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SPECIAL SECTION

Hunting impacts male wild turkey space use and resource selection: insights from a hunted and non-hunted population

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Abstract

Predation risk is known to influence prey behaviors. Risk from human predators can be more influential on prey responses than risk from natural predators. The wild turkey (*Meleagris gallopavo*) is a widely distributed game species, and growing literature suggests that hunting activity influences various behavioral metrics of males, including rates of vocalizations, resource selection, and movements. However, previous studies have made inferences about potential influences of hunting activity on male resource selection and movement behaviors solely by studying hunted populations, using a before-during-after treatment design, wherein the treatment was the onset of hunting. A more appropriate design would rely on matching individual males from both hunted and non-hunted populations to better account for individual variation in behaviors, hence improving causal inference. We compared space use, minimum daily distance moved, roost fidelity, and resource selection of male wild turkeys in a hunted population on the Webb Wildlife Management Area Complex during 2014–2018 to males in a non-hunted population on the Savannah River Site during 2020–2023 in South Carolina, USA. We found that male wild turkeys in the hunted population maintained 53% smaller home ranges and 69% smaller core use areas once hunting

began compared to the non-hunted population, but this reduction in space use was temporary. We found no differences in minimum daily distance traveled, whereas males in the hunted population generally exhibited greater fidelity to roost sites. Males in the non-hunted population selected areas closer to openings and secondary roads, whereas males in the hunted population exhibited the reverse pattern of selection until hunting ceased. Our findings contribute to a growing body of literature suggesting that male wild turkeys react to risk associated with hunting activity by altering their behaviors, although these alterations appear to be short in duration.

KEYWORDS

hunting, *Meleagris gallopavo*, movement ecology, predation risk, resource selection, South Carolina, wild turkey

Understanding factors that influence wildlife movement and resource selection is essential to understanding wildlife population dynamics (Morales et al. 2010, Abrahms et al. 2021). Wildlife move and select resources based on a combination of intrinsic factors, such as physiological needs (Nathan et al. 2008, Jachowski and Singh 2015), reproductive requirements (McNitt et al. 2020, Taylor et al. 2020), and social interactions (Sells and Mitchell 2020, Hansen et al. 2024), and extrinsic factors, such as habitat characteristics (Valeix et al. 2010, Ulrey et al. 2023*a*), environmental conditions (Avgar et al. 2013, Riotte-Lambert and Matthiopoulos 2020), and human disturbances (Wilson et al. 2020, Doherty et al. 2021). Unraveling the influences of these drivers provides valuable insights into a behavioral ecology of a species, which enhances effective management and conservation of animal populations (Jacoby et al. 2012). Predation risk is one driver of animal movement and resource selection that has garnered much attention (Lima and Dill 1990, Peacor et al. 2020, Gaynor et al. 2021).

Predation risk causes prey to alter their behaviors to reduce encounter rates with predators, often at the cost of losing foraging and reproductive opportunities (Villepique et al. 2015, Marantz et al. 2016, Smith et al. 2017, Roth et al. 2024). A risk-induced trait response occurs when prey alter behavior to reduce predation risk, which can result in population- and community-level effects (Zanette et al. 2011, Suraci et al. 2019, Peacor et al. 2020, Crawford et al. 2022). In addition to natural predators, game species are often killed at increased rates by humans; thus, humans represent a unique dominant predator (Darimont et al. 2015). Human predation risk often elicits greater trait responses compared to risk from natural predators and has increased potential for population-level effects (Frid and Dill 2002, Suraci et al. 2019, Gaynor et al. 2021, Wightman et al. 2023*a*). Specifically, human predation risk has been found to affect movement and resource selection by game species (Cleveland et al. 2012, Marantz et al. 2016, Little et al. 2016*b*, Picardi et al. 2019). Therefore, understanding how hunting affects game species movement and resource selection is imperative for informing conservation and management.

The wild turkey (*Meleagris gallopavo*) is a nonmigratory upland game bird indigenous to North America whose populations have experienced declines in abundance and recruitment across much of their range in the last decade (Byrne et al. 2015*a*, Eriksen et al. 2015, Chamberlain et al. 2022). For male wild turkeys, human harvest is the primary cause of mortality and occurs during the breeding season, potentially influencing reproduction through hunting-induced behavioral changes (Chamberlain et al. 2012, 2018; Wightman et al. 2024). Studies have shown that hunting significantly affects reproductive vocalizations and influences movements and resource selection, at times greater than natural predators (Chamberlain et al. 2018; Wightman et al. 2019, 2023*a*, 2023*b*; Wakefield et al. 2020*b*).

Previous studies examining effects of hunting on male movement behaviors found substantial interindividual variation, with some males increasing and others decreasing daily distances traveled, roost fidelity, and range area with the onset of hunting; however, collectively, these studies concluded that hunting had little to no biologically important effect on these movement metrics (Gross et al. 2015, Collier et al. 2017, Wakefield et al. 2020*a*). Likewise, contemporary literature on resource selection has noted that males tend to avoid areas of increased human activity during the onset of hunting for a short period, when risk is high, before returning to normal use after hunting pressure subsides (Wightman et al. 2023*a*, Roth et al. 2024). Specifically, male wild turkeys avoid areas closer to primary and secondary roads as they are often associated with increased hunter activity (Gerrits et al. 2020, Wightman et al. 2023*a*, Roth et al. 2024).

Male wild turkeys are intensively hunted across much of their range, making prior research focused on the effects of hunting on turkey behavior being conducted in hunted populations, while studies incorporating both hunted and non-hunted populations have been largely limited to research on vocalizations (Lehman et al. 2005, Wightman et al. 2019). In the absence of data on a non-hunted population, previous works relied on a before-during-after treatment (onset of hunting) approach to investigate the effects of hunting on movement and resource selection (Collier et al. 2017, Wakefield et al. 2020*a*, Wightman et al. 2023*a*, Roth et al. 2024). However, given that movement and resource selection vary markedly among individuals (Gross et al. 2015, Collier et al. 2017) and are likely driven by many factors, such as reproduction (Chamberlain et al. 2018), social status (Healy 1992, Ulrey et al. 2023*b*), and predation risk (Wightman et al. 2023*a*), the possibility of biased causal inference exists. A more appropriate approach for estimating effects requires the comparison of individuals in hunted and non-hunted populations (Ribas et al. 2021). By matching individuals with similar movement metrics before hunting occurs, in both hunted and non-hunted populations, one can account for individual variation and increase the accuracy of causal inference.

Our objective was to compare space use, daily movements, resource selection, and roost fidelity between hunted and non-hunted populations of male wild turkeys. We hypothesized that male wild turkeys modify their movement behavior and habitat use in response to hunting activity to reduce the risk of predation by hunters. Specifically, we predicted that males in the hunted population would use smaller home ranges and core areas while exhibiting reduced daily movements to minimize encounters with hunters. Additionally, we predicted that males in the non-hunted population would exhibit greater fidelity to roost sites compared to the hunted population, as hunting pressure may drive more frequent roost-site shifts. Lastly, we predicted that resource selection would be similar between populations, except that males in the hunted population would avoid primary and secondary roads, as these features represent areas of increased hunter risk.

STUDY AREA

We conducted research on 2 study sites in South Carolina, USA, approximately 60 km apart along the eastern banks of the Savannah River (Figure 1). Climate was subtropical, with annual temperatures ranging from 5.9°C to 26.5°C and annual precipitation ranging from 92.5 cm to 256.5 cm (www.prism.oregonstate.edu, accessed 5 May 2024). We collected data during 2014–2018 on the hunted study site, which was the Webb Wildlife Management Area (WMA) complex in Hampton and Jasper counties. The Webb WMA complex was approximately 10,000 ha located 6 km from Garnett in the middle Atlantic coastal plains' ecoregion (Griffith et al. 2002). The Webb WMA complex was managed by the South Carolina Department of Natural Resources (SCDNR) for hunting and conservation of white-tailed deer (*Odocoileus virginianus*), wild turkeys, and northern bobwhite (*Colinus virginianus*). Forest types on the Webb WMA complex were primarily composed of hardwood bottomlands (47%) dominated by various species of oak, (*Quercus* spp.), hickory (*Carya* spp.), sweet gum (*Liquidambar styraciflua*), mixed pine-hardwood stands (<1%), and upland planted-pine stands (33%) consisting of longleaf (*Pinus palustris*) and loblolly pine (*P. taeda*). Understory species consisted of sweet gum, American holly (*Ilex opaca*), wild grape (*Vitis* spp.), flowering dogwood (*Cornus florida*), and briars (*Rubus* spp.). Wildlife openings (3%) were present on the landscape in the form of maintained

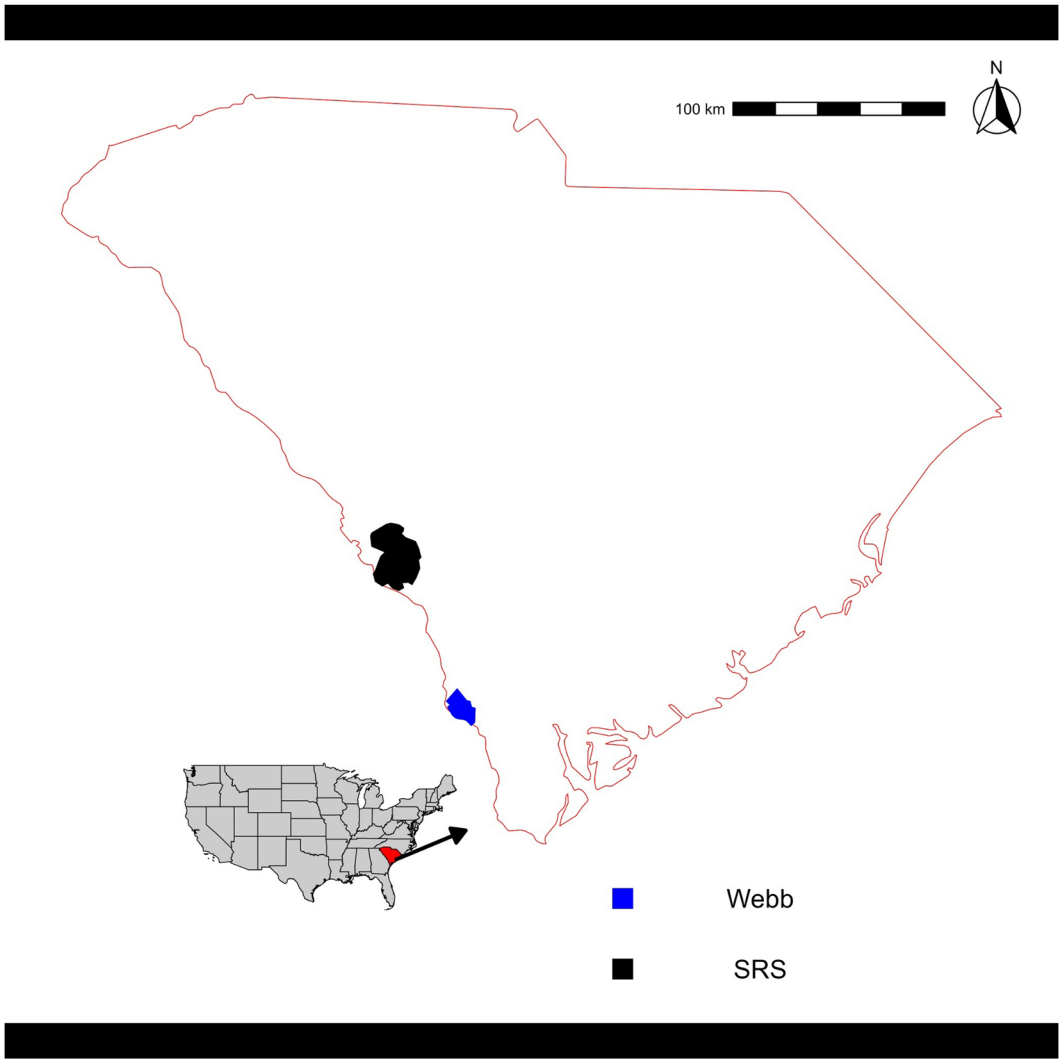

FIGURE 1 Location of the Webb Wildlife Management Area Complex (Webb) and the portion of the Savannah River Site (SRS) used for studying male eastern wild turkey movement and resource selection in South Carolina, USA, during 2014–2018 at Webb and 2020–2023 at SRS.

rights-of-way and small (<3 ha) openings in wooded areas. Wild turkey hunting season opened on 1 April and closed on 1 May (31 days) in 2014–2015 and 5 May (35 days) in 2016–2018, with annual youth hunts occurring on the Saturday before the season. The total length of primary and secondary roads was 91 km and 173 km, respectively, corresponding to densities of 0.91 km/km² and 1.73 km/km². Legal hunting hours were 30 minutes before sunrise to 30 minutes after sunset and no hunting was permitted on Sundays (Gerrits et al. 2020). During 2014–2015, hunters in South Carolina could harvest up to 5 male wild turkeys; this bag limit was reduced to 3 in 2016. During 2014 to 2018, the Webb WMA Complex averaged 876 turkey hunters per year, with 70% of hunting activity occurring before April 15th and the highest concentration of hunters during the first week of the season (Gerrits et al. 2020). For more information about Webb WMA see Wightman et al. (2019).

We collected data during 2020–2023 on the non-hunted study site, which was the United States Department of Energy's Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell counties.

The SRS was approximately 78,000 ha located 30 km south of Aiken in the southeastern plains' ecoregion of South Carolina (Griffith et al. 2002). Forest composition on SRS was comprised of approximately 29,805 ha of pine (38%), 13,281 ha of hardwoods (17%), and approximately 2,073 ha (3%) of small wildlife openings (<3 ha). The total length of primary and secondary roads was 327 km and 1,872 km, respectively, corresponding to densities of 0.42 km/km² and 2.4 km/km². Management activities were conducted by the United States Forest Service (USFS) and consisted of prescribed fire, timber management, and roadside mowing. Forest composition and management strategies on SRS were like that of the Webb WMA complex.

METHODS

Capture and monitoring

We captured wild turkeys from January–March using rocket nets baited with cracked corn (Austin et al. 1972, Delahunt et al. 2010). Captured wild turkeys were sexed based on physical characteristics and aged by the ninth and tenth primary feathers (Pelham and Dickson 1992). Each individual was banded with a uniquely-numbered, aluminum rivet leg band (National Band and Tag Company, Newport, KY, USA). At the Webb WMA Complex, captured wild turkeys were fitted with GPS-VHF backpacks manufactured by Biotrack Ltd (Wareham, Dorset, UK). Transmitters were programmed to record a single night location (roost) at 2358:58 local time, followed by locations every 30 minutes between the hours of 0500 and 2000 throughout the spring and summer until the battery expired or the unit was recovered (Collier et al. 2017, Chamberlain et al. 2018). Once released from the capture site, we monitored individuals ≥3 times per week, with data downloads occurring twice per month using handheld very-high-frequency (VHF) units.

On SRS, we fitted wild turkeys with backpack-style Global Positioning System (GPS) transmitters (Guthrie et al. 2011; Lotek Wireless, Newmarket, ON, Canada; e-obs GmbH, Gruenwald, Germany). Transmitters recorded locations from 0500 through 2000 daily and one roost location nightly (2358:58) until the battery expired or the transmitter was recovered. Transmitters recorded locations hourly in 2020–2021 and every 15 minutes during 2022–2023 when the bird was active above a 50-cm/second threshold, determined by accelerometer variance, reverting to hourly when below this threshold. Activity was assessed using accelerometer data collected on 3 axes every 2 minutes, with movement bursts triggering more frequent GPS fixes when variance on the Z-axis exceeded the threshold. If variance remained below this threshold, the GPS reverted to a lower-resolution collection interval to conserve battery life. These thresholds were calibrated to align with turkey specific activity patterns. We monitored wild turkeys >2 times/week using telemetry and downloaded GPS data using handheld antennas and receivers (UHF/VHF) once per week.

Movement analyses

We restricted our analysis to data collected on adult males as a limited number of juveniles were captured at both sites due to project objectives and because hunters target and harvest mostly adult males (Wightman et al. 2024). We divided the datasets into pre-hunt, hunt, and post-hunt phases. We used season dates for the South Carolina spring turkey hunting season specific to the Webb WMA Complex (excluding a one-day youth hunt) to delineate phases, and each phase was 32 days. In 2014–2015, the hunting season was 31 days compared to 35 for the remainder of our study. However, we delineated a uniform period of 32 days for each phase across years because we assumed that including one extra day of non-hunting as a hunting day at the end of the 2014–2015 season and excluding the last 3 days of the hunting season in 2016–2018 would not bias our results. Previous research has demonstrated that hunting activity is low by the end of the season and male turkeys typically alter their movement

and resource selection early in the season when hunting activity is high (Roth et al. 2024). Furthermore, using this approach allowed us to evenly divide each 32-day phase into 4 8-day periods to investigate changes before, during, and after hunting, as well as temporal changes within the hunting season given hunter activity varies temporally across the season (Gerrits et al. 2020). We only included individual males in the 8-day period analyses if they had complete data for the entire 8 days. We conducted all data management and analysis in Program R version 4.3.2 (R Core Team 2023).

To investigate potential influences of hunter activity on movement behaviors, we first calculated 50% core areas and 95% home ranges for each 8-day period using a dynamic Brownian Bridge Movement Model (dBBMM) from package move (Cohen et al. 2018, Kranstauber et al. 2023, Moscicki et al. 2023). We used a margin of 3, window size of 7, and a location error of 21 m (Byrne et al. 2014*b*). The window size determines the number of consecutive locations used to estimate Brownian motion variance, ensuring sufficient data for detecting movement patterns. A margin of 3 specifies a buffer of locations on each end of the window where breakpoints cannot occur, stabilizing variance estimates. Location error, set at 21 m, accounts for GPS uncertainty in position estimates and informs movement variance calculations within the dynamic Brownian bridge movement model. For our second movement metric, we calculated the average minimum daily Euclidean distance traveled of each individual male for each 8-day period. We calculated daily distances using the move and adehabitatHR packages (Calenge and Fortmann-Roe 2023, Kranstauber et al. 2023) by summing the step lengths between all hourly locations recorded between 0500 and 2000. Although 30-minute and 15-minute intervals were available for some individuals, we chose to use only hourly fixes to ensure consistency and avoid comparisons across varying collection schedules. We estimated roost-site fidelity by developing a roost index (RI) following methods outlined in Byrne et al. (2015*b*) and Wakefield et al. (2020*a*). We extracted daily roost locations and calculated distances between roost sites, with roost locations buffered by 27.5 m to determine uniqueness. We calculated RI values for each individual during each period by subtracting the total unique roosts divided by the number of total roosts from 1 (RI = 1 − [total unique roosts/total roosts]). An RI value close to 1 would indicate a single roost site was used, whereas values approaching 0 would represent an increase in the number of unique roost locations.

To investigate the potential influence of hunting on the movement metrics, we used a before-during-after treatment study design to compare estimates from our hunted and non-hunted populations, where hunting was defined as the treatment. To reduce bias when estimating causal effects using observational data, it is advantageous to implement matching methods that account for individuals with similar behavioral metric distributions in the treated and control groups before treatment (Ho et al. 2007, Ribas et al. 2021). We performed matching analysis using the package MatchIt, which offers several matching methods that include nearest neighbor, optimal pair, optimal full, generalized full, genetic, exact, coarsened exact, subclassification, and profile matching (Ho et al. 2011). To determine which matching method best balanced individuals from the hunted and non-hunted populations before treatment, based on core area, range area, daily distance, and roost fidelity, we implemented the matching methods mentioned above and assessed balance using variance ratios, empirical cumulative distribution function plots, and standardized mean differences (Ho et al. 2007, Austin 2009, Ali et al. 2014).

The best matching method for our data, given the above approach, was subclassification. Subclassification is a coarse matching method that divides metrics of interest into bins and uses propensity scores to provide weights, which are used to account for differences in the matched individual's metric distribution in subsequent analysis (Austin 2010, Hong 2010, Desai et al. 2017). We used 6 subclasses and set the distance parameter equal to ridge (Ho et al. 2011). To estimate the marginal effects of hunting on each of the movement metrics, we used a method known as g-computation or regression estimation (Schafer and Kang 2008, Snowden et al. 2011). Specifically, we fit a linear model for each movement metric as the response variable, where study population, phase, and 8-day periods were the interacting predictors. We then set weight equal to the propensity scores calculated from the matching analysis (lm function, R Core Team 2023). We calculated the average treatment effect and predictions with confidence intervals using the package marginaleffects (Arel-Bundock et al. 2024). We considered differences in predictions with non-overlapping 95% confidence intervals significant.

Resource selection

We calculated step-selection functions for movement paths in each 8-day period before, during, and after hunting season to test for potential differences in resource selection between hunted and non-hunted populations (Duchesne et al. 2010, Thurfjell et al. 2014, Muff et al. 2020, Wightman et al. 2023*a*). We used distance to primary and secondary roads as covariates, as they represent areas with increased hunter activity and are known to influence male wild turkey resource selection (Gerrits et al. 2020, Wightman et al. 2023*a*, Roth et al. 2024). We obtained road data for SRS from the USFS and Webb WMA Complex from SCDNR and used 2019 USGS Tiger/Line data (Topologically Integrated Geographic Encoding and Referencing) to delineate roads outside the primary study sites. We calculated the nearest distance from each turkey use and associated random points to primary and secondary roads using the Euclidean distance tool in ArcGIS 10.5.1 (Environmental System Research Institute, Inc., Redlands, CA, USA). We also used distance to land cover types of hardwoods, pines, and openings as covariates, as these land cover types have been found to influence turkey resource selection (Felix et al. 1986, Vangilder and Kurzejeski 1995, Little et al. 2016*a*, Wightman et al. 2023*a*, Roth et al. 2024). We quantified land cover types using 30 × 30-m raster layers from the United States Department of Agriculture, National Agricultural Statistical Service for each site and year. We calculated Pearson's correlation coefficients to test for collinearity between each covariate and excluded those when $r > 0.60$.

We compared the aforementioned distance and land cover covariates at the end point of each actual step (a straight line connecting consecutive GPS locations) with a set of 50 random steps (Duchesne et al. 2010, Muff et al. 2020). We generated random steps by fitting a gamma distribution to the observed step lengths and a von Mises distribution to the relative turning angles specific to each individual, rather than the overall population, using the amt package (Signer et al. 2019). All tracks were standardized to 30-minute intervals using the track resample

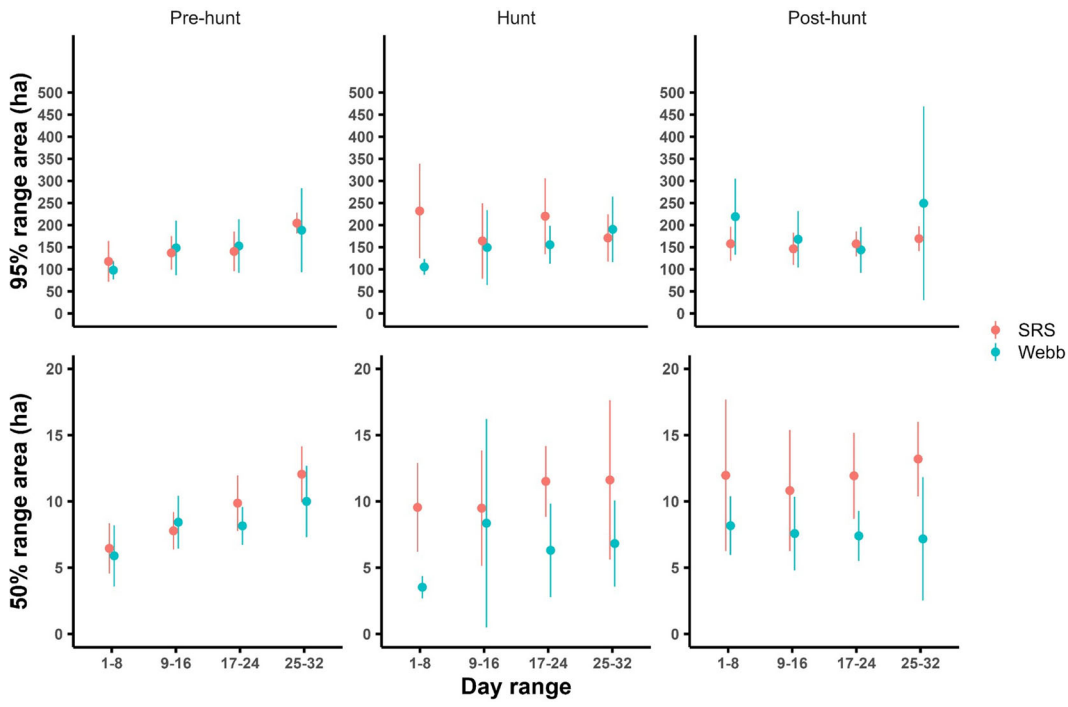

FIGURE 2 The predicted 95% home range area (ha) and 50% core area (ha) of male eastern wild turkey for 8-day periods before (Pre-hunt), during (Hunt), and after (Post-hunt) hunting season on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, during 2014–2018 at Webb and 2020–2023 at SRS.

function in the amt package to account for variation in collection schedules between 0500 and 2000 (Signer et al. 2019). Our approach created a stratified dataset of realized and random step locations, which we analyzed using a conditional Poisson regression, modeling stratum-specific intercepts as a random effect (Muff et al. 2020). We predefined the variance to a large value to ensure that stratum-specific intercepts did not converge toward their overall mean (Muff et al. 2020). We conducted statistical analyses using the glmmTMB package (Brooks et al. 2017), and included independent individual-specific slopes and intercepts for all covariates to account for individual variations in response to available conditions and unbalanced sampling (Muff et al. 2020). We did not use a model selection technique to rank candidate models because our global model incorporated the complete set of covariates previously used to study resource selection in male wild turkeys and all covariates were of interest. To determine the significance of the relationships, we examined the 95% confidence intervals for each beta coefficient and approximated the relative likelihood of selection for each covariate (Fortin et al. 2005).

RESULTS

We captured and marked 44 adult male wild turkeys on Webb WMA during 2014–2018 and 52 on SRS during 2020–2023. For the matching and subsequent analyses, we used GPS data from 37 adult males at Webb WMA and 39 from SRS. The remaining 20 males lacked data for the entirety of the pre-hunt phase due to mortality or transmitter failure. The mean 8-day period home ranges before, during, and after hunting season at the Webb WMA were 108 ha (SD = 118, min–max = 5–736), 114 ha (SD = 118, min–max = 6–521), and 129 ha (SD = 118, min–max = 5–622), respectively. The mean 8-day period home ranges at SRS were 198 ha (SD = 125, min–max = 25–456),

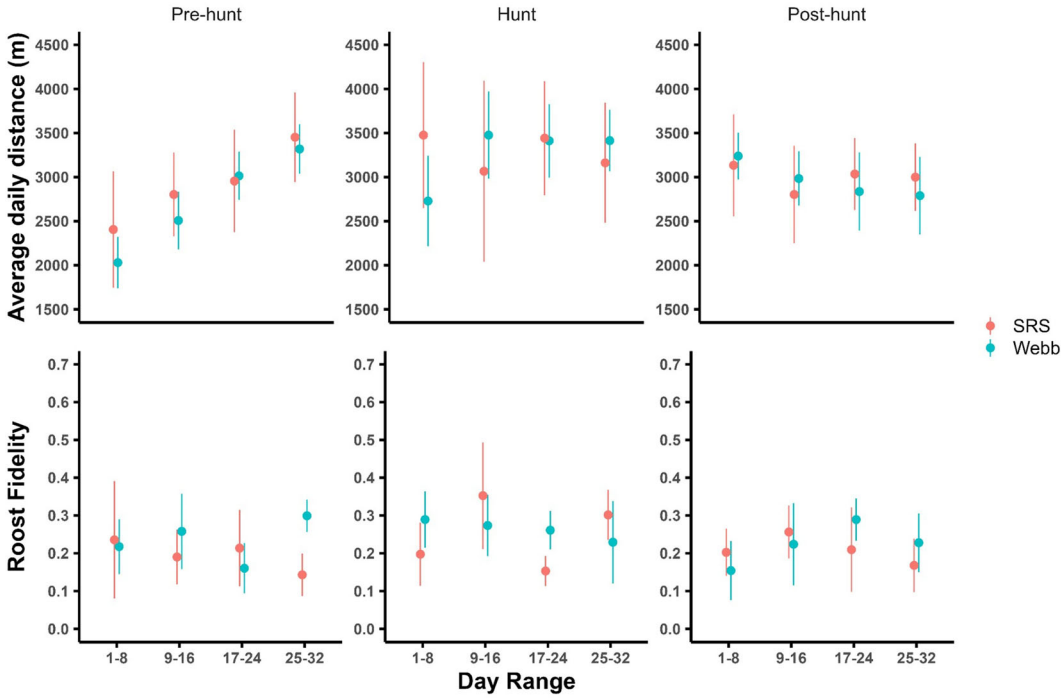

FIGURE 3 The predicted average daily distance (m) and roost fidelity of male eastern wild turkey for 8-day periods before (Pre-hunt), during (Hunt), and after (Post-hunt) hunting season on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, during 2014–2018 at Webb and 2020–2023 at SRS.

245 ha (SD = 129, min–max = 7–1,185), and 171 ha (SD = 125, min–max = 9–429), respectively. We observed a significantly smaller predicted home range area on the Webb WMA during the first 8 days of the hunting season, with an estimated reduction of 126.6 ha (95% CI = 1.0–257.8 ha), representing a 55% decrease relative to SRS (Figure 2). The mean 8-day period core areas before, during, and after hunting season at the Webb WMA were 6.9 ha (SD = 7.6, min–max = 0.4–21.5), 4.1 ha (SD = 7.7, min–max = 0.1–26.7), and 8 ha (SD = 7.7, min–max = 0.8–33.3), respectively. The mean 8-day period core areas at SRS were 10.1 ha (SD = 8.8, min–max = 0.6–44.1), 13.2 ha (SD = 8.8, min–max = 0.7–66.5), and 12.1 ha (SD = 8.8, min–max = 0.6–49.9), respectively. We observed significantly smaller predicted core areas on the Webb WMA during the first 8 days of the hunting season, with an estimated reduction of 6.1 ha (95% CI = 1.8–10.2 ha), representing a 64% decrease relative to SRS (Figure 2).

The 8-day period average daily distance traveled before, during, and after hunting season at the Webb WMA was 2,438.9 m (SD = 1,190.9, min–max = 606.7–5,396), 3,057.0 m (SD = 1,191.2, min–max = 667.5–6,001.1), and 2,793.5 m (SD = 1,190.7, min–max = 591–4,564.9), respectively. At SRS, average daily distance traveled before, during, and after hunting season were 3,530.2 m (SD = 1,202.4, min–max = 1,098.4–5,911.6), 3,972.5 m (SD = 1,215.5, min–max = 956.8–7,971.7), and 3,327.3 m (SD = 1,200.2, min–max = 737.6–5,625.1), respectively. We did not find any differences in the predicted average daily distance traveled during any 8-day period for males on the Webb WMA and SRS (Figure 3).

Mean 8-day period RI scores before, during, and after hunting season at the Webb WMA were 0.25 (SD = 0.19, min–max = 0–0.88), 0.3 (SD = 0.19, min–max = 0–0.88), and 0.28 (SD = 0.19, min–max = 0–0.75), respectively. At SRS, mean 8-day period RI scores before, during, and after hunting season were 0.19 (SD = 0.19, min–max = 0–0.75), 0.2 (SD = 0.19, min–max = 0–0.88), and 0.22 (SD = 0.19, min–max = 0–0.71), respectively. We observed increased RI scores on the Webb WMA during the last 8 days before the hunting season, with an estimated increase of 0.16 (95%

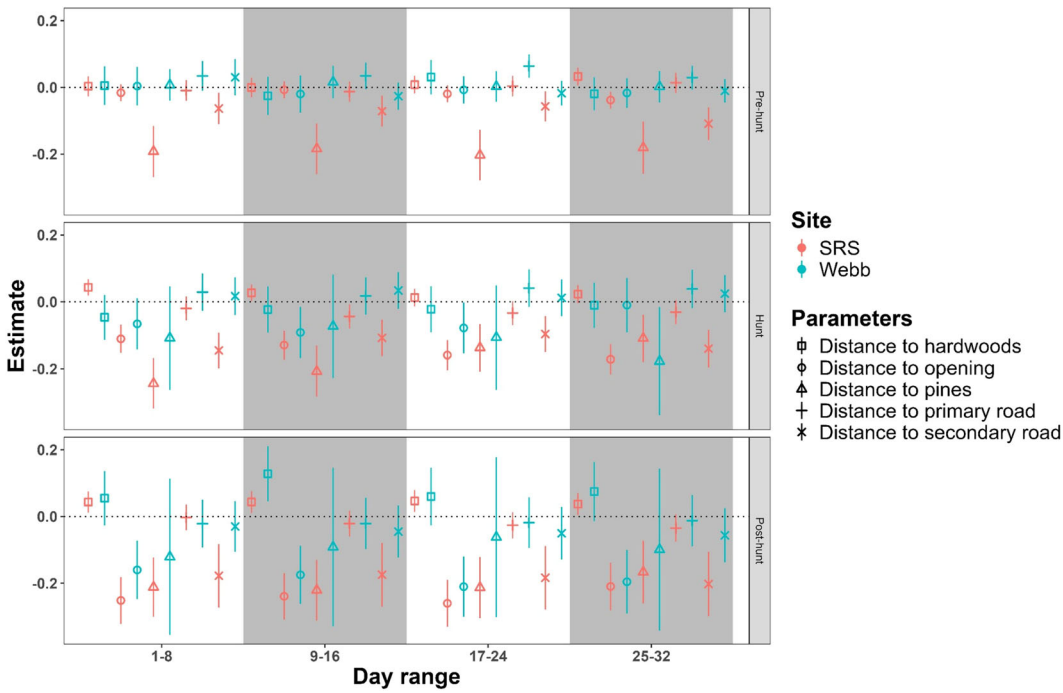

FIGURE 4 Parameter estimates of full model for 8-day step selection functions for male eastern wild turkeys on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, during 2014–2018 at Webb and 2020–2023 at SRS.

CI = 0.06–0.25), representing a 114% increase relative to SRS (Figure 3). Furthermore, we observed increased RI scores on the Webb WMA during the third 8-day period of the hunting season, with an estimated increase of 0.15 (95% CI = 0.02–0.20), representing a 100% increase relative to SRS (Figure 3).

On SRS, males selected to be closer to pines and secondary roads throughout the entire study period (Figures 4–6). Males also selected areas closer to primary roads later in March as the peak of breeding approached (i.e., end of pre-hunting phase; Figures 4, 7). Males began to exhibit selection for areas closer to openings as the hunting season approached. This selection became stronger and more pronounced during the remaining periods (Figures 4, 8). Conversely, males at SRS selected areas farther from hardwoods as the hunting phase approached. This selection generally continued throughout the remaining periods and phases (Figures 4, 9).

On the Webb WMA, patterns of selection for land cover metrics were less clear than on SRS, in that males did not generally exhibit strong selection for any land cover types (Figures 4–6). However, once hunting ended, males selected for areas closer to openings, similar to males on SRS (Figures 4, 8). Before hunting, we observed no significant selection for secondary roads but note that the selection coefficients suggested that males shifted from using areas farther from roads to areas closer to roads as that phase progressed (Figures 4, 5). However, this pattern changed with the onset and cessation of hunting; the direction of selection during hunting season was always farther away from secondary roads, but was closer after hunting ceased (Figures 4, 5). Although males on the Webb WMA Complex showed no selection for or against primary roads, beta estimates were positive during both the pre-hunt and hunting season phases, whereas they were negative once hunting season ended (Figures 4, 7). Lastly, we

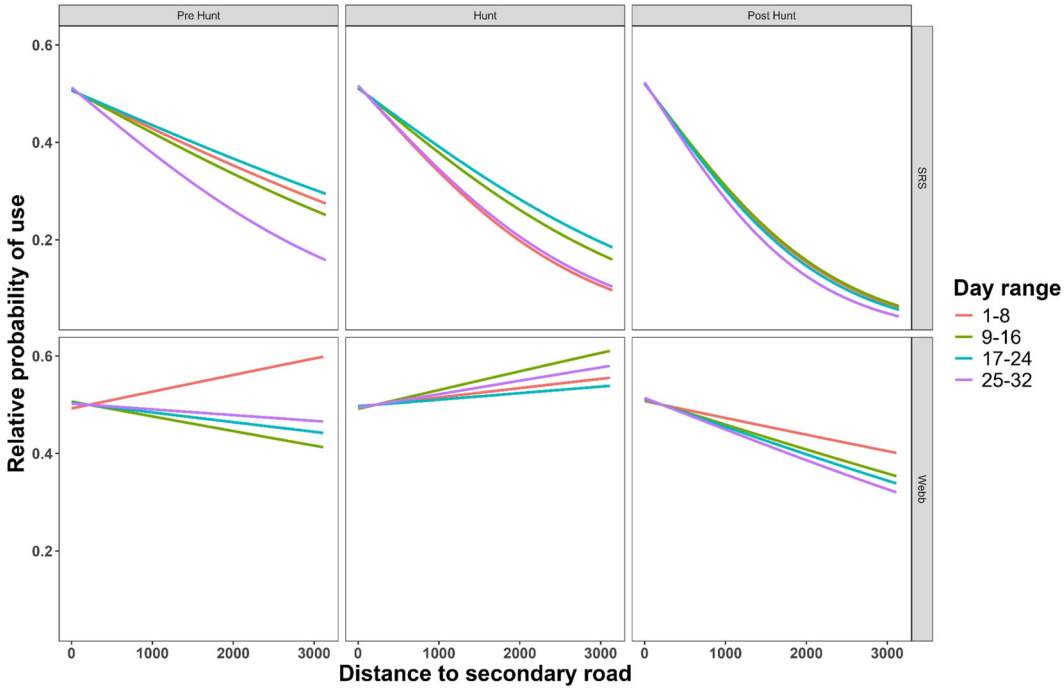

FIGURE 5 Relative probability of use from 8-day step selection functions for male eastern wild turkey on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, relative to distance (m) to secondary roads, during 2014–2018 at Webb and 2020–2023 at SRS. Predictions for the focal variable were generated by holding other non-focal variables at their mean value and based on the fixed-effects conditional model (i.e., averaged across random effect of individual). The 95% confidence intervals are omitted to better illustrate resource selection trendlines.

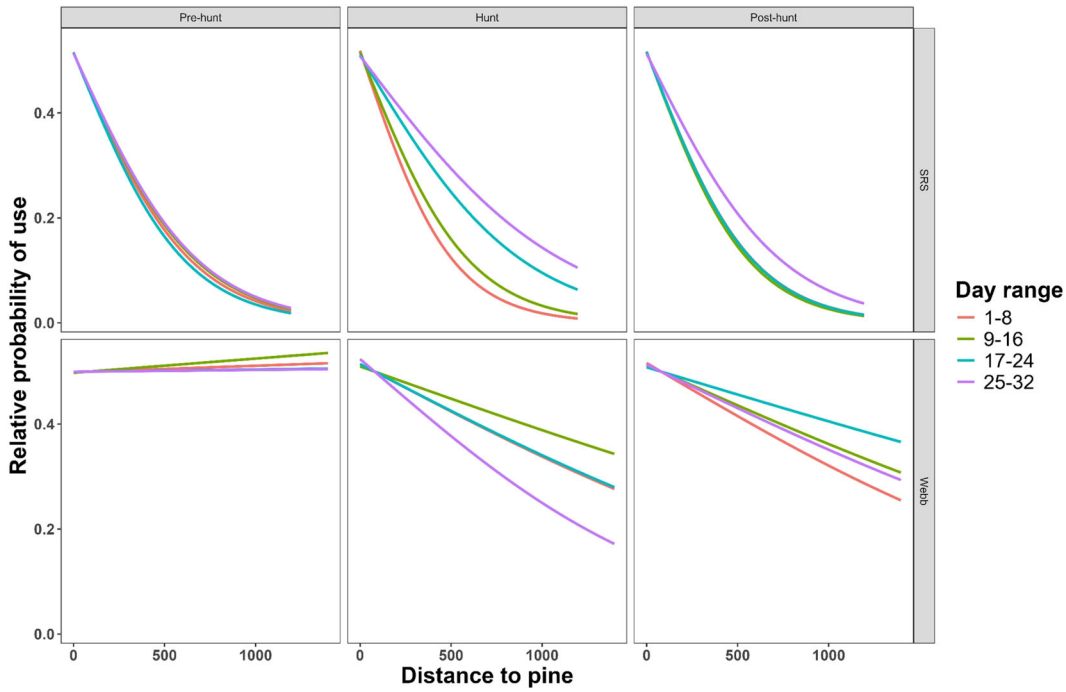

FIGURE 6 Relative probability of use from 8-day step selection functions for male eastern wild turkey on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, relative to distance (m) to pines, during 2014–2018 at Webb and 2020–2023 at SRS. Predictions for the focal variable were generated by holding other non-focal variables at their mean value and based on the fixed-effects conditional model (i.e., averaged across random effect of individual). The 95% confidence intervals are omitted to better illustrate resource selection trendlines.

observed that males exhibited no selection for or against hardwoods before or during hunting season, but selection coefficients suggested this pattern reversed after hunting ended.

DISCUSSION

Predation risk prompts prey to alter their behaviors both spatially and temporally; risks associated with human predators can disproportionately influence prey response relative to other predators (Gaynor et al. 2021, Wightman et al. 2023*a*). Contemporary literature has demonstrated that predation risk from hunting can alter various behaviors of hunted species (Little et al. 2016*b*, Mohlman et al. 2019, Wakefield et al. 2020*b*, Wightman et al. 2023*b*). We used matching methods to pair males with similar distributions of each behavioral metric to reduce bias when estimating causal effects of hunting on male wild turkey behavior. We found that males in the hunted population maintained smaller home range and core use areas once hunting season began, but these responses dissipated after approximately the first week of hunting season. We also observed that males in the non-hunted population selected areas closer to openings and secondary roads, whereas males in the hunted population tended to exhibit the reverse until hunting season ceased. Our findings contribute to a growing body of literature suggesting that male wild turkeys alter their behaviors in response to hunting activity, but these alterations do not persist.

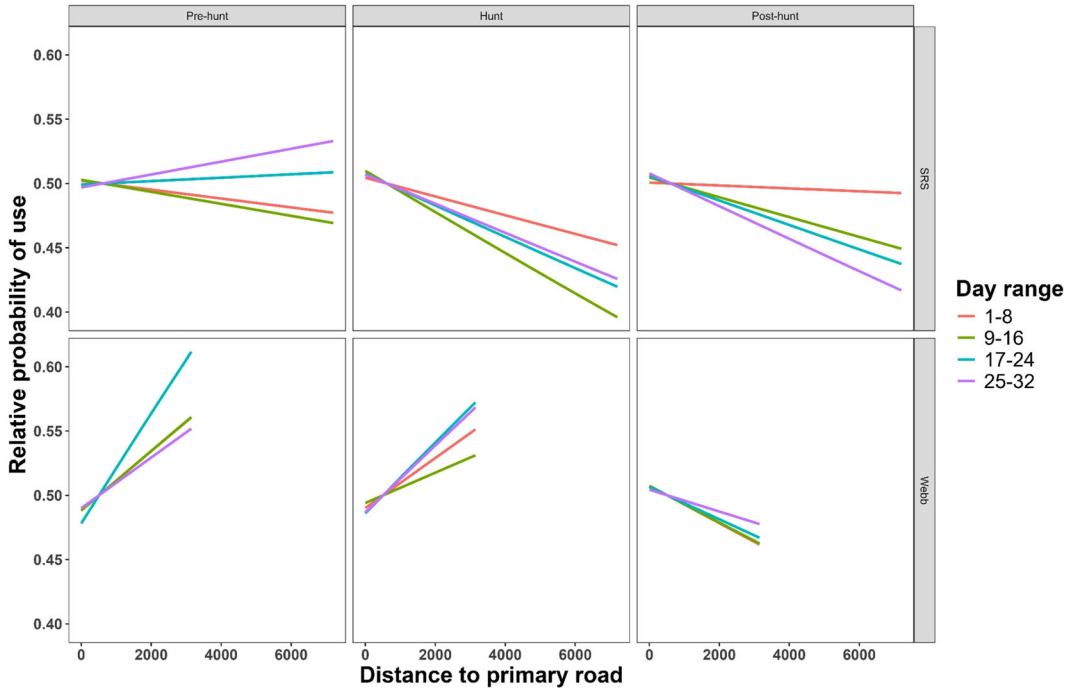

FIGURE 7 Relative probability of use from 8-day step selection functions for male eastern wild turkey on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, relative to distance (m) to primary roads, during 2014–2018 at Webb and 2020–2023 at SRS. Predictions for the focal variable were generated by holding other non-focal variables at their mean value and based on the fixed-effects conditional model (i.e., averaged across random effect of individual). The 95% confidence intervals are omitted to better illustrate resource selection trendlines.

We observed that male wild turkeys exposed to spring hunting exhibited a decrease in home range and core areas during the 8-day period after hunting season began, corresponding with the peak of hunter activity and hunting pressure (Hubbard and Vangilder 2005, Gerrits et al. 2020). Using data from our hunted site, Roth et al. (2024) noted similar patterns, with males altering behaviors immediately after the onset of hunting, primarily through the avoidance of secondary roads and areas with greater risk of hunter activity. Similarly, Gross et al. (2015) reported that male wild turkeys responded to the onset of hunting activity by reducing space use, a response also observed in other game species (Marantz et al. 2016). We speculate that reduction of space use by male wild turkeys with the onset of hunting season results from 2 potential and non-mutually exclusive behavioral responses. Specifically, previous works have noted that in response to hunting, many game species spend more time being vigilant (Schuttler et al. 2017, Wilson et al. 2020, Crawford et al. 2022) and use a smaller, reduced set of more familiar locations within their home range to reduce predation risk (Yoder et al. 2004, Forrester et al. 2015, Gehr et al. 2020). Collectively, it is plausible that increased vigilance and use of familiar locations in an individual's range likely contribute to temporal reductions in space use, offering a potential explanation for the observed reductions in space use by male wild turkeys after the onset of hunting season.

Extensive literature has detailed how game species alter movements in response to hunting, ranging from instances of individuals substantially increasing movements (Cleveland et al. 2012, Brown et al. 2020) to those noting the opposite (Ciuti et al. 2012, Hodges et al. 2014, Picardi et al. 2019). We failed to detect any differences in average minimum daily distance traveled for male wild turkeys between a hunted and non-hunted population, consistent with

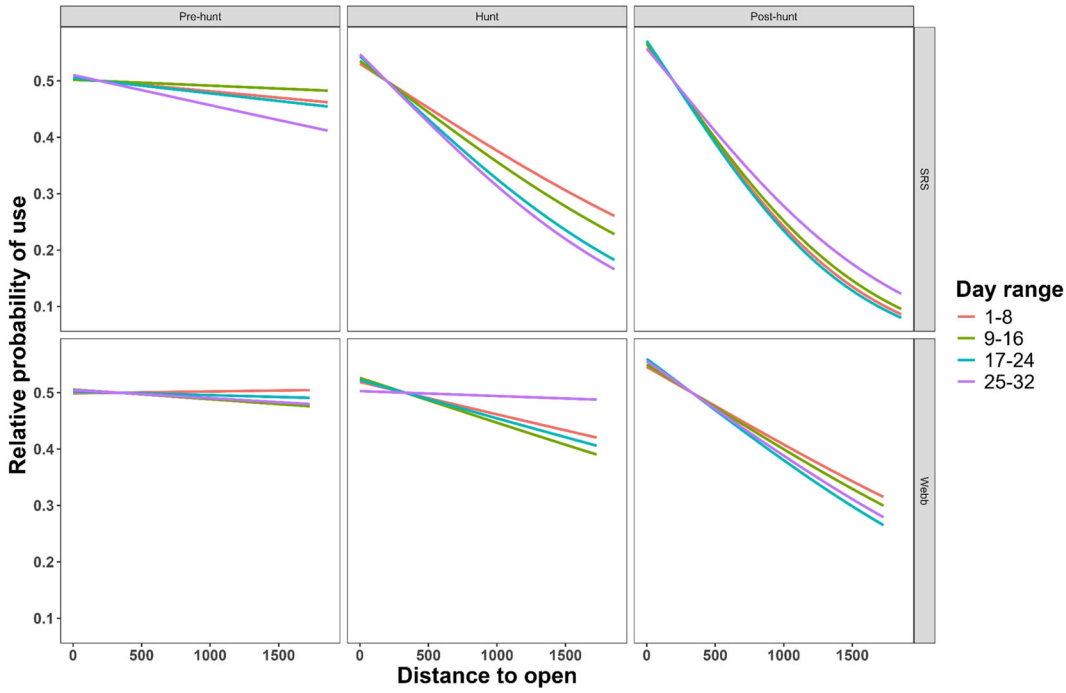

FIGURE 8 Relative probability of use from 8-day step selection functions for male eastern wild turkey on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, relative to distance (m) to openings, during 2014–2018 at Webb and 2020–2023 at SRS. Predictions for the focal variable were generated by holding other non-focal variables at their mean value and based on the fixed-effects conditional model (i.e., averaged across random effect of individual). The 95% confidence intervals are omitted to better illustrate resource selection trendlines.

studies on other game species demonstrating little influence of hunting season on individual movements (Hodges et al. 2000, Neumann and Ericsson 2018). However, we note that the greatest separation in estimates of average daily movements between sites occurred during the first 8 days after hunting season began and suspect this separation was a weak signal of differences in movements already captured in our estimates of space use. Furthermore, Wightman et al. (2023*a*) found that male wild turkeys increased movement to flee the area directly after encountering a hunter. We postulate that this could dilute any relationship at the average daily distance traveled scale, as turkeys may initially increase movements in the presence of hunters but then decrease distances traveled to reduce future encounters. Future studies should incorporate higher-resolution GPS collection schedules when comparing daily distances to better capture fine-scale movements, as coarser hourly intervals may overlook travel patterns. Regardless, we also observed that the overall trend for males in both populations was increasing daily distances traveled as the study period progressed before decreasing gradually as the study period ended, similar to findings detailed by Chamberlain et al. (2018). Last, we observed highly variable estimates of roost fidelity between populations, although males in our hunted population did exhibit greater fidelity to roosts immediately before and during hunting season. Gross et al. (2015) noted that male wild turkeys used greater distances between consecutive roosts during hunting season and speculated that males may perceive risks associated with hunters and adjust their roosting behaviors accordingly, similar to findings detailed in Wakefield et al. (2020*a*).

Previous studies have noted the influence that roads have on various aspects of wild turkey behavior (Thogmartin and Johnson 1999, Yeldell et al. 2017, Wood et al. 2019, Roth et al. 2024). We found that male wild

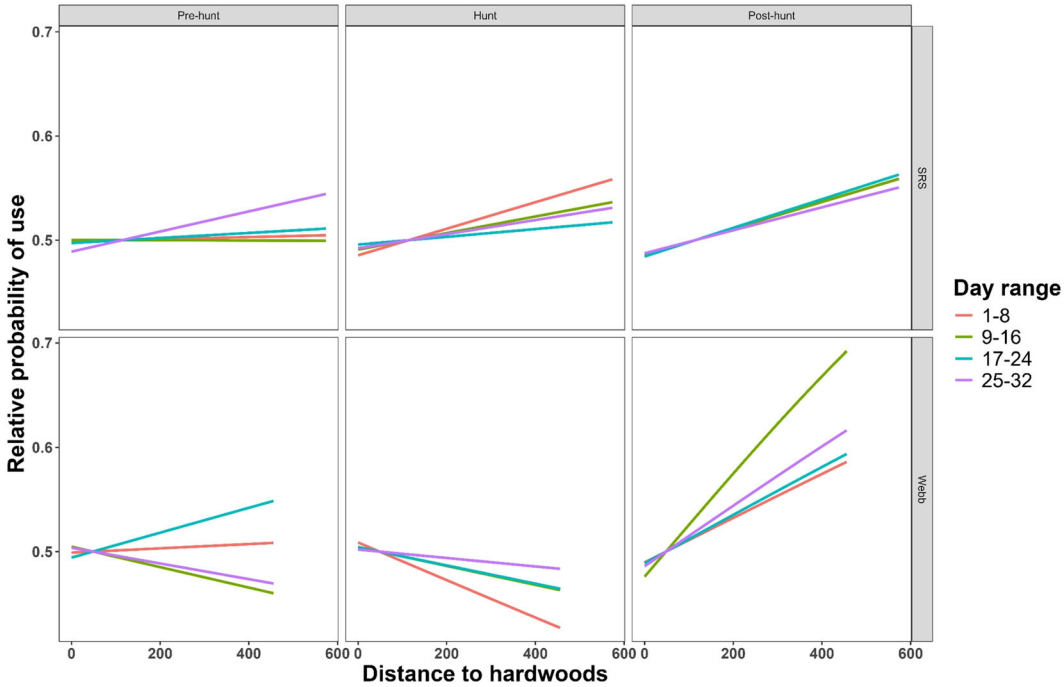

FIGURE 9 Relative probability of use from 8-day step selection functions for male eastern wild turkey on the Webb Wildlife Management Area Complex (Webb) and Savannah River Site (SRS) in South Carolina, USA, before (Pre-hunt), during (Hunt), and after (Post-hunt) spring wild turkey hunting season, relative to distance (m) to hardwoods, during 2014–2018 at Webb and 2020–2023 at SRS. Predictions for the focal variable were generated by holding other non-focal variables at their mean value and based on the fixed-effects conditional model (i.e., averaged across random effect of individual). The 95% confidence intervals are omitted to better illustrate resource selection trendlines.

turkeys not exposed to hunting consistently selected areas closer to secondary roads, whereas those exposed to hunting did not exhibit similar selection. Although not significant, beta estimates for male responses to secondary roads in our hunted population were positive throughout all phases of the hunting season, suggesting that males exhibited avoidance of secondary roads. Our finding is not surprising, as contemporary literature on wild turkeys continues to report an avoidance of roads and the corresponding predation risk that roads pose after hunting season begins (Wightman et al. 2023*a*, 2023*b*; Roth et al. 2024).

In pine-dominated landscapes containing hardwood forests at lower elevations, wild turkeys typically constrain habitat selection to hardwood forests during winter before shifting selection to upland pine forests and areas containing openings (Palmer et al. 1996, Miller et al. 1999, Byrne et al. 2014*a*, Wood et al. 2018). We observed this trend by males on the non-hunted site, as they progressively selected areas farther from hardwoods as the study period progressed, while also exhibiting an increasingly pronounced selection for pine forests and openings. Conversely, patterns of resource selection by males on our hunted site were more variable, in contrast to those same patterns in the absence of hunting. Males on our hunted site showed no selection for openings either before or during hunting season, but did select openings once hunting season ended, a behavior also observed in other hunted wild turkey populations (Wightman et al. 2023*a*). Reduced or altered use of open areas, where prey species are visible or otherwise vulnerable to predators and face elevated predation risk, is well documented for many prey species (Camp et al. 2012, Kohl et al. 2019). Our finding of no selection for or against pines by males in the hunted population also mirrors findings of Wightman et al. (2023*a*), which focused on a different hunted population of wild turkeys.

Roth et al. (2024) noted that hunter activity increased closer to pine landcover types, offering a plausible explanation for these differences in selection of pine between males in a hunted and non-hunted population.

We note that previous studies have provided equivocal conclusions relative to how male wild turkeys alter movement behaviors in response to hunting, mostly driven by substantive interindividual variability in responses of males during periods when hunting occurred or did not. For instance, Collier et al. (2017) reported that on our hunted site, males decreased movements in response to hunting but suggested that such decreases were not biologically significant, concluding instead that individual variation in movements most influenced their results. The authors recommended that accounting for individual variation of male movements should be prioritized to better understand how hunting may influence wild turkey behaviors.

Contemporary literature continues to demonstrate the importance of inter-individual variation in behavioral traits, with studies stressing the importance of focusing analyses on individuals to improve inferences (Merrick and Koprowski 2017). We used a matching analysis and paired individuals with similar movement metrics from a hunted and non-hunted population, thereby accounting for some individual variation in behavioral responses to hunting (Ribas et al. 2021). We offer that our findings contribute to improved and more accurate causal inference pertaining to how male wild turkeys respond to hunting activity. Future studies interested in how hunting activities influence wild turkey behavior, such as gobbling activity, would benefit from using similar methods to compare the behavior of individuals from a hunted and non-hunted population. Furthermore, we recommend that future studies incorporate a similar matching-based analytical approach to better infer potential influences of other factors, such as disease prevalence or habitat management strategies, on wild turkey behavior and fitness.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (protocol No. A2023 04-017-Y1-A0) and the Louisiana State University Agricultural Center (protocol Nos. A2014-013 and A2015-07).

DATA AVAILABILITY STATEMENT

Data available on reasonable request from the authors.

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