Impacts of wild pigs *(Sus scrofa*) on the breeding and non-breeding season movements and space use of wild turkeys (*Meleagris gallopavo*)

by

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Abstract

Wild pigs (*Sus scrofa*) are an impactful invasive species that have saturated the southeastern United States over the last three decades. During this same period, wild turkeys (*Meleagris gallopavo*) have experienced notable declines in productivity. Previous camera studies have suggested a negative temporal relationship between wild pigs and wild turkeys; however, the spatial aspect of this relationship has never been investigated. We explored the relationship between wild pig densities and the movement ecology of wild turkeys in central-eastern Alabama during the pre-breeding period and spring reproduction season of wild turkeys. We found that wild pig density had a range of negative impacts on wild turkey space use across seasons. We believe that wild turkeys perceived wild pigs as disturbance risk and avoided areas with high wild pig densities. Efforts to decrease wild pig populations may alter movements and have positive impacts on condition and production of wild turkeys.

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Chapter 1: Wild pigs impact reproductive season movements and space use of wild turkeys

Abstract

Impacts of invasive species on the movements and space use of native fauna have major implications during the reproductive period. Over the last three decades, wild pigs (*Sus scrofa*) have become an impactful invasive large mammal in the southeastern United States. Additionally, throughout the southeastern United States there has also been a notable decline in productivity of native wild turkeys (*Meleagris gallopavo*). Camera surveys have shown that the presence of wild pigs negatively impacts detection of wild turkeys in areas of overlapping use. We explored whether avoidance of wild pigs by wild turkeys can define population-level space use by wild turkeys during breeding season. We deployed 22 GPS units on wild turkeys prior to the spring reproductive season and conducted a 1-km^2 gridded camera survey in early summer to estimate densities of wild pigs across our 9,000-ha study area in east-central Alabama. We addressed reproductive season movement ecology of wild turkeys in relation to relative densities of wild pigs in terms of (1) step length, (2) daytime space use, (3) roost site selection, and (4) nest site selection. We hypothesized that wild turkeys would exhibit longer step lengths and avoid daytime use, nighttime roost selection, and nest placement in areas with greater densities of wild pigs. We found that density of wild pigs negatively impacted movement metrics of wild turkeys. Specifically, greater densities of wild pigs were associated with longer step lengths and lower probabilities of daytime use, roost site selection, and nest site selection in wild turkeys. Rate of movement and probability of use are associated with preference for the ecological attributes of an area. Our results suggest that wild turkeys avoided or were excluded from areas with greater densities of wild pigs due to perceived disturbance risk or wild pigs making areas

less usable. Our results have implications for interspecific spatial interactions as well as management activities to reduce the impacts of invasive wild pigs on native species.

Background

Wild turkeys (*Meleagris gallopavo*) are an important cultural and ecological game species of North America. With hunting of wild turkeys generating an annual estimated $7 billion in economic activity in the United States (U.S.) (Boone et al 2023), maintaining huntable populations remains a critical objective of wildlife management. Therefore, the documented decline in productivity of wild turkeys over the past several decades in the southeastern U.S. has been met with concern (Godfrey 1988, Clontz et al. 2021). Myriad factors have been suggested to contribute to diminished recruitment including decreases in habitat availability, overharvest through hunting activities, increases in predator populations, and interactions with introduced species (Cathey et al. 2007, Tapley et al. 2011, Byrne et al, 2015, Eriksen et al. 2015). An introduced species of particular interest is the wild pig (*Sus scrofa*) which has seen pronounced increases in range and density across the southeastern U.S. over the past three decades (McDonough et al. 2022). Wild pigs have been documented to impact native fauna through nest depredation, disease transmission, competition for resources, degradation of habitat, predation, and potentially exclusionary behaviors due to perceived disturbance risk (McDonough et al. 2022). The latter is of particular interest in the context of interspecific spatial interactions during reproductive periods due to potential downstream impacts on recruitment.

Native species can exhibit changes in fine-scale space use due to perceived risk from invasive competitors that subsequently impact population-level distribution patterns (Perez et al. 2017). Avoidance of encounters with invasive competitors such as wild pigs can result in shifts in patterns of resource selection (Silveira de Oliviera et al 2020, Dykstra et al. 2023, Garabedian et al 2023). Evidence suggests that wild pigs can impact species richness, resource availability, and spatiotemporal resource use by native fauna (Hegel et al. 2019, Osugi et al. 2019). Changes in rates and patterns of movement in relation to resource selection can have fitness implications (Berggren et al. 2002, Hodges et al. 2014, Wiens et al. 2014, Chamberlain et al. 2019). Perceived risk can play a role in resource selection, which has been documented in elk (*Cervus canadensis*) that shifted population-level spatiotemporal resource selection due to perceived risk from hunting activity and had the greatest impacts on reproductively active females (Spitz et al. 2019). Recent research has suggested potential negative spatiotemporal interactions between wild pigs and wild turkeys (Lewis et al. 2022, McDonough 2023, Smith 2023). Variation in observations of wild turkeys with respect to wild pig abundance may be driven by (1) wild turkey recruitment improving due to greater nest success or brood survival, or (2) wild turkeys avoiding or being excluded from areas with greater densities of wild pigs.

We evaluated whether wild turkeys avoided areas based on variation in density of wild pigs during the reproductive period for wild turkeys in east-central Alabama (1 March to 1 June 2022). We used a camera survey to estimate wild pig densities in areas where wild pigs and wild turkeys co-existed. We used GPS-tagged wild turkeys and developed resource selection functions (RSF) for wild turkey movements. We focused on whether there existed a relationship between relative densities of wild pigs and movement metrics of wild turkeys (including step length, daytime space use, roost site selection, and nest site selection). We hypothesized that areas with greater densities of wild pigs would observe greater step lengths and lower probabilities of daytime use, roost site selection, and nest site selection. Greater step lengths are associated with faster rates of movement (Wakeling et al. 2022), which would potentially indicate an avoidance behavior (Lima and Dill 1990). Reduced daytime use, roost site selection, and nest site selection would also indicate lower preference for areas with greater densities of wild pigs (Stankowich and Blumstein 2005, Broekhuis et al. 2013).

Study Area

Our study was conducted on 9,186 ha of contiguous privately-owned properties comprised of seven adjoining landowners. Located in the upper coastal plain in east-central Alabama, the study area was comprised of 5,562 ha of forest cover (60.5%), including 3,333 ha of pine (36.3%), 1,330 ha of hardwood (14.5%), and 899 ha of mixed pine-hardwood (9.8%). Open cover comprised 1,823 ha (19.9%) of the study area. The region had a subtropical climate with warm wet winters and hot humid summers (average annual temperature of 18 °C and approximately 133 cm of annual rainfall; Long 1974). Land management objectives on these properties were primarily timber production and promotion of game species such as white-tailed deer (*Odocoileus virginianus*), northern bobwhite (*Colinus virginianus*), mourning dove (*Zenaida macroura*), and wild turkey. Forests were dominated by longleaf (*Pinus palustris*) and loblolly (*Pinus taeda*) pine, with intermixed hardwood stands of oaks (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and elm (*Ulmus* spp.) (Godfrey 1988, Samuelson 2020). Noteworthy, the 476 ha property in the southeastern corner of the study area (camera locations 3-6 and 10-12) was enclosed by an 2.5 m fence and had no wild pigs (Figure 1).

Methods

Deployment of GPS units on wild turkeys

We deployed 31 backpack-style GPS-VHF units (Lotek UK Ltd, Wareham, UK) on wild turkeys (13 males, 18 females) captured with rocket nets over areas baited with cracked corn during January-March 2022 (Henry 1968, Bakner et al. 2023). Age was determined by presence of barring on ninth and tenth primary feathers and sex was determined by breast feather coloration (Pelham et al. 1992). Individuals were each outfitted with an aluminum rivet leg band (National Band and Tag Co., Newport, Kentucky, U.S.), and all capture and handling procedures were approved by Auburn University IACUC (PRN: 2021-3994). Each GPS-VHF unit was programmed to collect locations every two hours between 0600 and 2000 daily, with an additional point taken at 0000 for roost location. Units were also programmed to emit a mortality signal after 18 hours of no detected movement. There were nine individuals (3 males, 6 females) that died prior to data collection, two within the 14-day window of capture myopathy (Brunjes et al 2007). The remaining 22 wild turkeys (10 males and 12 females) were monitored weekly with Yagi antennas throughout the 1 March to 1 June 2022 study period.

Executing camera survey

We conducted a camera survey in May 2022 following methods described by Lewis et al. (2022) and McDonough (2023) to estimate densities of wild pigs across the study area. A 1-km^2 grid was applied over the study area in ArcGIS Pro™ (Esri, Redlands, California, U.S.) to determine locations for camera deployment. Grid cells that were < 25% within the bounds of the study area were excluded, creating 51 unique 1-km^2 cells. A camera was placed within a 300-meter radius buffer of the center of each grid cell (Figure 1.1). We based our spacing of cameras as 1-km^2 is less than the average home range size of wild pig sounders in the study area during the study period ($\bar{x}$ =3.45 km^2; Gomez-Maldonado n.p.).

Camera sites were initially baited with 11 kg of whole corn and rebaited every 3-4 days throughout the survey period. Cameras (ReconyxTM PC800 Hyperfire Professional IR Cameras, Reconyx Inc., Holmen, Wisconsin, U.S.) were deployed 7 days after the initial establishment of bait sites. Cameras were oriented north-south on trees, 1 m from the ground, 5 m from bait, with any visual obstruction removed. The cameras were programmed to take three images each time movement was detected with a one-minute buffer period between triggers. Cameras were deployed for seven days (Williams et al. 2011).

Estimating densities of wild pigs

We used TimeLapse2 V2.2.3.9 (University of Calgary, Calgary, CA) to estimate densities of wild pigs across the study area. We estimated the density of wild pigs in each grid cell to be the total number of unique individuals per camera. Individuals were identified by size, sex, pelage, unique physical characteristics, sounder association, and non-overlapping timing of visitation (Gomez-Maldonado et al. 2024). The camera survey took place outside peak reproduction season for wild pigs and without perturbation of wild pig populations (Ditchkoff et al. 2012), so we assumed a stable local population for the three-month study period (1 March to 1 June 2022). We note that our timeline is also shorter than the length of gestation (~115 days) in wild pigs, so we assumed no major influence of reproduction on the wild pig population (Henry 1968, Chinn et al. 2022).

Statistical analysis

We standardized counts of wild pigs per cell across the 51 surveyed grid cells as relative densities per 1 km^2. Relative density values were determined by ranking cell counts as percentiles (lowest = 0.0 and greatest = 1.0). Each percentile was assigned to a respective grid cell. Relative densities were assigned in ArcGIS Pro™ in 1 km^2 raster cells via the kernel density estimate tool. A 1 km buffer was created around the outside of the survey bounds to form the total study area, with buffer cell values determined as the average of adjacent survey cells (Pollentier et al. 2017, McClure et al. 2018, Crawford et al. 2021). No buffer was applied to cells bordering the high-fenced property (southeastern corner) because (1) the wild pig values within the fence were all zero and (2) the fence should not influence adjacent areas outside the fence (Figure 1.2). The camera and buffer values were re-interpolated in 30-m raster cells to match the resolution of the National Land Cover Data 2021 (NLCD 2021) to standardize raster cell size (Figure 1.1; Dewitz 2021).

We extracted land cover data at 30-m resolution from NLCD 2021 delineated as categories of pine forest, hardwood forest, mixed forest, open cover and riparian area. These land cover types had previously been determined to be biologically relevant cover types for wild turkeys (Holbrook et al. 1987, Chance et al. 2020). Pine cover was defined as evergreen (pine) trees > 5 m tall that occupy > 20% of total vegetation cover, with > 75% of total tree cover present belonging to species that retain leaves year-round. Hardwood cover was defined as deciduous (hardwood) trees > 5-m tall that occupy > 20% of total vegetation cover, with > 75% of tree cover present belonging to species that lose leaves with seasonal change. Mixed cover was defined as having > 20% vegetation cover of trees > 5 m tall while neither evergreen nor deciduous species consist of > 75% of total tree cover. Forest cover types of pine, hardwood, and mixed forest were each coded as present (1) or absent (0). Open cover types in NLCD 2021 of cropland, grassland, shrub, and road were combined as Open and coded as present (1) or absent (0). Riparian cover type was classified as present (1) or absent (0) within a 100 m buffer of water or wetland area. We used these land cover variables as interactions with wild pig density to determine the magnitude of effect wild pigs had on probability of use by wild turkeys in each cover type.

Movement data for wild turkeys was cleaned to remove erroneous fix locations with dilution of precision (DOP) > 7 and points outside the study area (Gupte et al. 2022). Movement data were then grouped into the following categories: ALL, MALES, BREEDING FEMALES, and NONBREEDING FEMALES. Females were categorized as BREEDING FEMALES from the start of the reproductive season (March 1) until the individual termination of nesting or brooding (Wightman et al. 2019, Wakefield et al. 2020). Females were categorized as NONBREEDING FEMALES from the first full day of inactivity from nesting or brooding to the end of the survey period (June 1). Step length and utilization distribution metrics for resource selection were determined via dynamic Brownian bridge movement models in package move in Program R (Kranstauber et al. 2012, R Core Team 2024). Step length was calculated as the Pythagorean distance between two consecutive points. Resource selection was evaluated via second-order selection of all point by grouping within the bounds of the study area (e.g., all daytime space use points for BREEDING FEMALES grouping; Johnson 1980).

We applied a generalized linear model to examine step length relative to estimated densities of wild pigs. Step length calculations were extracted for step-to points. Relative wild pig density was extracted to points by grouping (ALL, MALES, BREEDING FEMALES, and NONBREEDING FEMALES). Land cover variables were not included in this portion of the analysis because line segments could cross multiple cover types in each step. We applied an RSF to compare known and random points to determine selection or avoidance behaviors in association with relative wild pig densities for daytime space use. An equal number of random points to known points were created within the available space for each grouping (ALL, MALES, BREEDING FEMALES, and NONBREEDING FEMALES). We employed the model selection methodology of Bakner et al. (2024) for inclusion of land cover types with known importance in wild turkey ecology (hardwood, mixed, open, pine, and riparian). We used a generalized linear model for interactions between relative wild pig density and land cover types.

We examined impacts of wild pigs and interactions with land cover type on roost site selection by using an RSF for known and random nighttime roost sites. Roost site locations were selected as midnight locations (Cohen et al. 2018, Bakner et al. 2023). An equal number of random points were assigned within the MCP of all roosting sites within the study area for each grouping (ALL, MALES, BREEDING FEMALES, and NONBREEDING FEMALES). Predictor variables of relative wild pig density and land cover variables were extracted to both roost and random points. Again, we employed the model selection methodology of Bakner et al. (2024) for inclusion of land cover types with known importance in wild turkey ecology (hardwood, mixed, pine, and riparian). We used a generalized linear model for interactions between relative wild pig density and land cover types. Open cover type was included for BREEDING FEMALES because female wild turkeys roost on the ground during nesting and brooding activities (Lehman et al. 2010, Carpenter et al. 2023).

During the reproductive season, females were monitored twice per week to determine nesting activity. If actively nesting, then females were checked daily with VHF to monitor nest fate. Nests were checked in-person within 24 hours of nest termination or after 28 days post initiation of incubation. There were 16 nests within the study area that were verified in-person. Two nests successfully hatched poults which were verified in-person as having the presence of egg pipping. Due to low sample size of nests, five times the number of known points (80 total) were assigned as random points within the MCP of all nesting sites within the study area. The generalized linear model for was applied as an RSF for known and random nests to examine second-order use-availability selection for nest site in relation to relative wild pig density. Land cover interactions were not included due to low sample size of nest sites.

Results

A total of 22 wild turkeys (10 males, 12 females) were monitored during the 1 March to 1 June 2022 study period. All 12 females nested and thus were classified as BREEDING FEMALES from the beginning of the study period (1 March 2022) until the cessation of individual nesting or brood rearing. One female was predated while nesting, so we classified 11 females as NONBREEDING FEMALES from the first day post individual nesting or brooding until the end of the study period (1 June 2022). Raw densities of wild pigs from the camera survey ranged from 0-42 pigs/km^2 and were standardized to 0.0-1.0 pigs/km^2.

Relative density of wild pigs was positively associated with step length for ALL grouping, NONBREEDING FEMALES, and MALES (Table 1.1). The average step length was 253.5 m for the ALL grouping, 231.8 for BREEDING FEMALES, 216.6 for NONBREEDING FEMALES, and 288.5 m for MALES. For every 10% increase in relative wild pig density, we observed a 12.5 m increase in step length for the ALL grouping ($P < 0.001$), a 43.6 m increase in step length for NONBREEDING FEMALES ($P < 0.001$), and a 7.0 m increase in step length for MALES ($P < 0.001$).

We observed a negative relationship between wild pig density and probability of daytime use by wild turkeys for the ALL grouping ($\beta = -2.17$, $P < 0.001$), BREEDING FEMALES ($\beta = -3.83$, $P < 0.001$), NONBREEDING FEMALES ($\beta = -1.62$, $P < 0.001$), and MALES ($\beta = -3.63$, P

< 0.001; Table 1.2; Figure 1.3). We also observed a negative relationship between wild pig density and probability of daytime use across multiple land cover types. Wild pig density had a negative relationship with probability of daytime use in pine cover for the ALL grouping ($\beta = -1.63$, $P < 0.001$), BREEDING FEMALES ($\beta = -1.87$, $P < 0.001$), and MALES ($\beta = -1.52$, $P < 0.001$). Wild pig density also had a negative relationship with probability of daytime use in hardwood cover for the ALL grouping ($\beta = -0.83$, $P < 0.001$). However, BREEDING FEMALES had a positive relationship between wild pig density and probability of use in hardwood cover ($\beta = 0.89$, $P = 0.017$). Wild pig density had a negative relationship with probability of daytime use in mixed cover for the ALL grouping ($\beta = -1.86$, $P < 0.001$) and MALES ($\beta = -1.58$, $P = 0.001$). In riparian cover, wild pig density had a negative relationship with probability of daytime use for the ALL grouping ($\beta = -3.26$, $P < 0.001$), BREEDING FEMALES ($\beta = -2.05$, $P < 0.001$), NONBREEDING FEMALES ($\beta = -0.70$, $P = 0.029$), and MALES ($\beta = -2.31$, $P < 0.001$). Additionally, wild pig density had a negative relationship with probability of daytime use in open cover for NONBREEDING FEMALES ($\beta = -0.81$, $P = 0.045$). When examining wild pig density by quantile, we also found a stepwise reduction in predicted probability of daytime use by grouping as wild pig density increased (Table 1.3). From the lowest (0.0) to the greatest (1.0) wild pig density, we observed a decrease in predicted probability of daytime use of 52.3% for the ALL grouping, 73.6% for BREEDING FEMALES, 37.8% for NONBREEDING FEMALES, and 67.8% for MALES.

Probability of roost site selection was negatively related to wild pig density for the ALL grouping ($\beta = -4.40$, $P < 0.001$), BREEDING FEMALES ($\beta = -5.12$, $P < 0.001$), NONBREEDING FEMALES ($\beta = -3.16$, $P < 0.001$), and MALES ($\beta = -5.55$, $P < 0.001$; Table 1.4; Figure 1.4). The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had

12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals. The direction and significance (P) of the β-estimate indicates the log-odds ratio of effect of the interaction term. The "Pig *Open" interaction was included for BREEDING FEMALES because female wild turkeys roost on the ground during nesting and brooding. Additionally, wild pig density had a negative relationship with probability of roost site selection in hardwood cover for MALES ($\beta = -3.98$, $P = 0.027$). When examining wild pig density by quantile, we found a stepwise reduction in predicted probability of nighttime roost selection by grouping as wild pig density increased (Table 1.5). From the lowest (0.0) to the greatest (1.0) wild pig density, we observed a decrease in predicted probability of nighttime roost selection of 69.2% for the ALL grouping, 75.5% for BREEDING FEMALES, 53.4% for NONBREEDING FEMALES, and 57.8% for MALES.

A total of 16 nests were initiated by the 12 females in the BREEDING FEMALES grouping, as renesting occurred (Figure 1.5). The average relative density of wild pigs was 0.31 for all nest sites and 0.41 for random nest sites, with the two successful nests respectfully at 0.14 and 0.44. Additionally, nest site selection by BREEDING FEMALES was negatively related to wild pig density ($\beta = -0.62$, $P = 0.016$; Figure 1.6).

Discussion

We found that wild pigs had a range of predicted negative impacts on wild turkeys, suggesting a potential for wild pig density to influence movements and space use of wild turkeys. Namely, we observed evidence of variation in metrics of step length, daytime space use, roost site selection, and nest site selection related to wild pig density. Our results suggest that selection by wild turkeys for areas with lower densities of wild pigs indicated that (1) wild pigs were perceived as disturbance risk or (2) areas with greater densities of wild pigs were perceived as less favorable. Furthermore, while wild pigs may not serve as predators of adult wild turkeys, we posit that the drivers of differences in space use by wild turkeys are (1) inherent avoidance of areas associated with wild pigs or (2) exclusion from areas by wild pigs due to perceived risk of disturbance.

Whereas temporal avoidance or exclusion by wild pigs has been proposed for wild turkeys in previous camera survey studies (Walter et al. 2022, McDonough 2023, Smith 2023), a driver of variability or an explanation of spatial impacts has never been explored. The relationship between use of an area and selection for ecological attributes of that area is established in ecological theory (McIntyre et al. 1999, Potts et al. 2014). There is also precedent that areas avoided contain ecological attributes that are less favorable or invoke perceived risk (Stankowich and Blumstein 2005, Broekhuis et al. 2013). Inherent avoidance is supported in the context of wild pigs and wild turkeys by Walters and Osbourne (2021) in which rates of detection for wild turkeys decreased in areas of overlapping use with wild pigs. Prior research has also found that wild turkeys disproportionally used areas with reduced risk of predation (Wood et al. 2019, Wakefield et al. 2020). Again, while wild pigs may not pose a threat to adult wild turkeys in the form of predation, we believe the wild turkeys in our study perceived wild pigs as disturbance risk, leading to spatiotemporal avoidance or exclusion from areas of overlapping use.

We found that step lengths of wild turkeys were greater in areas with greater densities of wild pigs for the ALL, NONBREEDING FEMALES, and MALES groupings. Step length acts as an indicator for rate of movement and increases in rates of movement are associated with avoidance behaviors from perceived risks (Lima and Dill 1990, Wilson et al. 2015, Thompson et al. 2024). Pusenius et al. (2020) suggested that moose (*Alces alces*) adjusted rates of movement in relation to presence of grey wolves (*Canis lupus*). Similarly, Laundré et al. (2001) suggested that elk (*Cervus elaphus*) and bison (*Bison bison*) displayed behavioral responses to the presence of wolves that exceeded actual risk of predation. While not driven by risk of predation, we believe that wild turkeys exhibited disturbance-driven risk avoidance behaviors by increasing rates of movement in areas with greater densities of wild pigs. By moving quicker through areas of perceived risk, wild turkeys spent less time potentially exposed to disturbance threats associated with wild pigs. This potentially has downstream implications for condition in terms of energy use, feeding activity, and vulnerability to predation, as well as recruitment in terms of breeding activity and brood rearing.

We found a series of negative effects of wild pig density on movement rates of wild turkeys; however, whether these effects have biological significance is unknown. Step length serves as a representation of how space use affects daytime biological operations, including foraging efficiency and awareness of predatory threats (Thompson et al. 2024). An aspect of optimal foraging theory focuses on how rate of movement influences foraging efficiency, and variations from a given movement rate with respect to the optimal would result in reduced individual fitness (Pyke et al. 1977). Elevated movement rates due to risk aversion are associated with reduced foraging efficiency (Lima and Dill 1990, Wilson et al. 2015). Increased movement rates of turkeys in our study could theoretically have resulted in reduced foraging efficiency due to perceived disturbance risk by wild pigs. Step length is measured as linear distance (Thompson et al. 2024), and animals that are restricted to more linear movements may have enhanced risk of predation (Gilliam and Fraser 2001, Wilson et al. 2015). Adam and Stuart-Smith (2000) found that woodland caribou (*Rangifer tarandus*) had greater rates of predation when restricted to linear corridors. Similarly, Prokopenko et al. (2016) found that increases in linear movements by red deer (*Cervus elaphus*) resulted in greater rates of predation. Therefore, the influence of wild pigs to restrict movement patterns of wild turkeys via perceived disturbance risk may expose wild turkeys to greater risk of predation to predators such as bobcats and coyotes (Melville et al. 2015). Increased linearity of movement is also associated with faster rates of movement (Dickie et al. 2020). Thus, wild pigs may have influenced both the linearity and speed of movements of wild turkeys, resulting in longer step lengths through areas of greater wild pig density.

We observed wild turkeys exhibiting less daytime space use in areas with greater densities of wild pigs. A negative relationship between temporal use by wild turkeys in relation to wild pig density has been supported by several camera survey studies (Walters 2022, Hoskin 2023, McDonough 2023, Smith 2023). While these studies reported that wild pigs decreased detection or temporally displaced wild turkeys, our results indicate that the heterogeneity of space use by wild turkeys was influenced by the heterogeneity of wild pig density across the study area. We believe that wild turkeys either deliberately avoided areas associated with wild pigs or were actively excluded from areas by wild pigs. While we observed numerous negative interactions between wild pig density and land cover variables for probability of daytime use across groupings, we also found that wild turkeys in the ALL, BREEDING FEMALES, AND MALES groupings did not select against open cover in association with wild pig density. We believe that the value of open cover during the reproductive period may exceed the perceived disturbance risk incurred with wild pigs. Open areas are important for courting displays by male wild turkeys (Krakauer 2005, Sullivan et al. 2022), as well as valuable foraging areas during the reproductive period (Moore 2006, Sullivan et al. 2022). Therefore, when individuals became reproductively inactive (e.g. NONBREEDING FEMALES), the perceived disturbance risk associated with wild pigs manifested in a negative association with probability of daytime use in open cover. With open cover limited in availability in the study area, there were also no alternatives to openings used by wild pigs.

We also found a decrease in probability of roost site selection across each grouping of wild turkeys in relation to density of wild pigs. Suitable roost sites are important in wild turkey ecology to mitigate environmental exposure or risk of predation, which is greatest during crepuscular periods when roost sites are selected (Boeker and Scott 1969, Bakner et al. 2022b, Adey et al. 2023). Wild pigs are highly active during crepuscular and nighttime periods (Clontz et al. 2021), so avoidance of areas where wild pigs are present during these periods could mitigate perceived disturbance risk (Stankowich et al. 2005, Garabedian et al. 2023). Furthermore, avoidance of these areas during the daytime would likely lead to avoidance when selecting a place to roost as well. Similarly, roosting in areas with lower densities of wild pigs would likely lead to daytime use of areas with lower densities of wild pigs. Previous studies have found that condition and survival of wild turkeys has been linked to disproportionate roost selection near supplemental food sources or areas that reduced risk of environmental exposure or predation (McIntyre and Wiens 1999, Kane et al. 2007). Adey et al. (2023) suggested that avoidance of predation risk was the primary factor driving roost site selection for wild turkeys in Canada. Similarly, we believe that the wild turkeys in our study selected against roost sites located in areas with greater densities of wild pigs to reduce risk of disturbance by wild pigs. We posit that this was due to wild turkeys perceiving wild pigs as threats during vulnerable crepuscular periods in which roost sites were selected.

Wild turkey females disproportionally nested in areas with lower densities of wild pigs as well. We believe that these results indicate evidence that nesting females may perceive wild pigs as a threat to reproductive success. The most vulnerable time during the life history of a mature female wild turkey is during the four-week nest incubation and first two weeks of brood rearing in which females roost on the ground (Little 1980, Miller et al. 1998, Carpenter et al. 2023). Selecting a nest site that minimizes perceived disturbance risk would best serve to promote reproductive success. Therefore, nesting in areas with lesser densities of wild pigs would serve to minimize risk of disturbance while nesting. Our study observed an above average rate of nest failure (87.5%, average = 59-76%; Wood et al. 2019, Crawford et al. 2021) and brood failure (100%, average = 64-76%; Wood et al. 2019, Bakner et al. 2022a) for wild turkeys in the southeastern U.S. This could indicate that the female wild turkeys in our study area may be selecting less suitable areas to nest (1) to minimize risk of encounters with wild pigs, or (2) due to exclusion from more suitable nesting grounds by wild pigs. Nesting in less suitable areas can potentially expose nesting females to greater rates of nest failure due to predation or environmental exposure (Byrne et al. 2015, Bakner et al. 2024). Ulrey et al. (2022) examined predator populations in relation to wild turkey reproduction and found greater abundance indices of wild pigs in areas with unsuccessful wild turkey nests. Our results are particularly important for wild turkeys in the southeastern U.S when we consider declining rates of productivity and recruitment, as well as diminishing quality of nesting and brooding habitat (Chamberlain et al. 2022).

While wild pigs may not pose a meaningful predatory threat to mature wild turkeys, our study establishes a precedent that wild pigs have negative impacts on the movement ecology and resource selection of wild turkeys during breeding season. We believe that wild turkeys perceived encounters with wild pigs as disturbance risk and selected for areas with lower densities of wild pigs to reduce these encounters. With this, we postulate that areas with greater densities of wild pigs were perceived as less favorable and therefore became less usable to wild turkeys. We also propose that the drivers of these differences in space use observed by wild turkeys were avoidance of areas associated with wild pigs or exclusion from areas by wild pigs.

Conclusion

Our study provides an approach to explaining the spatiotemporal relationship between an ecologically impactful invasive large mammal and an economically important native ground-nesting bird. Through the application of an RSF to camera trapping of wild pigs and GPS-VHF movement data of wild turkeys, we described the impacts of perceived disturbance risk of wild pigs on avoidance in wild turkeys. Invasive species pose the second greatest threat to biodiversity across the globe (Wilcove et al. 1998), with wild pigs acting as a major threat to declining and imperiled species (McClure et al. 2018). The impacts of wild pigs on the movements of native species likely does not end with the spring reproductive season of wild turkeys, so future work should continue to examine impacts on movement, reproduction, and survival of declining or threatened species that share overlapping ranges with wild pigs.

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Tables

Table 1.1: Change in step length (β in meters) per 1% increase in relative density of wild pigs (*Sus scrofa*) by grouping of wild turkey (*Meleagris gallopavo*) during reproductive season (1 March to 1 June 2022) in east-central Alabama. The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had 12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals.

Grouping	β	P	95% Confidence Interval
ALL	1.25	< 0.001	0.95-1.55
BREEDING FEMALES	-0.06	0.867	-0.71-0.59
NONBREEDING FEMALES	4.36	< 0.001	3.86-4.87
MALES	0.70	< 0.001	0.22-1.18

Table 1.2: Daytime space use by grouping of wild turkey (*Meleagris gallopavo*) in relation to relative density of wild pigs (*Sus scrofa*) and landcover interactions during reproductive season (1 March to 1 June 2022) in east-central Alabama. The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had 12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals. The direction and significance (P) of the β-estimate indicates the log-odds ratio of effect of the interaction term.

Grouping	Land Cover Interaction	β	Standard Error	P
ALL				
	Pig	-2.17	0.166	< 0.001
	Pig *Pine	-1.63	0.207	< 0.001
	Pig *Hardwood	-0.83	0.248	< 0.001
	Pig *Mixed	-1.86	0.307	< 0.001
	Pig *Riparian	-3.26	0.326	< 0.001
	Pig *Open	-0.10	0.200	0.611
BREEDING FEMALES				
	Pig	-3.83	0.260	< 0.001
	Pig *Pine	-1.87	0.329	< 0.001
	Pig *Hardwood	0.89	0.374	0.017
	Pig *Mixed	-0.65	0.493	0.189
	Pig *Riparian	-2.05	0.327	< 0.001
	Pig *Open	-0.50	0.337	0.137
NONBREEDING FEMALES				
	Pig	-1.62	0.310	< 0.001
	Pig *Pine	-0.21	0.358	0.557
	Pig *Hardwood	0.55	0.443	0.215
	Pig *Mixed	-0.34	0.552	0.534
	Pig *Riparian	-0.70	0.322	0.029
	Pig *Open	-0.81	0.404	0.045
MALES				
	Pig	-3.63	0.280	< 0.001
	Pig *Pine	-1.52	0.333	< 0.001
	Pig *Hardwood	-0.04	0.403	0.915
	Pig *Mixed	-1.58	0.493	0.001
	Pig *Riparian	-2.31	0.380	< 0.001
	Pig *Open	-0.68	0.399	0.087

Table 1.3: Predicted probability of daytime space use (0.0-1.0) for groupings of wild turkey (*Meleagris gallopavo*) by relative density quantile (0.0-1.0) of wild pigs (*Sus scrofa*) during reproductive season (1 March to 1 June 2022) in east-central Alabama. The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had 12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals.

Grouping	Wild pig density quantile	Predicted probability of use
ALL		
	0.00	0.76
	0.25	0.61
	0.50	0.47
	0.75	0.34
	1.00	0.23
BREEDING FEMALES		
	0.00	0.84
	0.25	0.66
	0.50	0.43
	0.75	0.22
	1.00	0.10
NONBREEDING FEMALES		
	0.00	0.64
	0.25	0.54
	0.50	0.44
	0.75	0.34
	1.00	0.26
MALES		
	0.00	0.75
	0.25	0.55
	0.50	0.33
	0.75	0.17
	1.00	0.08

Table 1.4: Roost site selection by grouping of wild turkey (*Meleagris gallopavo*) in relation to relative density of wild pigs (*Sus scrofa*) and landcover interactions during reproductive season (1 March to 1 June 2022) in east-central Alabama. The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had 12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals. The direction and significance (P) of the β-estimate indicates the log-odds ratio of effect of the interaction term. The "Pig *Open" interaction was included for BREEDING FEMALES because female wild turkeys roost on the ground during nesting and brooding.

Grouping	Land Cover Interaction	β	Standard Error	P
ALL				
	Pig	-4.40	0.522	< 0.001
	Pig *Pine	-0.16	0.568	0.778
	Pig *Hardwood	0.02	0.701	0.982
	Pig *Mixed	0.05	0.864	0.954
	Pig *Riparian	0.83	0.520	0.111
BREEDING FEMALES				
	Pig	-5.12	1.034	< 0.001
	Pig *Pine	-0.41	1.045	0.697
	Pig *Hardwood	-0.67	1.201	0.576
	Pig *Mixed	-0.03	1.454	0.982
	Pig *Riparian	0.38	0.829	0.651
	Pig *Open	1.93	1.114	0.082
NONBREEDING FEMALES				
	Pig	-3.16	0.275	< 0.001
	Pig *Pine	-0.91	0.825	0.271
	Pig *Hardwood	0.94	0.953	0.326
	Pig *Mixed	-1.41	1.412	0.319
	Pig *Riparian	-1.20	0.740	0.104
MALES				
	Pig	-5.55	1.243	< 0.001
	Pig *Pine	-0.14	1.288	0.912
	Pig *Hardwood	-3.98	1.800	0.027
	Pig *Mixed	-2.03	1.905	0.287
	Pig *Riparian	-0.62	1.372	0.650

Table 1.5: Predicted probability of roost site selection (0.0-1.0) for groupings of wild turkey (*Meleagris gallopavo*) by relative density quantile (0.0-1.0) of wild pigs (*Sus scrofa*) during reproductive season (1 March to 1 June 2022) in east-central Alabama. The ALL grouping consisted of 22 wild turkeys, BREEDING FEMALES had 12 individuals, NONBREEDING FEMALES had 11 individuals, and MALES had 10 individuals.

Grouping	Wild pig density quantile	Predicted probability of use
ALL		
	0.00	0.72
	0.25	0.46
	0.50	0.22
	0.75	0.09
	1.00	0.03
BREEDING FEMALES		
	0.00	0.78
	0.25	0.49
	0.50	0.21
	0.75	0.07
	1.00	0.02
NONBREEDING FEMALES		
	0.00	0.59
	0.25	0.40
	0.50	0.23
	0.75	0.12
	1.00	0.06
MALES		
	0.00	0.58
	0.25	0.26
	0.50	0.08
	0.75	0.02
	1.00	0.01

Figures

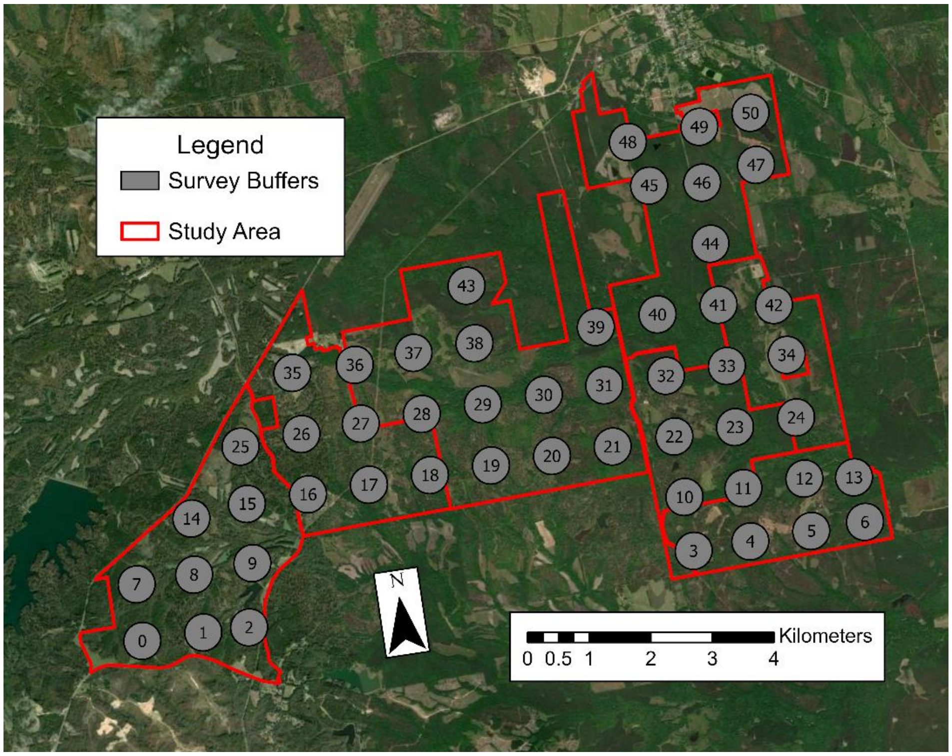

Figure 1.1: Study area map of seven adjoining properties in east-central Alabama with survey buffers denoted in grey circles and study area bounds outlined in red. The property in the southeastern corner (survey buffers 3-6 and 12-13) is surrounded by a high fence and is pig-free.

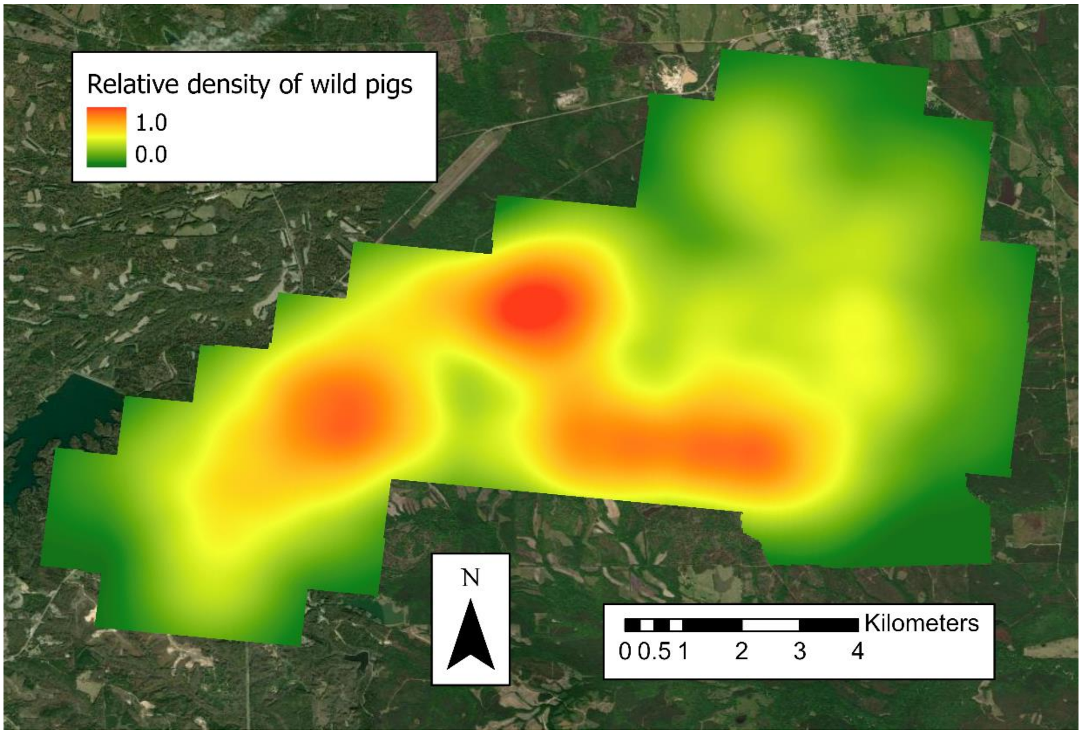

Figure 1.2: Relative density of wild pigs across buffered study area (0.0-1.0) in east-central Alabama in 30-m resolution for the May 2022 camera survey. Lower densities are denoted in green and greater densities are denoted in red.

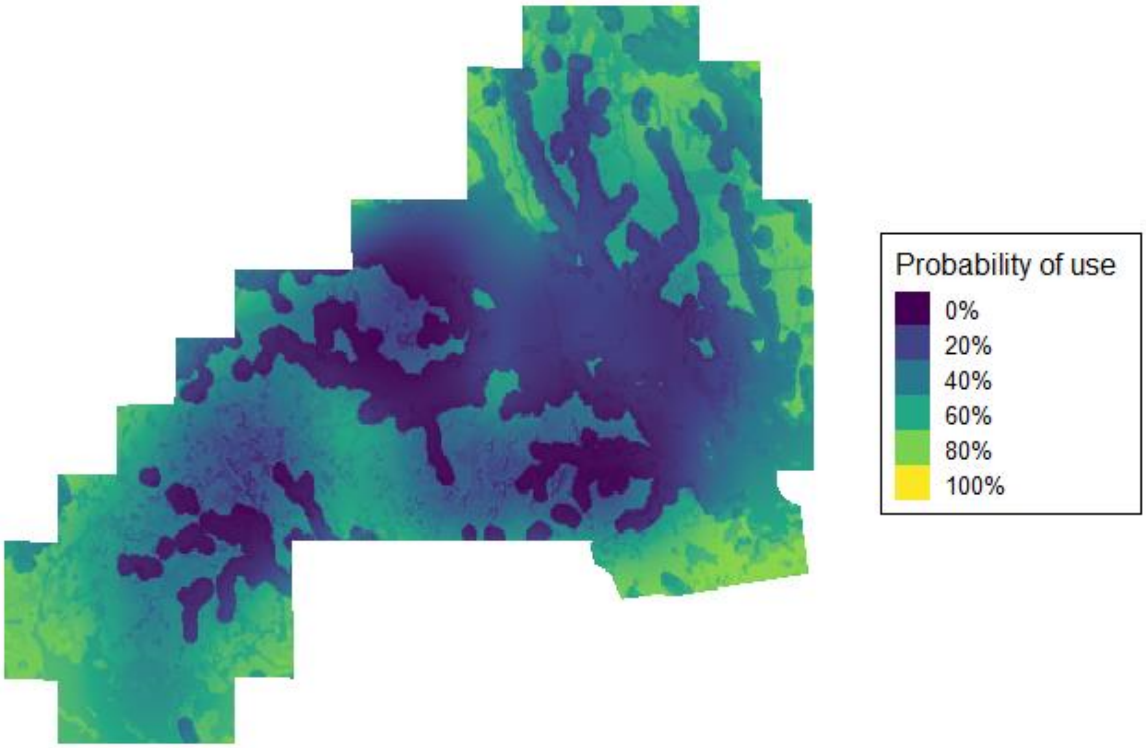

Figure 1.3: Impact of wild pig (*Sus scrofa*) density and land cover type on the probability of daytime use for the 22 wild turkeys (*Meleagris gallopavo*) in the ALL grouping during the reproductive season (1 March to 1 June 2022) in east-central Alabama. Darker blue shades indicate lower probability of use while lighter yellow shades indicate greater probability of use.

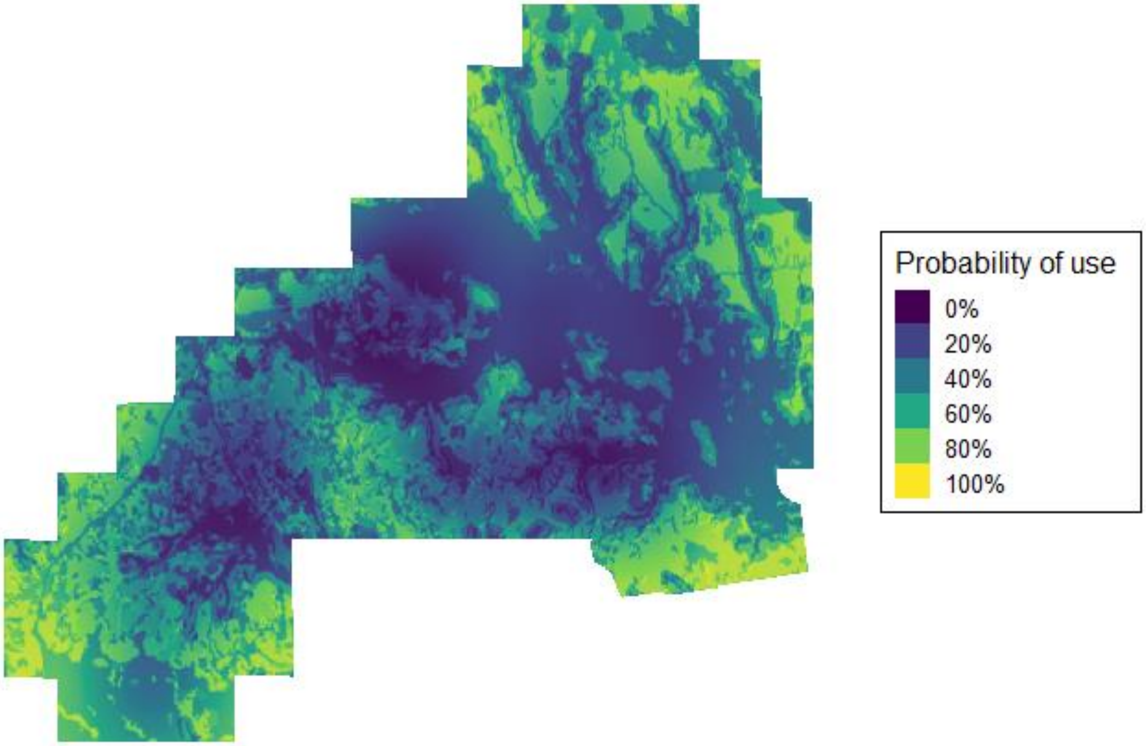

Figure 1.4: Impact of wild pig (*Sus scrofa*) density and land cover type on the probability of roost site selection for the 22 wild turkeys (*Meleagris gallopavo*) in the ALL grouping during the reproductive season (1 March to 1 June 2022) in east-central Alabama. Darker blue shades indicate lower probability of use while lighter yellow shades indicate greater probability of use.

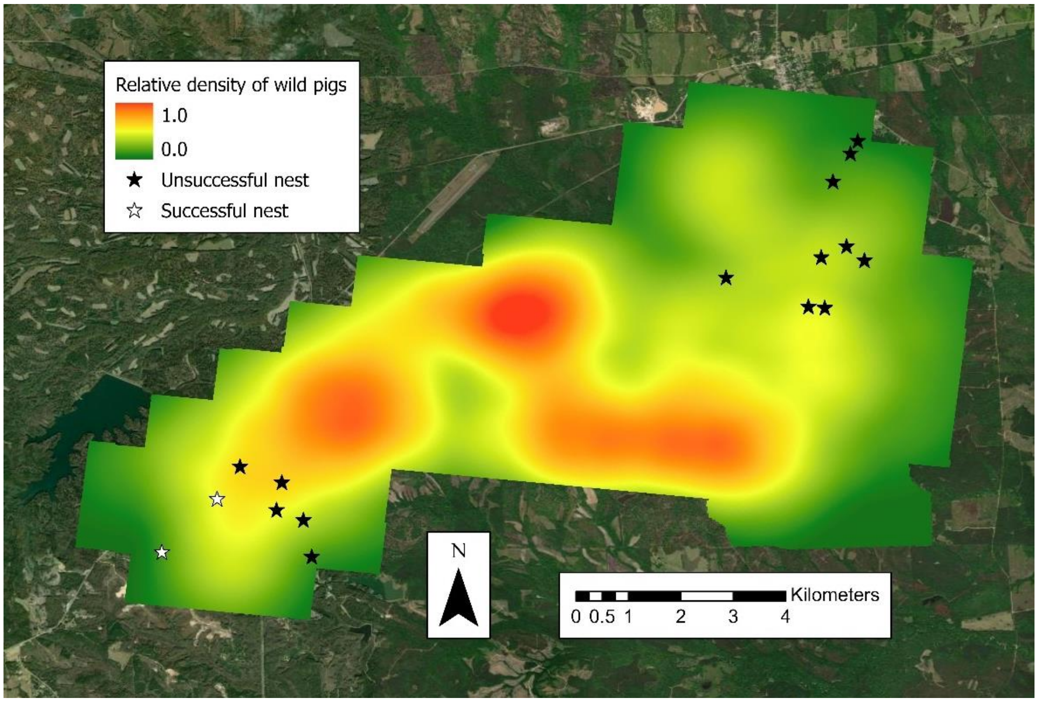

Figure 1.5: Nest locations of 16 wild turkeys (*Meleagris gallopavo*) in east-central Alabama during the reproductive season (1 March to 1 June 2022) relative to density estimates of wild pigs (*Sus scrofa*) from the May 2022 camera survey at 30-m resolution. Lowest densities of wild pigs (0.0) are denoted in green and greatest densities of wild pigs (1.0) are denoted in red. Unsuccessful nests are denoted as black stars and successful nests are denoted as white stars.

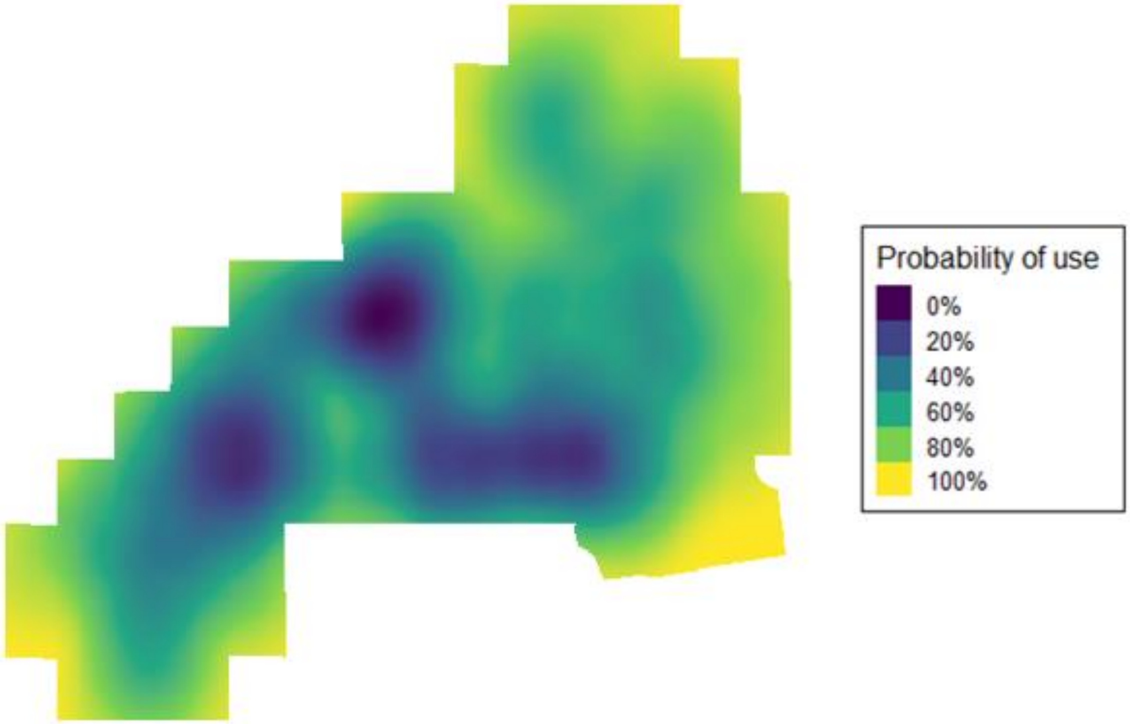

Figure 1.6: Impact of wild pig (*Sus scrofa*) density on the probability of nest site selection for the 12 female wild turkeys in the BREEDING FEMALES grouping during the reproductive season (1 March to 1 June 2022) in east-central Alabama. Darker blue shades indicate lower probability of use while lighter yellow shades indicate greater probability of use.

Chapter 2: Impacts of wild pigs on space use and movements of wild turkeys during autumn and winter

Abstract

Wild pigs (*Sus scrofa*) affect native flora and fauna in the areas they invade. Results from camera surveys have suggested that wild pigs have spatiotemporal impacts on resource selection of wild turkeys (*Meleagris gallopavo*). The autumn and winter seasons serve as an important period for spring breeders like wild turkeys. We explored the relationship between wild pig density estimates and wild turkey space use in Alabama during the autumn and winter seasons. We concurrently monitored GPS units on wild turkeys and conducted an autumn camera survey to estimate wild pig densities across our 9,000-ha study area. We hypothesized that wild turkeys would exhibit reduced use and altered movement rates in areas with greater densities of wild pigs. We found that wild turkeys displayed an avoidance of wild pigs during the daytime and when selecting roost sites and moved at slower rates in areas of high wild pig density. Avoidance of wild pigs was particularly pronounced in hardwood forests during the daytime. We believe wild turkeys avoided wild pigs due to perceived disturbance risk. We also believe wild pigs competed with wild turkeys for hard mast such that wild turkeys avoided hardwood forests. Wildlife management activities aimed at reducing wild pig abundance could increase use of areas by wild turkeys.

Introduction

Wild pigs (*Sus scrofa*) are an invasive introduced species in North America with a wide range of documented environmental and ecological impacts (McDonough et al. 2022). Over the past 30 years, populations of wild pigs have saturated the southeastern U.S. and are currently present in every county in Alabama, Arkansas, Florida, Georgia, Mississippi, and South Carolina (USDA 2024). Wild pigs negatively impact native species through direct predation (Jolley et al. 2010), competition for resources (Fay et al. 2023), and destruction of habitat (Strickland et al. 2020). There is also evidence that wild pigs may impact native species through perceived disturbance risk and resource partitioning (Hegel et al. 2019, Osugi et al. 2019). Responses to perceived risk can be measured by the magnitude of effect that potential encounters have on movement patterns (Sabal et al. 2020). Resource partitioning explains the mechanism by which the competition between species for resources such as space and forage lead to a division of use (Walter 1991).

There has been particular concern for wild pigs regarding impacts on ground-nesting birds (McDonough et al. 2022). Some artificial nest studies have speculated that wild pigs may impact nesting success of gallinaceous birds such as northern bobwhite (*Colinus virginianus*) and wild turkeys (*Meleagris gallopavo*; Tolleson et al. 1993, Sanders et al. 2020, McInnis 2021). Additionally, Carpio et al. (2023) examined fecal samples of wild pigs and found evidence of direct consumption of red-legged partridge (*Alectoris rufa*), a gallinaceous bird of conservation concern in Spain. Recent research has also suggested a spatiotemporal displacement of wild turkeys by wild pigs (McDonough et al. 2022). Several camera survey studies have found a negative relationship between abundance metrics of wild pigs and temporal use patterns by wild turkeys (Walters and Osbourn 2021, Lewis et al. 2022, McDonough 2023, Smith 2023). While the results of these studies have suggested a potential spatial aspect of this relationship, there is currently a lack of quantification or understanding of the mechanisms driving the impacts of wild pigs on resource selection and space use of wild turkeys.

The role seasonality plays in how wild pigs affect wild turkeys and other native species is also understudied. There is, however, some evidence that wild pigs compete with or temporally shift resource use by native species during the autumn and winter season. Fay et al. (2023) conducted a camera survey baited with acorns during autumn and winter (September to February) and found that wild pigs were significant competitors for hard mast. Additionally, Dykstra et al. (2023) conducted an autumn baited camera survey (September to November) and found that raccoons (*Procyon lotor*) and eastern gray squirrels (*Sciurus carolinensis*) shifted temporal activity patterns when wild pigs were present. In terms of spring breeders like wild turkeys, the autumn and winter seasons play a critical role in reproductive success due to a seasonal reduction in forage availability (Wunz and Hayden 1975, Porter et al. 1980, Vander Haegan et al. 1988). The autumn and winter seasons are important to wild turkeys for maintaining or improving condition prior to the energetically demanding spring reproductive period (McShea and Healy 2002). Therefore, interspecific interactions that limit or reduce access to food resources during autumn and winter have to potential to substantially impact productivity.

Hard masts like acorns play an important role in the nutrition of wild turkeys during autumn and winter, and changes in availability can shift space use (Gardner and Arner 1968, Porter et al. 1983, Rumble and Anderson 1996, Nguyen et al. 2004). Specifically, wild turkeys can shift resource selection away from hardwood areas when less acorns is available (Vander Haegen et al. 1989, Roberts et al. 1995, Lehman et al. 2007, Baici and Bowman 2023). Such shifts potentially impact condition, reproduction, and survival in the following spring (Burhans et al. 2000, Lehman et al. 2007). Wild pigs share seasonal dietary overlap with wild turkeys for acorns (McDonough et al. 2022, Fay et al. 2023). Competition for this limited pulse resources has potential to impact spring breeding in wild turkeys in areas with high densities of wild pigs or during years of low acorn abundance (Wood and Barrett 1979, McDonough 2023). Acorn availability is primarily constrained to hardwood stands, so a reduction in use of these areas by wild turkeys due to competition with wild pigs could impact reproductive success of wild turkeys the following spring.

Our study examined the impacts of wild pigs on movements and space use of wild turkeys in the autumn and winter seasons, with our study period from 1 October 2022 to 1 January 2023. Our specific objectives were to adjoin camera survey data for wild pigs with GPS-movement data of wild turkeys during the autumn and winter seasons to quantify the effects of wild pig abundance on use by wild turkeys. We applied resource selection functions (RSFs) to analyze density estimates of wild pigs across the study area and movement metrics of wild turkeys (step length, daytime selection, and roost site selection). We hypothesized that greater densities of wild pigs would be associated with greater step lengths and less roost site selection. We also hypothesized that we would observe less daytime selection of areas with greater densities of wild pigs, particularly in hardwood stands where competition for hard mast would be the greatest. Changes in rates of movement or reduced use of areas with greater pig densities would indicate a potential spatiotemporal avoidance behavior of wild pigs by wild turkeys.

Study Area

Our study was comprised of seven contiguous private properties (9,186 ha total) in east-central Alabama. The region was characterized by warm wet winters and hot humid summers typical of the southeastern U.S. (average temperature = 18 °C; annual rainfall ≈ 133 cm; Long 1974). The study area consisted of 1,823 ha of open cover [9.9%] and 5,562 ha of forest cover

[60.5%] (3,333 ha pine [36.3%], 1,330 ha hardwood [14.5%], and 899 ha mixed pine-hardwood [9.8%]). The properties were managed for timber production (longleaf [*Pinus palustris*] and loblolly pine [*Pinus taeda*]) and wildlife game species (white-tailed deer [*Odocoileus virginianus]*, northern bobwhite [*Colinus virginianus*] mourning dove [*Zenaida macroura*], and wild turkey). Among the pine-dominated landscape were intermixed hardwood stands of oaks (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and elm (*Ulmus* spp.) (Godfrey 1988, Samuelson 2020). The 476-ha property in the southeastern corner of the study area (camera locations 3-6 and 10-12) was enclosed by a 2.5-m fence and free from wild pigs (Figure 2.1).

Methods

GPS-unit deployment on wild turkeys

We deployed 12 GPS-VHF units (Lotek UK Ltd., Wareham, UK) on wild turkeys (7 females, 5 males) between January and March 2022. Individuals were captured with rocket nets over areas baited with cracked corn (see Bakner et al. 2023) with handling procedures approved by Auburn University IACUC (PRN: 2021-3994). Individuals were each outfitted with a GPS-VHF unit and an aluminum rivet leg band (National Band and Tag Co., Newport, KY, USA). Age class was determined by presence of barring on nineth and tenth primary feathers and sex was differentiated by breast feather coloration (Pelham and Dickson 1992). The GPS-VHF units collected locations from 1 October 2022 to 1 January 2023. Daytime locations were recorded every two hours between 0600 and 2000, with an additional location recorded at 0000 for nighttime roost site. Wild turkeys were monitored weekly during the 1 October 2022 to 1 January 2023 study period with Yagi antennas and GPS-downloading devices.

Camera survey for wild pigs

We conducted a camera survey in mid-October 2022 to determine abundances of wild pigs across the study area according to Lewis et al. (2022) and McDonough (2023). We applied a 1-km^2 grid over the study area in ArcGIS Pro^{TM} (Esri, Redlands, CA, U.S.) to determine locations for camera deployment and excluded grid cells that were < 25% within the bounds of the study area. A camera was placed within a 300-meter radius buffer of the center of each of the 51 unique 1-km^2 grid cells (Figure 2.1). The camera spacing of 1-km^2 was used because it was less than the home range size of wild pigs that were monitored on the study site ($\bar{x}$ =3.45 km^2, Gomez-Maldonado n.p.). We baited each camera site with 11 kg of whole corn one week prior to camera deployment, with an additional 11 kg of whole corn rebaited every 3-4 days during the study period. Game cameras were deployed one week after initial baiting (ReconyxTM PC800 Hyperfire Professional IR Cameras, Reconyx Inc., Holmen, WI, U.S.). Camera sites faced north-south on trees and were placed 1 m from the ground and 5 m from bait with visual obstructions removed. Cameras were programed to take three images upon detection of motion with a one-minute buffer period between triggers. Cameras were taken down after the one-week camera survey period (Williams et al. 2011).

Abundance estimates of wild pigs

We employed TimeLapse2 V2.2.3.9 (University of Calgary, Calgary, CA) to estimate wild pig densities at each of the 51 1-km^2 grid cells. Total counts at each grid were determined as the total number of unique individual wild pigs per respective camera. Individual wild pigs were differentiated by size, sex, pelage, unique physical characteristics, sounder association, and non-overlapping timing of visitation (Williams et al. 2011, Gomez-Maldonado et al. 2024). We used a three-month study period (1 October 2022 through 1 January 2023) during the autumn and winter. We assumed a stable local wild pig population across the study area because there were no hunting or removal efforts of wild pigs during the study period. Furthermore, this timeline was shorter than the length of gestation (~115 days) in wild pigs, so we assumed no significant influence of reproduction on the population during the study period (Henry 1968, Ditchkoff et al. 2012, Chinn et al. 2022).

Counts of wild pigs were standardized across the study areas as relative densities per 1 km^2. Relative density values were ranked as percentiles (0.0-1.0/km^2) ranging from lowest (0.0) to greatest (1.0) density. These percentiles were assigned to respective grid cells in ArcGIS Pro™ in 1-km^2 raster cells via the kernel density estimate tool. We elected to add a 1-km buffer around the outside of the survey bounds because the average home range of wild pigs that were monitored in the study area was greater than the spacing of our cameras ($\bar{x}$ =3.45 km^2, Gomez-Maldonado n.p.). Buffer values were assigned as the average of adjacent survey cell values. The buffer was omitted for cells bordering the fenced property in the southeastern corner of the study area that was free from wild pigs, as the nature of these cells having no wild pigs should not influence the estimates of wild pigs outside the fence (Figure 2.2; Machtans et al. 1996, Pollentier et al. 2017, Crawford et al. 2021). Grid cell values were re-interpolated to 30-m resolution to match the National Land Cover Data 2021 (NLCD 2021; Figure 2.1; Dewitz 2023).

Statistical analysis

We extracted land cover data from NLCD 2021 at 30-m resolution for land cover types that have known biological importance for wild turkeys: pine forest, hardwood forest, mixed forest, open cover, and riparian (Holbrook et al. 1987, Chance et al. 2020). Pine forest cover type was delineated as evergreen (pine) trees occupying > 20% of total vegetation cover with trees > 5-m tall that retain leaves year-round making up > 75% of total tree cover. Hardwood forest cover type was delineated as deciduous (hardwood) trees occupying > 20% of total vegetation cover with trees > 5-m tall making up > 75% of total tree cover. Mixed forest cover type was delineated as trees > 5-m tall making up > 20% of total tree cover with neither evergreen or deciduous trees making up > 75% of total tree cover. Forest cover types of pine, hardwood, and mixed forest were each coded as present (1) or absent (0). The open cover type was a combined category of cropland, grassland, shrub, and road cover types, coded as present (1) or absent (0). A 100-m buffer around water and wetland areas was created for the riparian cover type and was classified as present (1) or absent (0). Location fixes outside the study area or with dilution of precision (DOP) > 7 were removed (Bakner et al. 2023), with movement data then grouped into the following categories: ALL, FEMALES, and MALES. The ALL grouping consisted of all 12 individuals, the FEMALES grouping consisted of the seven females, and the MALES grouping consisted of the five males.

We used a dynamic Brownian bridge movement model in package move in Program R to calculate movement metrics (R Core Team, Vienna, Austria). The linear distance between consecutive points was used for step length. We used a linear model framework to analyze the relationship between step length and wild pig density. We excluded land cover interactions for step length analyses because each step could cross multiple cover types. We applied a resource selection function (RSF) framework to analyze daytime and roost site selection in relation to wild pig density. Daytime points from 0600 to 2000 were used for daytime selection, with a point at 0000 used for roost site selection. A minimum convex polygon (MCP) was created around each category of points (i.e., all roost site locations for the FEMALES grouping; Johnson

1980). An equal number of random to actual points were created within the MCP of respective groupings. For each analysis of daytime and roost site selection, we followed the model selection methodology of Bakner et al. (2024) for inclusion of land cover types with known importance in wild turkey ecology. Interactions between land cover variables and wild pig density estimates were used for daytime and roost site selection to determine the magnitude of effect wild pigs had on probability of use by wild turkeys in respective land cover types. We used generalized linear models for daytime selection for the ALL, FEMALES, and MALES groupings with interactions between land cover variables (pine, mixed, hardwood, open, riparian) and estimated wild pig density to predict probability of use. We also used generalized linear models for roost site selection for the ALL, FEMALES, and MALES groupings with interactions between land cover variables (pine, mixed, hardwood, open) and estimated wild pig density to predict probability of use. Riparian cover was excluded from the roost site model due to low sample size.

Results

A total of 12 wild turkeys (5 males, 7 females) were monitored during the 1 October 2022 to 1 January 2023 study period. Estimates of wild pig densities per camera ranged from 0-13 pigs/km^2 which were standardized to relative densities (0.0-1.0/km^2). The average step length was 148.6 m for the ALL grouping, 111.5 for FEMALES, and 196.2 for MALES. Wild pig density was negatively associated with step length for the ALL and MALES groupings (Table 2.1). For every 10% increase in wild pig density, we observed an 80.7 m decrease in step length for the ALL grouping ($P < 0.001$) and a 76.8 m decrease in step length for MALES ($P < 0.001$).

Probability of daytime selection by wild turkeys was negatively related to wild pig density for the ALL ($\beta = -1.98$, $P < 0.001$), FEMALES ($\beta = -2.14$, $P < 0.001$), and MALES groupings (β = -4.08, P < 0.001; Table 2.2; Figure 2.3). Additionally, we observed a negative relationship between probability of daytime selection and wild pig density across multiple land cover types. Wild pig density was negatively related to probability of daytime selection of hardwood cover for the ALL (β = -1.78, P < 0.001), FEMALES (β = -2.14, P < 0.001), and MALES groupings (β = -1.52, P < 0.001). Wild pig density also had a negative relationship with probability of daytime selection of riparian cover for FEMALES (β = -0.94, P = 0.003). However, we also observed a positive relationship between probability of daytime selection and wild pig density across several land cover types. Wild pig density was positively related to probability of daytime selection of pine cover for the ALL (β = 0.75, P = 0.002), FEMALES (β = 0.74, P = 0.004), and MALES groupings (β = 1.23, P < 0.001). Wild pig density was also positively related to probability of daytime selection of mixed cover for the ALL grouping (β = 0.65, P = 0.025) and FEMALES (β = 1.45, P < 0.001). In riparian cover, wild pig density had a positive relationship with probability of daytime selection for FEMALES (β = 0.08, P = 0.013) and MALES (β = 1.34, = 0.009). Additionally, wild pig density had a positive relationship with probability of daytime selection of open cover for the ALL (β = 0.70, P = 0.013), FEMALES (β = 1.18, P = 0.003), and MALES groupings (β = 1.22, P = 0.005). When examining wild pig density by quantile, we also found a stepwise reduction in predicted probability of daytime selection by grouping as wild pig density increased (Table 2.3). From the least (0.0) to the greatest (1.0) wild pig density, we observed a decrease in predicted probability of daytime selection of 43.5% for the ALL grouping, 45.9% for FEMALES, and 70.6% for MALES.

Probability of roost site selection was negatively related to wild pig density for the ALL (β = -1.51, P = 0.043), FEMALES (β = -1.85, P = 0.045), and MALES groupings (β = -5.68, P = 0.003; Table 2.4; Figure 2.4). For FEMALES, we also observed a negatively relationship between wild pig density and probability of roost site selection in hardwood cover (β = -5.00, P = 0.016). Conversely, wild pig density had a positive relationship with probability of roost site selection for FEMALES in mixed cover (β = 4.82, P = 0.013) as well as for MALES in pine cover (β = 4.51, P = 0.028). When examining wild pig density by quantile, we also found a stepwise reduction in predicted probability of roost site selection by grouping as wild pig density increased (Table 2.5). From the least (0.0) to the greatest (1.0) wild pig density, we observed a decrease in predicted probability of roost site selection of 20.6% for the ALL grouping, 27.0% for FEMALES, and 40.1% for MALES.

Discussion

We observed a suite of effects of wild pig density on movements and space use of wild turkeys during the autumn and winter seasons. Wild turkeys had lower predicted probabilities of daytime selection of areas with greater wild pig densities. Evidence from camera surveys have supported a negative temporal relationship between use by wild pigs and detection of wild turkeys (Walters and Osbourne 2021, Smith 2023), however the spatial relationship has not been examined. Lewis (2021) conducted baited camera surveys for wild turkeys and reported that probability of use of a site increased by 11% and detection increased by 9% when wild pig sounders were absent. McDonough (2023) found that 100% removal of the original baseline estimate of wild pigs led to an average of 2.0 times the detection and 1.5 times the population estimate of wild turkeys compared to prior to removal. Similar results were found for the Lord Howe Island woodhen (*Tricholimnas sylvestris*) in which areas that underwent wild pig removal observed increased use by woodhens (Miller and Mullette 1985). Wild pigs posed some predatory risk to woodhens, and though adult wild turkeys are not considered to be prey for wild pigs, we believe that wild turkeys in our study avoided wild pigs due to perceived risk.

A negative relationship between daytime selection and wild pig density was also demonstrated in hardwood cover for the ALL and FEMALES groupings, which is potentially explainable by competition for hard mast. Hard mast (e.g., acorns) is spatiotemporally constrained to hardwood stands during autumn and winter (Godfrey 1988, McWilliams 1992). Acorns are an integral forage for wild turkeys during the autumn and winter seasons due to high fat content and metabolizable energy, comprising 20-33% of total diet during the autumn and winter (Ellis and Lewis 1967, Zwank et al. 1988, McShea and Healy 2002). As such, limited access to hard mast in the months leading up to the reproductive season may have negative effects on condition, production, and survival in spring (Porter et al. 1983, Vangilder and Kurzejeski 1995, McShea and Healy 2002, Lehman et al. 2007). Acorns are also important food sources for wild pigs (Ditchkoff and Mayer 2009, Schlichting et al. 2015), sometimes comprising > 75% of total dietary dry mass during autumn and winter (Wood and Roark 1980). Fay et al. (2024) conducted a camera survey baited with acorns from October 2018 to February 2019 and found that wild pigs consumed the greatest percentage of acorns of any species (23%). Competition for a spatiotemporally limited forage like hard mast can lead to reduced rates of consumption and increased use of other foraging areas (MacArthur 1958, Walter 1991). We believe consumption of hard mast by wild pigs could reduce availability of hard mast, leading to reduced use of hardwood areas by wild turkeys.

In addition to observing a negative association of wild turkeys with wild pigs in hardwood areas, we found a positive association with wild pigs in several other land cover types. Multiple studies reported that wild turkeys shift resource use away from hardwood forests when hard mast is limited (Vander Haegen et al. 1989, Roberts et al. 1995, McShea and Healy 2002). Wild pigs may reduce hard mast availability (Fay et al. 2023), particularly in hardwood areas, which may lead to increased selection of other cover types by wild turkeys. The effects of wild pigs on wild turkeys may also be different in hardwood areas than other cover types. Walters and Osborne (2021) examined occurrence patterns of wild turkey in relation to wild pigs and suggested that the presence of wild pigs in an area may exclude or alter space use of wild turkeys, leading to increased use of land cover types by wild turkeys that they would otherwise not typically use in the absence of wild pigs.

We also observed a negative relationship between wild pig density and roost site selection for wild turkeys. Roost sites are typically mature hardwood and pine trees with branches 3 to 10 m high (Austin and Degraaf 1975, Kilpatrick et al. 1988). Avoidance of predation risk and environmental exposure have been suggested as primary attributes in the selection of suitable roost sites among wild turkeys (Adey et al. 2023, Gonnerman et al. 2023). During the evening when roost sites are selected (Adey et al. 2023), wild pig activity is generally high (Clontz et al. 2021, Garabedian et al. 2023). Wolfson et al. (2023) reported that ≥ 70% of activity by wild pigs occurred during crepuscular and nighttime periods during autumn and winter. Wild turkeys also have poor vision during crepuscular and nighttime periods and thus could be at greatest risk of disturbance or predation during this time (Miller 2018). Although wild pigs are not considered to be predators of adult wild turkeys, turkeys may still avoid areas with high wild pig activity to minimize perceived risk (Stankowich and Blemstien 2005). Wild turkeys also avoided areas with high wild pig density during the daytime, so it is possible that this led to an avoidance when selecting a roost site.

We observed reduced step lengths by wild turkeys in areas with greater wild pig densities for the ALL and MALES groupings, which is contrary to what has previously been reported. In Chapter 1 (studying this same population of wild turkeys), step length increased for wild turkeys in areas with greater wild pig densities during the spring reproduction period. We believe that the selfish herd hypothesis as proposed by Hamilton (1971) and the abatement effect hypothesis as proposed by Turner and Pitcher (1986) could help explain these seasonal differences. The selfish herd hypothesis suggests that gregarious behaviors help to improve foraging efficiency and reduce risk of predation (Hamilton 1971, Morton et al. 1994, Quinn and Cresswell 2006, Hammer et al. 2023). Similarly, the abatement effect hypothesis suggests that forming cohesive groups can decrease predation and disturbance by increasing dilution and vigilance (Turner and Pitcher 1986, Warburton and Lazarus 1991, Wrona and Dixon 1991, Viscido et al. 2001). Wild turkeys are a sentinel gregarious species that flock during the autumn and winter but separate at the initiation of the spring breeding season (Wright 1915, Watts and Stokes 1971, Vangilder and Kurzejeski 1995). Measures of step length during the autumn and winter are therefore more than a representation of the movement of an individual but also the movement of the flock. While the response of an individual (such as during the spring breeding period) to risk may be to escape and increase rate or linearity of movement (see Chapter 1; Lima and Dill 1990, Adam and Stuart-Smith 2000, Prokopenko et al. 2016, Thompson et al. 2024), the response of the flock could be to reduce speed and decrease linearity of movement to increase vigilance (Watts and Stokes 1971, Hatle and Faragher 1998, Persons et al. 2001, Sabal et al. 2020, Wirsing et al. 2020).

Management implications

We believe that the impacts of wild pigs on wild turkeys varies by season, with impacts greatest in hardwood stands during autumn and winter. Similar to the spring reproductive period (see Chapter 1), wild turkeys demonstrated an avoidance of areas with high wild pig density during the daytime and when selecting a roost site. However, wild turkeys reduced movements when in high wild pig densities, the opposite response to the reproductive period. While impacts of wild pigs on space use and movements of wild turkeys during the autumn and winter seasons appear less ubiquitous across land cover types than during the reproductive period, negative impacts on daytime selection of hardwood stands may have significant implications for condition, reproductive success, and survival the following spring. Efforts to decrease densities of wild pigs may alter wild turkey movement metrics and habitat use, and potentially have positive impacts on condition and fitness. Utilizing strategic approaches such as whole sounder removal (Ditchkoff and Bodenchuk 2020, Lewis et al. 2022) would likely have the greatest positive impact on wild turkeys due to the potential to substantially decrease wild pig populations.

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Tables

Table 2.1: Change in step length (β in meters) per 1% increase in relative density of wild pigs (*Sus scrofa*) by grouping of wild turkeys (*Meleagris gallopavo*) during autumn and winter (study period: 1 October 2022 to 1 January 2023) in central-eastern Alabama. The ALL grouping consisted of 12 wild turkeys, FEMALES had 7 individuals, and MALES had 5 individuals.

Grouping	β	P	95% Confidence Interval
ALL	-8.07	< 0.001	-9.97-(-6.17)
FEMALES	0.49	0.620	-1.45-2.43
MALES	-7.68	< 0.001	-11.08-(-4.28)

Table 2.2: Daytime selection by grouping of wild turkeys (*Meleagris gallopavo*) in relation to relative density of wild pigs (*Sus scrofa*) and landcover interactions during autumn and winter (study period: 1 October 2022 to 1 January 2023) in central-eastern Alabama. The ALL grouping consisted of 12 wild turkeys, FEMALES had 7 individuals, and MALES had 5 individuals. The direction and significance (P) of the β-estimate indicates the log-odds ratio of effect of the interaction term.

Grouping	Land Cover Interaction	β	Standard Error	P
ALL				
	Pig	-1.98	0.222	< 0.001
	Pig *Pine	0.75	0.237	0.002
	Pig *Hardwood	-1.78	0.309	< 0.001
	Pig *Mixed	0.65	0.291	0.025
	Pig *Riparian	0.08	0.294	0.787
	Pig *Open	0.70	0.284	0.013
FEMALES				
	Pig	-2.14	0.324	< 0.001
	Pig *Pine	0.71	0.348	0.041
	Pig *Hardwood	-2.06	0.425	< 0.001
	Pig *Mixed	1.45	0.403	< 0.001
	Pig *Riparian	-0.94	0.406	0.021
	Pig *Open	1.18	0.404	0.003
MALES				
	Pig	-4.08	0.350	< 0.001
	Pig *Pine	1.23	0.370	< 0.001
	Pig *Hardwood	-0.30	0.498	0.552
	Pig *Mixed	-0.20	0.472	0.676
	Pig *Riparian	1.34	0.513	0.009
	Pig *Open	1.22	0.437	0.005

Table 2.3: Predicted probability of daytime selection (0.0-1.0) for groupings of wild turkey (*Meleagris gallopavo*) by relative density quantile (0.0-1.0) of wild pigs (*Sus scrofa*) during autumn and winter (study period:1 October 2022 to 1 January 2023) in east-central Alabama. The ALL grouping consisted of 12 wild turkeys, FEMALES had 7 individuals, and MALES had 5 individuals.

Grouping	Wild pig density quantile	Predicted probability of use
ALL		
	0.00	0.62
	0.25	0.50
	0.50	0.37
	0.75	0.27
	1.00	0.18
FEMALES		
	0.00	0.62
	0.25	0.49
	0.50	0.36
	0.75	0.25
	1.00	0.16
MALES		
	0.00	0.75
	0.25	0.53
	0.50	0.29
	0.75	0.13
	1.00	0.05

Table 2.4: Roost site selection by grouping of wild turkeys (*Meleagris gallopavo*) in relation to relative density of wild pigs (*Sus scrofa*) and landcover interactions during autumn and winter (study period:1 October 2022 to 1 January 2023) in central-eastern Alabama. The ALL grouping consisted of 12 wild turkeys, FEMALES had 7 individuals, and MALES had 5 individuals. The direction and significance (P) of the β-estimate indicates the log-odds ratio of effect of the interaction term.

Grouping	Land Cover Interaction	β	Standard Error	P
ALL				
	Pig	-1.51	0.745	0.043
	Pig *Pine	1.53	0.888	0.084
	Pig *Hardwood	-0.80	1.268	0.528
	Pig *Mixed	-0.65	1.297	0.614
FEMALES				
	Pig	-1.85	0.924	0.045
	Pig *Pine	0.60	1.365	0.663
	Pig *Hardwood	-5.00	2.071	0.016
	Pig *Mixed	4.82	1.930	0.013
MALES				
	Pig	-5.68	1.919	0.003
	Pig *Pine	4.51	2.050	0.028
	Pig *Hardwood	-0.73	3.451	0.832
	Pig *Mixed	-27.41	24.990	0.273

Table 2.5: Predicted probability of roost site selection (0.0-1.0) for groupings of wild turkey (*Meleagris gallopavo*) by relative density quantile (0.0-1.0) of wild pigs (*Sus scrofa*) during autumn and winter (study period: 1 October 2022 to 1 January 2023) in east-central Alabama. The ALL grouping consisted of 12 wild turkeys, FEMALES had 7 individuals, and MALES had 5 individuals.

Grouping	Wild pig density quantile	Predicted probability of use
ALL		
	0.00	0.29
	0.25	0.22
	0.50	0.16
	0.75	0.12
	1.00	0.08
FEMALES		
	0.00	0.35
	0.25	0.25
	0.50	0.17
	0.75	0.12
	1.00	0.08
MALES		
	0.00	0.40
	0.25	0.14
	0.50	0.04
	0.75	0.01
	1.00	< 0.01

Figures

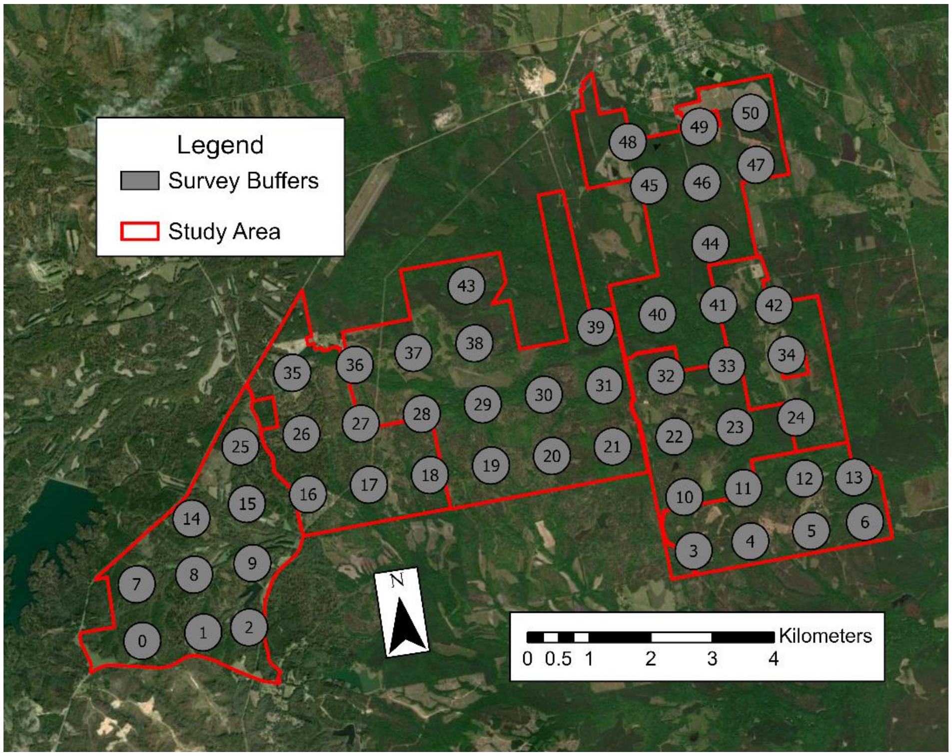

Figure 2.1: Study area map of seven adjoining private properties in east-central Alabama with survey buffers shaded grey and study area bounds outlined in red. The southeastern property (survey buffers 3-6 and 12-13) was surrounded by a 2.5-m fence and free from wild pigs.

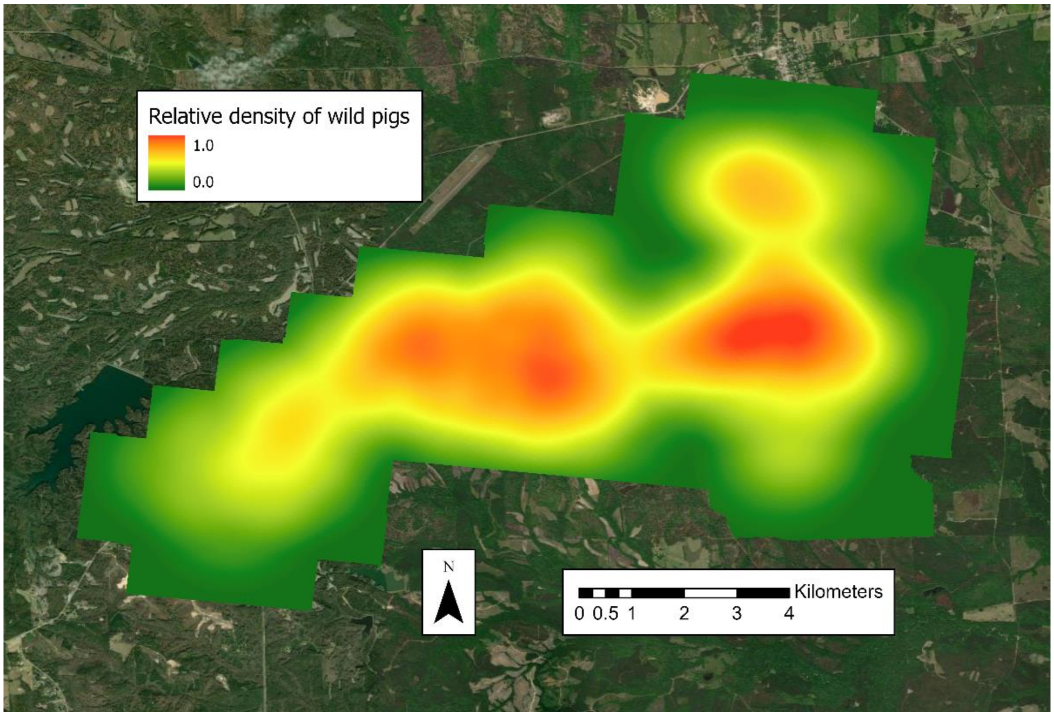

Figure 2.2: Relative density of wild pigs across buffered study area (0.0-1.0) in east-central Alabama in 30 m resolution for the October 2022 camera survey. Lower densities are shaded green and greater densities are shaded red.

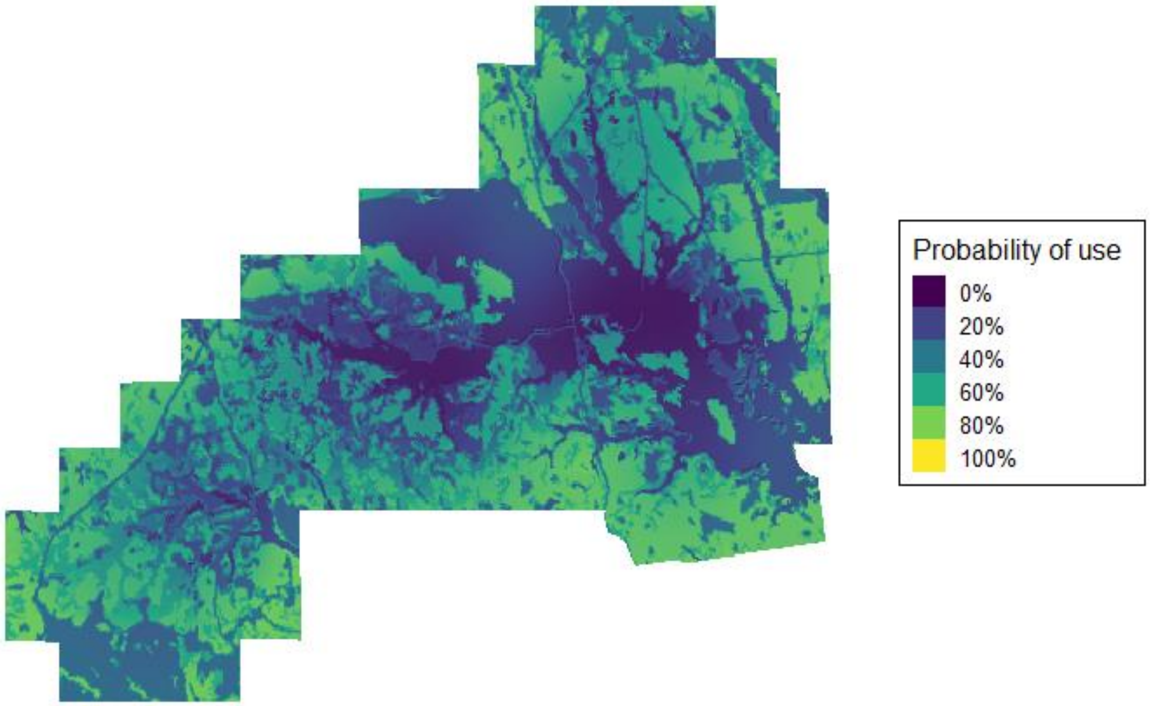

Figure 2.3: Impact of wild pig (*Sus scrofa*) density and land cover type on the probability of daytime selection for the 12 wild turkeys (*Meleagris gallopavo*) in the ALL grouping during autumn and winter (study period: 1 October 2022 to 1 January 2023) in east-central Alabama. Lower probability of daytime selection was shaded in darker blue and greater probability of daytime selection was shaded in lighter yellow shades.

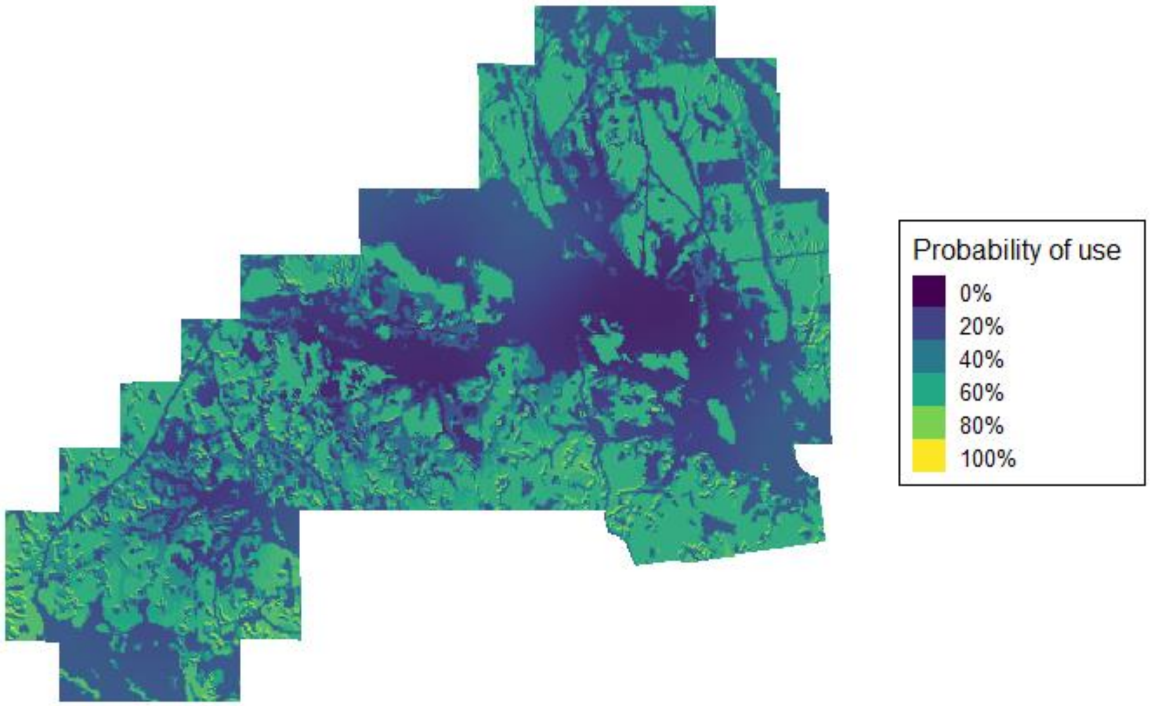

Figure 2.4: Impact of wild pig (*Sus scrofa*) density and land cover type on the probability of roost site selection for the 12 wild turkeys (*Meleagris gallopavo*) in the ALL grouping during autumn and winter (study period: 1 October 2022 to 1 January 2023) in east-central Alabama. Lower probability of roost site selection was shaded in darker blue and greater probability of roost site selection was shaded in lighter yellow shades.