge physiographic province of the Appalachian Mountain Range and spans 3,043 km^2. It is 96.8% forested (USGS 2019) with a forest age distribution of 77.9% late forest, 21.9% middle forest, and 0.2% early forest (USFS 2017). From 1979 to 2015, the frequency of timber harvest declined resulting in a mature forest age structure, as the 2 youngest age classes (0–10 years and 11–20 years) declined in coverage by 95% (Little et al. 2018). Northern hardwood communities occurred on north-facing slopes at elevations greater than 1,200 m and largely consisted of American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), and birch (*Betula* spp.) in the overstory and rhododendron (*Rhododendron maximum*) or striped maple (*Acer pensylvanicum*) in the understory (Little et al. 2018). Cove hardwoods occurred at elevations less than 1,200 m and were mesic communities dominated by American basswood (*Tilia americana*), northern red oak, and tulip poplar (*Liriodendron tulipifera*, Little et al. 2018). Mixed-pine hardwood communities generally occurred on south-facing slopes and predominantly consisted of red maple (*Acer rubrum*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. montana*), and yellow pine (*Pinus* spp.) in the overstory and mountain laurel (*Kalmia latifolia*) in the understory (Little et al. 2018). Upland hardwood communities were present on submesic to xeric sites of all elevations and were composed of white oak (*Q. alba*), black oak (*Q. velutina*), northern red oak, red maple, and hickories (*Carya* spp.) in the overstory and rhododendron or mountain laurel in the understory (Little et al. 2018). Streamside communities included eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) in the overstory and rhododendron in the understory (Little et al. 2018). Average annual temperatures range from 6.3 to 19.9° C and average annual rainfall and snowfall are 142 cm and 10.2 cm, respectively (based on weather data from Blairsville, Georgia; U.S. Climate Data 2019).

Blue Ridge and Coopers Creek WMAs had elevations ranging 592–1,302 m ($\bar{x}$ = 836, SD = 101) and slopes ranging 0–56 degrees ($\bar{x}$ = 18, SD = 8; USGS 2013). The WMAs were 97% forested with 49% deciduous, 39% mixed, and 9% evergreen forest types (USGS 2019). Eighty-six wildlife openings were located across both WMAs to provide food sources for wildlife (E. Mavity, USFS, unpublished data). Cool season openings were managed as perennial plantings to provide winter nutrition and act as buffers during poor mast years, while warm season openings were planted to annual crops to provide summer nutrition. Approximately 10–14 openings were planted on each WMA annually and were evenly split between the fall and spring planting seasons (F. Manning, Georgia Department of Natural Resources, personal communication). Typical cool season plantings included various combinations of wheat, oats, rye, chicory, white clover, and red clover. Typical warm season plantings included corn, grain sorghum, and buckwheat. Wildlife openings were maintained by mowing 1–3 times each year and those containing clover were fertilized in the fall. Wildlife openings averaged 0.71 ha (range = 0.07–3.33, SD = 0.60) and were connected to either administrative-only or public use roads (E. Mavity, USFS, unpublished data). The WMAs contained 230 km of county roads and USDA Forest Service roads that were open to vehicular traffic during hunts (U.S. Census Bureau 2015*a*, *b*; USFS 2020). An additional 279 km of county and USDA Forest Service roads were located within 1 km of the WMA boundaries (U.S. Census Bureau 2015*a*, *b*; USFS 2020). In addition, 87 km of hiking trails traversed the WMAs with an additional 42 km within 1 km of the WMA boundaries (USFS 2012).

One primitive weapons deer hunt and 2 firearms deer hunts occurred on each WMA during the 2018–2019 and 2019–2020 seasons. There was no limit to the number of hunters who could hunt on the WMAs. Hunters could sign up online or at kiosks located outside each WMA check station. During the 2018–2019 deer hunting season, most hunts were antlered-only with limited opportunities for antlerless harvest, whereas during the 2019–2020 season, hunts were antlered-only. Harvest of black bears (*Ursus americanus*) and wild pigs (*Sus scrofa*) was permitted during all deer hunts. Legal hunting hours were 30 minutes before sunrise until 30 minutes after sunset.

METHODS

Data collection

We recruited hunters on Blue Ridge WMA during the 2018–2019 and 2019–2020 hunting seasons and on Coopers Creek WMA during the 2019–2020 hunting season to carry handheld GPS units (eTrex 10, GARMIN, Olathe, KS, USA) that were programmed to record locations every 30 seconds. We intercepted hunters at the 2 WMA check stations and focused our recruitment efforts on the day prior to and during the days of primitive weapons and firearms deer hunts, including mornings before sunrise. We explained the research and asked hunters to participate by taking a GPS unit and completing a participation form. Hunters could keep the units for any length of time as long as they continued to hunt. When GPS units were returned, we downloaded data and cleared the units for re-deployment.

Data filtering and classification

All spatial analyses were conducted in ArcMap 10.7.1 and ArcGIS Pro 2.8 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We calculated the horizontal positional error of the GPS units by comparing 182 locations recorded by one unit while placed on top of a National Geodetic Survey benchmark in Blairsville, Georgia, USA to the actual benchmark coordinates. We used the distance from each recorded location to the true location to determine a 95% confidence interval root mean square error of 1.74 m (Bolstad 2019). To filter hunter GPS data, we first omitted locations not associated with legal hunting hours. We erased locations falling within 150 m of campgrounds, picnic areas, and other WMA facilities (Gerrits et al. 2020) and locations falling within 61 m of WMA check stations, which was based on the proximity of open hunting areas to those check stations. We clipped locations to a 610-m buffer around the WMAs. The buffer accounted for potential discrepancies between our GIS layer of WMA boundaries and boundary-indicating signs on the ground and also accounted for possible hunter ventures off the WMAs that were still within the Chattahoochee National Forest. We omitted locations associated with distances >84 m within 30 seconds, assuming those represented non-foot travel by hunters (Gross et al. 2015). Finally, we censored locations during legal shooting hours that were associated with overnight stays, indicating a camp site in a non-designated camping area.

We separated filtered data into hunting bouts, which were independent periods of hunting activity in a continuous spatial and temporal sequence (Gerrits et al. 2020). We considered a continuous string of hunting locations for ≥30 minutes as a hunting bout, thus a hunter could have >1 hunting bout per day. White-tailed deer hunters typically hunt from stationary locations called stands, where they spend most of their time. Deer hunters also travel to, from, and among stands and may engage in stalk hunting. Therefore, we separated hunting bouts further into individual stand locations and travel routes. To isolate stands, we calculated a point density surface for each hunting bout using a cell size equal to the GPS error, a radius equal to twice the GPS error, and an extent that incorporated a 30-m buffer around the minimum bounding rectangle of the corresponding hunting bout. We reclassified the point density surface to assign pixels with ≥1 location as one and all other pixels as NoData. We converted the reclassified surface to polygon and added a buffer equal to the GPS error. Then, we clipped the original hunting bout by the buffered polygon to extract all locations associated with the stand. We eliminated stands <25 minutes in duration. To produce one point location for each stand, we calculated the mean center of the stand locations. We created a merged dataset of all locations associated with stands and another merged dataset of all mean center locations. To create polygons of stand areas, we calculated a convex hull around all locations associated with each stand and added a buffer equal to the GPS error. To isolate travel routes, we censored locations within each hunting bout that fell within the stand area. Then, we removed all routes <5 minutes in duration (Figure 2). We merged all travel routes to create one travel dataset. Final hunting bouts included all travel-associated locations plus the mean center stand locations.

Resource selection analysis

We investigated hunter selection at 3 spatial scales: 1) WMAs, 2) individual hunter use areas, and 3) individual stands relative to corresponding travel paths. To compare used and available locations, we incorporated 8 environmental covariates into 7 different models (Table 1). The WMA scale represented a 2nd order RSF, where used locations were hunting bouts and available locations were randomly generated locations across the WMAs at a ratio of 1 used:10 available. The hunter use area scale represented a 3rd order RSF. We created a circular buffer area around each starting location for a hunting bout with a radius equal to the maximum distance from the starting location that the hunter travelled during the hunting bout. The buffer area represented the space available to the hunter given their desired starting location and maximum distance they were willing to travel from their starting location. Used locations were hunting bouts and available locations were randomly generated locations within the buffer area at a ratio of 1 used:10 available. The stand versus travel scale fell between a 3rd and 4th order RSF. Used locations were mean center stand locations and available locations were randomly selected locations from the hunter's travel path at a ratio of 1 used:5 available.

For our analyses, we extracted raster values of covariates to used and available locations using ArcGIS Pro 2.8 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We compared used to available locations in a binary logistic regression framework where used locations were coded as 1 and available locations were coded as 0. We implemented the regression as a generalized linear mixed-effects model using the glmer function in the lme4 package (Bates et al. 2015) in program R (R Core Team 2019). For the 2nd order analysis, we incorporated hunter identification (coded as a factor variable) as a random effect to account for variation among individual hunters (Gillies et al. 2006). For the 3rd order analysis, we created a unique ID to associate each hunting bout to the available locations generated within the hunting bout's buffer area and incorporated the unique ID as a random effect. For the 3rd–4th order analysis, we created a unique ID to associate each stand location to the randomly

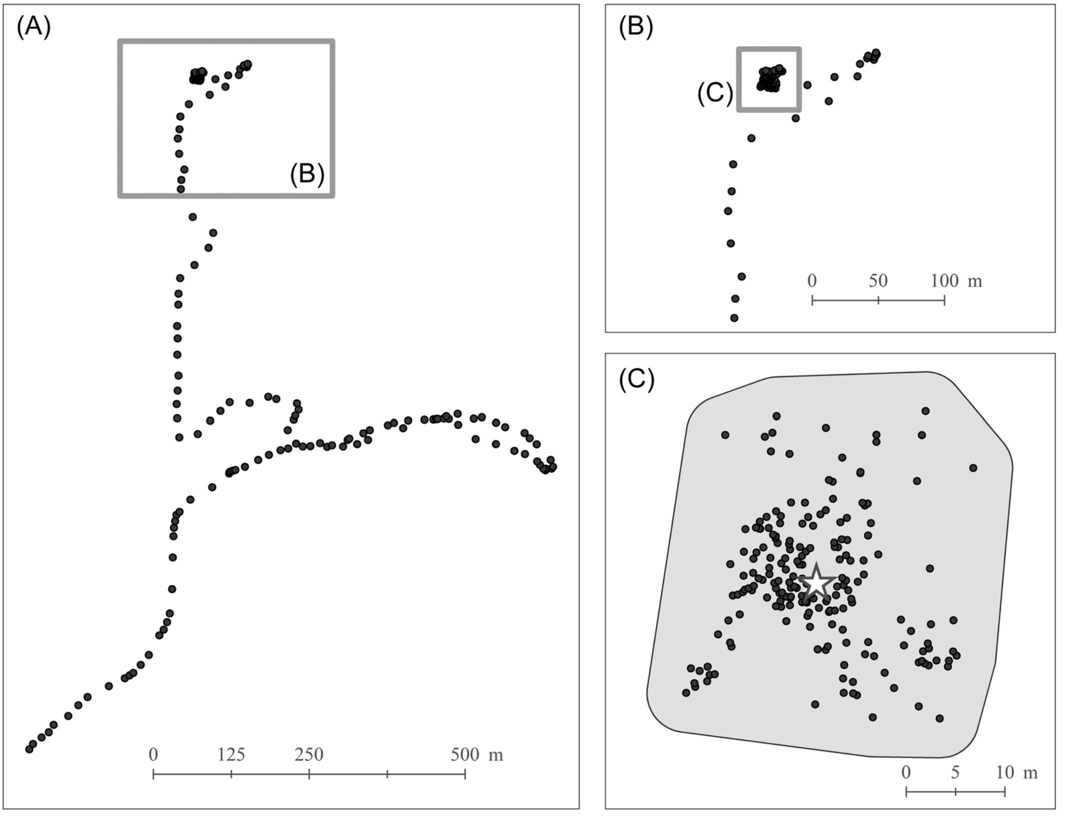

FIGURE 2 White-tailed deer hunters on Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, were tracked via GPS during the 2018–2019 and 2019–2020 hunting seasons. Hunter locations were separated into hunting bouts, which were independent periods of hunting activity in a continuous spatial and temporal sequence lasting ≥30 minutes. A sample of an original hunting bout is shown in (A). Hunting bouts were further separated into stands (B and C), based on the density of locations. Stand areas (gray area in C) were calculated using a convex hull around all stand locations plus a buffer equal to the GPS error. A single location for each stand was calculated using the mean center (star in C) of all stand locations. Travel paths were considered all hunting bout locations not associated with the stand that lasted ≥5 minutes. Final hunting bouts used in resource selection analyses included travel paths and mean center stand locations.

selected available locations along the corresponding travel path and incorporated the unique ID as a random effect. Prior to analysis, we standardized all covariate values for used and available locations by subtracting the mean and dividing by the standard deviation. Standardizing variables allows for the direct comparison of beta coefficients (Morris et al. 2016) and reduces model convergence issues. To eliminate potential multicollinearity among covariates, we evaluated Pearson correlations between each pair of covariates and calculated a variance inflation factor for each covariate. Among the 3 analyses, the greatest correlation coefficient ($|r|$) was 0.52 and all variance inflation factors were <2.0, suggesting that multicollinearity was not likely (Zuur et al. 2009, Dormann et al. 2013). We ranked models based on corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) using AICcmodavg package (Mazerolle 2020) in program R (R Core Team 2019). All models with $AIC_c < 4.0$ units from the top model were considered candidate models. We calculated odds ratios (OR) and associated 95% confidence intervals for each variable in our top model. We considered a variable to be statistically significant if $P < 0.05$ and/or its OR 95% confidence interval did not include 1. We used k-fold cross-validation (k = 10 folds) to assess model fit (Boyce et al. 2002).

TABLE 1 Generalized linear mixed-effects regression models evaluating the relative importance of 8 covariates on white-tailed deer hunter ($n = 58$) selection on 3 spatial scales within Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons.

Model	Variables[a]
Access	Roads[a] + Trails[b]
Topography	Elevation[c] + Slope[d]
Forest type	Deciduous[e] + Mixed[e] + Evergreen[e]
Landcover	Deciduous + Mixed + Evergreen + Openings[f]
Ease of travel	Slope*Roads[g]
Global	Roads + Openings + Trails + Deciduous + Mixed + Evergreen + Elevation + Slope
Null	None

[a]Euclidean Distance (m) to roads open for vehicular traffic (U.S. Census Bureau 2015*a*, *b*; USFS 2020); 30-m resolution.
[b]Euclidean Distance (m) to hiking trails and roads closed to vehicles (USFS 2012); 30-m resolution.
[c]Digital Elevation Model (USGS 2013); 10-m resolution.
[d]Slope surface (degrees) derived from Elevation.
[e]Euclidean Distance (m) from deciduous, mixed, or evergreen land cover classes (USGS 2019); 30-m resolution.
[f]Euclidean Distance (m) to wildlife openings (E. Mavity, USFS, unpublished data); 30-m resolution.
[g]*indicates interaction between variables.

WMA mapping

Using the Raster Calculator in ArcGIS Pro 2.8 (Environmental Systems Research Institute, Inc., Redlands, CA, USA), we mapped the relative probability of hunter selection across the WMAs. First, we standardized all covariate rasters by subtracting the mean and dividing by the standard deviation. Then, we incorporated the beta coefficients ($\beta_1 \ldots \beta_k$) from the top model in our 2nd order RSF and the standardized covariate rasters ($x_1 \ldots x_k$) to create a raster map, where the relative probability (p) of hunter selection at each 30-m pixel was equal to:

$$p = exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k)/(1 + exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k))$$

We reclassified the relative probability raster in 3 ways. First, to map and calculate the percentage of WMAs with a greater probability of hunter selection versus non-selection, we reclassified pixels with probabilities ≤0.50 as 0 and probabilities >0.50 as 1. Second, to map and calculate the percentage of WMAs that hunters would not select, we reclassified pixels with probabilities <0.01 as 1 and probabilities ≥0.01 as 0. Third, we divided the range of relative probability values into 5 equal intervals for a smoother visualization of probabilities relative to one another. Values depicted in the maps represented the relative probability of selection based on a used versus available framework, rather than the actual probability of use associated with a used versus un-used framework (Manly et al. 2002).

RESULTS

Summary statistics

We recruited 73 hunters to carry GPS units and 58 produced data usable for analyses. Data filtering resulted in 61,405 total hunting locations. We isolated 158 total hunting bouts (Table 2) with an average of 2.7 (SD = 2.0) hunting bouts per hunter. Hunters averaged 1.7 (SD = 1.2) hunting bouts/day and spent an average total time

TABLE 2 Summary statistics associated with 158 hunting bouts and 151 stands of white-tailed deer hunters (n = 58) on Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons.

	Hunting bouts					Stands				
			Percentile					Percentile		
Variable[a]	$\bar{x}$	SD	50th	75th	90th	$\bar{x}$	SD	50th	75th	90th
Roads	237	261	150	331	680	221	219	127	318	511
Openings	761	771	532	1041	1981	727	849	474	1041	2043
Trails	1,392	1,064	1,148	2,048	2,880	1,541	1,123	1,376	2,072	3,134
Deciduous	45	58	30	67	124	35	44	30	42	90
Mixed	54	90	30	60	150	42	63	30	60	95
Evergreen	230	249	150	296	540	253	292	150	319	649
Elevation	770	103	753	836	905	763	90	753	823	886
Slope	14	7	13	19	24	13	7	11	19	22

[a]See Table 1 for descriptions of variables.

hunting/day of 4 hr 47 min (SD = 2 hr 43 min). Hunting bouts averaged 3 hr 20 min (SD = 2 hr 3 min) in duration. Data spanned 10 hunts and 29 different hunting days over 2 hunting seasons providing 109 hunter-day combinations. Fifty-two percent of hunting activity occurred in the morning between 0600 and 1159 and 48% occurred in the afternoon or evening between 1200 and 1939.

We identified 151 stands (Table 2) composed of 42,660 locations (69% of total hunting locations) with an average of 2.6 (SD = 2.1) stands/hunter and 1.6 (SD = 1.2) stands/hunter/day. Hunters spent an average of 2 hr 32 min (SD = 1 hr 34 min) at each stand and an average of 3 hr 23 min (SD = 2 hr 15 min) at stands/day hunted. We identified 142 travel paths composed of 18,266 total locations. Travel per hunting bout averaged 1 hr 0 min (SD = 1 hr 1 min), across an average distance of 1.37 km (SD = 1.24), and average speed of 1.56 km/hr (SD = 1.20). Travel duration per day averaged 1 hr 28 min (SD = 1 hr 22 min) across an average distance of 1.96 km (SD = 2.05) and an average speed of 1.42 km/hr (SD = 0.92).

Hunter selection

For hunter selection on the WMAs, the global model was the top model with an AIC_c weight of 1 and k-fold cross-validation value of 0.9087 (i.e., model explains 91% of variation in the dependent variable; Table S1, available online in Supporting Information). Elevation and distance to deciduous forest had the greatest effect on hunter selection with elevation being the most important covariate (Table 3). Hunters selected for lower elevations ($\beta = -1.125$, SE = 0.012, OR = 0.325 ± 0.004) and areas closer to deciduous forest ($\beta = -0.543$, SE = 0.011, OR = 0.581 ± 0.007). Distance to trails and open roads were the least important covariates in hunter selection.

For hunter selection within individual use areas, the global model was the top model with an AIC_c weight of 1 and k-fold cross-validation value of 0.9044 (Table S2). Distance to wildlife openings and elevation had the greatest effect on hunter selection with distance to wildlife openings being the most important covariate (Table 4). Hunters selected for areas closer to wildlife openings ($\beta = -0.565$, SE = 0.024, OR = 0.568 ± 0.020) and higher elevations ($\beta = 0.459$, SE = 0.023, OR = 1.583 ± 0.054). Distance to mixed and evergreen forest were the least important covariates in hunter selection.

TABLE 3 Results for the top model (i.e., global model) evaluating the relative importance of 8 covariates on white-tailed deer hunter (n = 58) selection within Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons. Ranks were derived from ordering |β| from greatest (1) to least (8).

Variable[a]	Rank	β[b]	SE	Z	*P*	Odds ratio	Lower 95%	Upper 95%
Roads	7	−0.154	0.011	−14.595	<0.001	0.857	0.839	0.875
Openings	3	−0.485	0.009	−51.889	<0.001	0.615	0.604	0.627
Trails	8	0.021	0.009	2.318	0.020	1.021	1.003	1.039
Deciduous	2	−0.543	0.011	−48.697	<0.001	0.581	0.568	0.594
Mixed	6	0.241	0.011	22.053	<0.001	1.273	1.246	1.301
Evergreen	5	0.347	0.009	37.793	<0.001	1.415	1.390	1.441
Elevation	1	−1.125	0.012	−96.687	<0.001	0.325	0.317	0.332
Slope	4	−0.463	0.009	−51.690	<0.001	0.629	0.618	0.641

[a]See Table 1 for descriptions of variables.

[b]Standardized.

TABLE 4 Results for the top model (i.e., global model) evaluating the relative importance of 8 covariates on white-tailed deer hunter (n = 58) selection within hunter use areas on Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons. A hunter use area was defined as a buffer around a hunting bout starting location with a radius equal to the maximum distance the hunter travelled from the starting location. Ranks were derived from ordering |β| from greatest (1) to least (8).

Variable[a]	Rank	β[b]	SE	Z	*P*	Odds ratio	Lower 95%	Upper 95%
Roads	6	0.141	0.011	12.456	<0.001	1.151	1.126	1.177
Openings	1	−0.565	0.024	−23.412	<0.001	0.568	0.542	0.596
Trails	5	−0.281	0.030	−9.297	<0.001	0.755	0.712	0.801
Deciduous	4	−0.408	0.013	−32.423	<0.001	0.665	0.649	0.681
Mixed	8	−0.043	0.011	−3.853	<0.001	0.958	0.938	0.979
Evergreen	7	0.137	0.017	7.969	<0.001	1.147	1.109	1.186
Elevation	2	0.459	0.023	19.964	<0.001	1.583	1.513	1.656
Slope	3	−0.455	0.010	−47.864	<0.001	0.634	0.623	0.646

[a]See Table 1 for descriptions of variables.

[b]Standardized.

For hunter selection of stands, 5 models had $\Delta AIC_c < 4$ units (Table S3). We calculated β, OR, and confidence intervals using model averaging for covariates among the 5 models (Table 5). Hunters selected areas closer to deciduous forest (β = −0.327, SE = 0.127, OR = 0.721 ± 0.093) and farther from roads (β = 0.298, SE = 0.093, OR = 1.347 ± 0.126), relative to their travel paths.

Wildlife Management Area mapping revealed only 5% of the total WMA area contained a greater relative probability of hunter selection ($P > 0.50$; Figure 3) compared to the probability of non-selection. One percent of the total WMA area represented predicted areas that virtually no hunter would select ($P < 0.01$). The equal interval classification of relative probability values revealed relative hot spots for hunter selection across the WMAs. The

TABLE 5 Results for model averaging the top 5 models ($\Delta AIC_c < 4$) that evaluated the relative importance of 8 covariates on white-tailed deer hunter ($n = 58$) selection of stand sites relative to their travel paths on Blue Ridge and Coopers Creek Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons. Ranks were derived from ordering $|\beta|$ from greatest (1) to least (8).

Variable[a]	Rank	β[b]	SE	Odds ratio	Lower 95%	Upper 95%
Roads	2	0.298	0.093	1.347	1.122	1.617
Openings	3	−0.152	0.114	0.859	0.687	1.074
Trails	6	0.030	0.102	1.030	0.843	1.259
Deciduous	1	−0.327	0.127	0.721	0.562	0.926
Mixed	4	0.041	0.104	1.042	0.851	1.277
Evergreen	5	0.041	0.124	1.042	0.818	1.328
Slope	7	−0.019	0.097	0.981	0.811	1.187

[a]See Table 1 for descriptions of variables.
[b]Standardized.

northwestern corner of Blue Ridge WMA and sporadic areas throughout the southern half of Coopers Creek WMA had greater relative probabilities of hunter selection compared to the rest of the areas within the WMAs.

DISCUSSION

Past research on hunter movements mainly focused on 2 environmental characteristics: slope and distance to roads (Thomas et al. 1976, Fuller 1988, Lyon and Burcham 1998, Diefenbach et al. 2005, Gross et al. 2015). Hunters tend to avoid steep slopes and remain close to roads (Stedman et al. 2004, Diefenbach et al. 2005, Gross et al. 2015, Gerrits et al. 2020). Although slope and distance to roads had similar relationships to hunter selection on WMAs in our study as they did in previous studies, the covariates were not among the most important in explaining hunter selection on the WMAs. Elevation, distance to deciduous forest, and distance to wildlife openings had the greatest effect on hunter selection across the WMAs. Hunters selected for areas that had lower elevations and were closer to deciduous forest and wildlife openings. Hunters were likely tied to deciduous forest and wildlife openings because of the food resources available to deer. We acknowledge that deciduous forest is a broad category and we did not have data on individual tree species composition on the WMAs. However, it is probable that hunters targeted the oak component of the deciduous forest considering that the deer population on our study area is largely driven by availability of oak mast (Wentworth et al. 1990*a*, Wentworth et al. 1992, Carlock et al. 1993, Johnson et al. 1995, Kammermeyer and Carlock 2000). During poor mast years, deer may rely more heavily on wildlife openings (Wentworth et al. 1990*b*, Carlock et al. 1993), which are sources of quality forage. The higher relative importance (i.e., effect sizes) of distance to wildlife openings and distance to deciduous forest compared to other covariates in our study indicated that hunters pursuing deer in a low density population may prioritize areas with the best perceived chance of finding a deer over areas that provide easier access to hunting spots (i.e., distance from roads, slope).

Distance to open roads was a top covariate in our 3rd and 4th order analysis of stand sites. Stands were farther from roads compared to locations along the hunter's travel path, indicating that hunters started their hunting bouts on a road and travelled in a perpendicular fashion to reach their stand destinations. In our 2nd order analysis of the WMAs, hunters were less likely to select for areas as distance from roads increased. The different relationships between hunter selection and distance from roads among the various RSF orders highlights the importance of

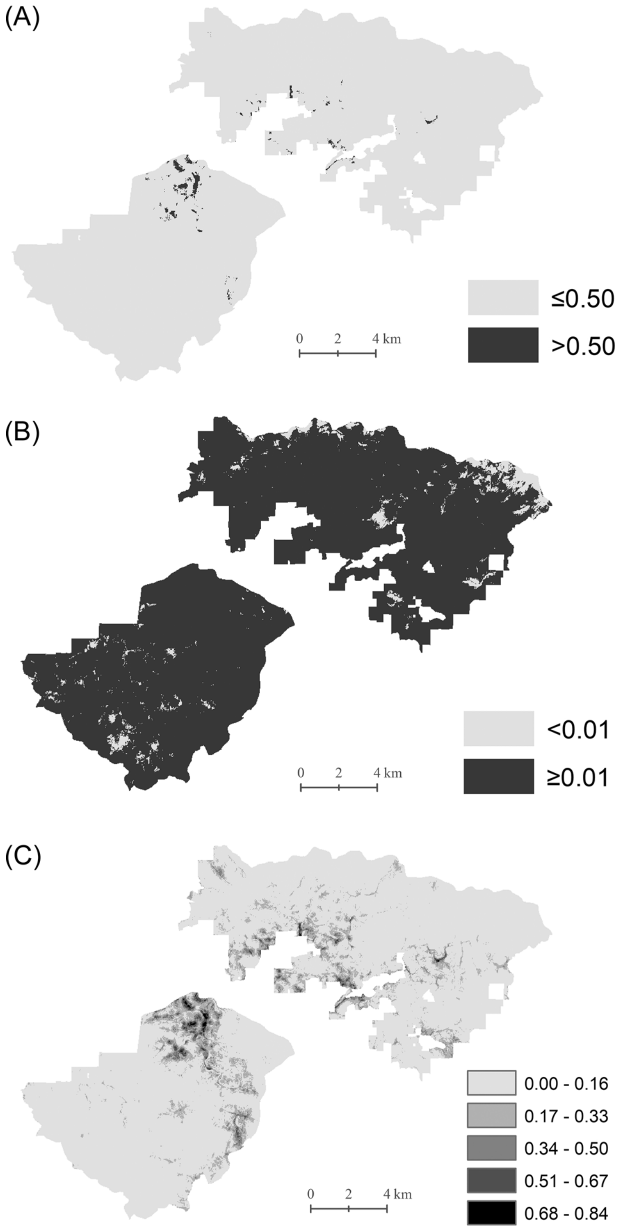

FIGURE 3 Second order RSF analysis for white-tailed deer hunters mapped across Blue Ridge (bottom left) and Coopers Creek (top right) Wildlife Management Areas in northern Georgia, USA, during the 2018–2019 and 2019–2020 hunting seasons (GDNR–WRDNC 2018). Values represent the relative probability of hunter selection based on a use versus availability framework. The map on the top (A) shows where there is a greater probability of hunter selection ($P > 0.50$) versus a greater probability of non-selection ($P \leq 0.50$). The center map (B) shows where there is virtually no relative probability of hunter selection ($P < 0.01$). The bottom map (C) shows relative probabilities of hunter selection classified into 5 equal intervals and indicates relative hot spots of hunter selection across the Wildlife Management Areas.

incorporating multiple spatial scales to explain hunter selection (Little et al. 2016*b*). Although distance from roads was less important in explaining hunter selection across the WMAs relative to other covariates, controlling access remains an essential tool in managing hunter distribution (Ranglack et al. 2017, Gerrits et al. 2020, Rowland et al. 2021). In our 3rd order analysis of hunting bouts relative to buffers surrounding a starting location, hunters tended to gravitate towards wildlife openings, which are typically associated with road access. Hunters were also less likely to traverse steeper slopes but selected areas with higher elevations. It seems that hunters drove to higher vantage points in their vehicles and stayed on high ground as they hunted.

Distance to trails was the least important covariate in the WMA-scale analysis, moderately important in the hunter use area analysis, and not important in the stand-scale analysis. Past research found that hunters pursuing different species, such as turkeys (Gerrits et al. 2020), elk, and mule deer (Rowland et al. 2021) were closely tied to trails. However, hunting for those species tends to involve greater mobility compared to white-tailed deer hunting which largely occurs from stands. We acknowledge that our spatial data likely did not include all available trails on our study area. For example, relic logging roads are present throughout the southern Appalachians but are not typically designated on maps. Administrative roads open only to foot traffic for hunters are also poorly documented across the WMAs. Overall, the low availability of trails on our study area may account for why hunters did not target them.

Mapping the results of our 2nd order RSF revealed a potential vast under-utilization of the WMAs by deer hunters. Only 5% of the WMAs contained areas where the probability of hunter selection was greater than non-selection, indicating that many areas of the WMAs likely provide ample *de facto* refugia for deer (Diefenbach et al. 2005). Refugia are effective at minimizing deer harvest (Diefenbach et al. 2005, Keenan 2010). The manipulation of refugia may be a useful tool for managers wanting to minimize the effects of hunting on the deer population without limiting the number of hunters (Diefenbach et al. 2005, Keenan 2010). Gross et al. (2015) found that turkey hunters on a WMA in Louisiana also under-utilized the amount of land available to them. Fifty percent of hunting pressure occurred on only 3% of the WMA area and 90% of hunting pressure occurred within 27% of the WMA area (Gross et al. 2015). An uneven distribution of hunters may lead to variable harvest vulnerability and hunting pressure, depending on the location of animal home ranges (Broseth and Pederson 2000, Gross et al. 2015). At the WMA scale in our analysis, deer likely receive little hunting pressure, however, there may be deer in localized areas that experience more pressure than others.

By incorporating environmental covariates into 3 orders of RSFs, we provided insights into how deer hunters in the southern Appalachians select locations across WMAs, locations within local use areas, and stand sites relative to their travel paths. Our analyses revealed the importance of variables other than slope and distance to roads, such as elevation, distance to deciduous forest, and distance to wildlife openings. Ultimately, our study should help managers understand hunting pressure and hunter selection in an area where hunting must be managed in the face of a declining, low-density deer population. Future research should focus on areas with a more typical deer density and similarly incorporate multiple landscape covariates to help provide a more comprehensive understanding of hunter selection.

MANAGEMENT IMPLICATIONS

Only 5% of the total WMA area had a greater relative probability of hunter selection compared to the relative probability of non-selection. Combined with the low hunter numbers on the WMAs, our results suggest that vast refuge areas for deer likely existed on the WMAs during our study period. Manipulating hunter distribution is not necessary to aid in sustaining deer on either WMA at this time. However, if managers want to ensure that hunting pressure does not negatively impact fitness of deer in key areas, closing roads, delineating refuges, or assigning hunters to hunt units are strategies that can be used to better distribute hunters as necessary. Research centered on the movement responses of deer to hunting pressure on WMAs would ultimately determine if steps to manipulate hunting pressure are necessary to minimize effects on the deer population.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

ETHICS STATEMENT

Our study was approved by the University of Georgia Institutional Review Board (Protocol ID#PROJECT00001075), ensuring that our methods relating to human subjects complied with applicable federal, state, and institutional policies and procedures.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website. Material includes AIC results tables for the 3 spatial orders of Resource Selection Function analyses.

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