

ARTICLE

Co-occurrence of native white-tailed deer and invasive wild pigs: Evidence for competition?

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Abstract

Understanding whether invasive and native species compete for shared resources where they co-occur is essential for mitigating the negative impacts of invasive species on native ecosystems. Here, we examined how the presence and density of an invasive species, wild pigs (*Sus scrofa*), affect native white-tailed deer (*Odocoileus virginianus*; hereafter, deer) on the Savannah River Site, SC, USA. We examined potential changes in deer areas of use, temporal overlap, and occupancy to evaluate the effects of wild pig occurrence and density on deer space use, diel activity, and co-occurrence with wild pigs across 9 months during 2018 and 2019. Wild pig density had the strongest effect on deer space use in high- and moderate-use areas. Declines in deer space use in response to wild pig density were most pronounced in March and October 2018 and April 2019 for females, while male space use declined in response to wild pig density in October and December 2018. Both species were largely nocturnal with high overlap in diel activity across months. Deer occupancy responses to wild pig density varied across months, with negative responses in May and October 2018 and positive responses in July 2018 and April 2019. Deer and wild pigs co-occurred at 30%–59% of camera stations across months, with broadscale co-occurrence patterns being unaffected by changes in shared cover or wild pig occurrence. Overall, our results suggest that deer make fine-scale behavioral adjustments to avoid wild pigs, providing evidence that competition is likely occurring even where wild pig density is relatively low. Such fine-scale behavioral plasticity in deer appears to mitigate the costs of competition with wild pigs and may be a mechanism enabling long-term co-existence of deer and wild pigs. Our study provides novel insight on the complexities of spatiotemporal relationships between invasive wild pigs and native deer and suggests that the negative effects of interactions between deer and wild pigs may be more pronounced when deer life history needs are particularly demanding. In areas where eradication of invasive wild pigs may be impossible, maintaining low wild pig densities may help mitigate, but may not eliminate, the negative effects of wild pigs on deer.

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KEYWORDS

behavior, control, density, interspecific competition, invasive species, non-native competitor, resource partitioning, space use, spatiotemporal interactions, suid, ungulate

INTRODUCTION

Invasive species present a significant threat to native wildlife in part because they can compete with and limit or exclude native wildlife (Colléony & Shwartz, 2020; Pyšek et al., 2020; Rogers & Kark, 2020) access to shared resources (Haynes et al., 2014; Kass et al., 2020). Where invasive and native species compete for shared resources, resource partitioning is one mechanism enabling co-occurrence (Chaudhary et al., 2020). Resource partitioning could occur in space or time, whereby native species adjust behaviors and shift use to different areas or times of day to avoid direct encounters with an invasive competitor (Chaudhary et al., 2020; Perez Carusi et al., 2017). Such competition with invasive species can have detrimental consequences for native wildlife populations by negatively affecting reproduction and survival (Wiens et al., 2014), even resulting in extirpation (Farris et al., 2017). Accordingly, knowledge about the nature of competition for shared resources can guide managers tasked with mitigating the detrimental effects of invasive species on native wildlife populations (Nie et al., 2019).

The extent to which native and invasive species partition shared resources in space or time may also be contingent on the density and social system of the invasive competitor (Bradley et al., 2019; de Boer & Prins, 1990) as increased density increases the likelihood of direct encounters with native species (Pintor et al., 2009). Consequently, increased density of invasive competitors may have a greater impact on native species' fine-scale behaviors compared with their occurrence alone (Stone et al., 2019). Such fine-scale behavioral adjustments may involve native species' avoidance of areas with increased density of the invasive competitor and/or reducing activity in an area at times the invasive competitor is most active (Frey et al., 2017). In some cases, behavioral adjustments by native species observed at fine spatial scales may manifest as population-scale shifts in distribution (Perez Carusi et al., 2017). Additionally, direct encounters between invasive competitors and native species may be more likely during seasonal resource pulses (Nie et al., 2019; Paolini et al., 2018; Schley & Roper, 2003), when shared hiding or escape cover is limited (Chitwood et al., 2015), or during demanding life history periods of native species (e.g., reproduction), any of which may increase the extent to which species partition resources.

Wild pigs (*Sus scrofa*) are a globally invasive species that have become a major concern throughout their introduced range due to their extensive negative impacts on native ecosystems. Wild pigs negatively impact native wildlife by modifying their habitat (Mori et al., 2020) and competing for resources (Focardi et al., 2000; O'Brien et al., 2019). Wild pigs can be extremely aggressive toward other species (Barrios-Garcia & Ballari, 2012; Casula et al., 2019), which can limit and even exclude native species from accessing shared resources (Mikulka et al., 2018; Osugi et al., 2019). Recent research also suggests the negative impacts of wild pigs on native wildlife could be exacerbated on sites with year-round availability of concentrated food resources, which can increase wild pig density via improved body condition and reproduction (Mayer et al., 2021). However, existing research on the nature of interactions between wild pigs and native wildlife has yielded mixed results. Some studies reported fine-scale nonaggressive interactions between wild pigs and native wildlife (Brook & Clarke, 2020), whereas others reported native wildlife avoid areas occupied by wild pigs (Hegel et al., 2019; O'Brien et al., 2019; Osugi et al., 2019), highlighting the importance of wild pig control to mitigate the negative effects on native wildlife (McDonough et al., 2022).

In the United States, invasive wild pigs are largely concentrated in the southern region (Lewis et al., 2019) where their distribution overlaps extensively with native species of management concern, including the culturally and economically important white-tailed deer (*Odocoileus virginianus*). White-tailed deer are vigilant to noise and movements of nonpredator species as observed at baited camera stations where multiple species aggregate (Lashley et al., 2014). Additionally, white-tailed deer (hereafter, deer) and wild pigs overlap extensively in diet and use of vegetation cover, which is likely to trigger competition among these species (de Oliveira et al., 2020; Elston & Hewitt, 2010; Mikulka et al., 2018; VerCauteren et al., 2020). Deer and wild pigs each have been shown to select for areas with hardwood canopy cover, often with dense understory vegetation, because this cover type offers food resources (particularly acorns; Kammermeyer & Carlock, 2000; Mikulka et al., 2018), thermal cover/refugia (Clontz et al., 2021a, 2021b; Gerard et al., 1991; Kay et al., 2017; Kilgo et al., 2021), and protection from predators. Wild pigs have even been reported to aggressively displace deer from feeding on acorns (Taylor & Hellgren, 1997), which may limit deer populations during periods of low

most availability (Kammermeyer & Carlock, 2000). Rooting and wallowing by wild pigs could also alter understory vegetation to an extent that foraging areas as well as bedding and escape cover are rendered less suitable to deer (Focardi et al., 2000; Putman, 1996). Consequently, deer may adjust space use in response to wild pigs due to the direct effects of interference competition for shared cover and food resources as well as indirectly due to resource exploitation (Ferretti & Fattorini, 2021; O'Brien et al., 2019; Seward et al., 2004). Such competition for shared cover and food resources may negatively impact deer population dynamics, and negative impacts may be exacerbated where wild pig populations are increasing in density (Focardi et al., 2000; Nie et al., 2019).

Although wild pig control is undertaken for a multitude of purposes, mitigating negative effects on native wildlife like deer is a frequent objective (Davis, Leland, et al., 2018). However, understanding the impact wild pigs have on deer requires information on the nature of spatiotemporal relationships between these species. In this study, we examined joint influences of shared resources and wild pig occurrence and density on spatiotemporal relationships with deer on the Savannah River Site (SRS), SC, USA. We assessed how wild pig occurrence and density affect deer space use, diel activity, and co-occurrence while controlling for the effects of a shared vegetation cover type selected by both species (i.e., hardwood canopy cover). We predicted that deer would shift space use to avoid areas and camera sites where wild pig density is high, resulting in reduced deer space use and occupancy of shared hardwood cover areas. Additionally, we predicted that wild pig density would have a greater impact on deer occupancy of hardwood areas than pig occurrence alone; therefore, deer occupancy of hardwoods would be inversely related to wild pig density. Finally, if wild pigs are the influential species relative to deer, pig occupancy should be unaffected or increase along a hardwood canopy cover gradient regardless of deer occurrence.

METHODS

Study site

The SRS, an 80,267-ha National Environmental Research Park owned and operated by the U.S. Department of Energy, is located on the Upper Coastal Plain and Sandhills physiographic provinces in South Carolina. The landscape of the SRS is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods and, although forest rotation lengths are longer than average for the area, the site is generally

representative of habitat in the region (Kilgo & Blake, 2005). The climate of SRS is humid subtropical with annual precipitation and temperature averaging 1225 mm and 18°C, respectively (Blake et al., 2005). Planted stands of loblolly (*Pinus taeda*), longleaf (*Pinus palustris*), and slash (*Pinus elliotii*) pines comprise 66% of the SRS and are managed on 50–120-year rotations, depending on species- and site-specific management goals. Bottomland hardwood, forested wetlands, and cypress (*Taxodium distichum*)–tupelo (*Nyssa aquatica* and *Nyssa sylvatica* var. *biflora*) comprise approximately 18,461 ha (23% of the SRS). The remaining 6421 ha of forested area on the site includes mixed-hardwood stands and water bodies/reservoirs (Imm & McLeod, 2005). Developed areas (i.e., facilities) comprise 3% of the SRS (Imm & McLeod, 2005).

The SRS white-tailed deer population is managed via annual harvest to maintain a low density (3–6 deer/km²) and minimize the risk of deer–vehicle accidents. The sex ratio is approximately even (Johns & Kilgo, 2005). The introduced population of wild pigs on the SRS has been present at least since the 1940s and likely since Colonial times (Mayer & Brisbin, 2012). Since 1965, the SRS wild pig population has been managed through annual public deer hunts (during which wild pigs were legally harvested) and a control program involving lethal removal of wild pigs through shooting, trapping, and hunting with dogs. Estimated wild pig density on SRS ranges from 3 to 20 pigs/km² (Keiter et al., 2017; Kilgo et al., 2021; Mayer, 2005).

Field methods and data acquisition

Wild pig density

We conducted camera trap surveys to estimate wild pig density every other month from March 2018 through August 2019 ($n = 9$ surveys) for 21 days during each month. We deployed 117 cameras (Reconyx Hyperfire 2 Professional White Flash, Holmen, WI) on a grid of 636 × 636 m cells to record deer and wild pig detections (Appendix S1: Figure S1); average distance between cameras was 466 m and ranged 225–873 m. We chose a grid cell size of 636 × 636 m (40 ha) for consistency with long-term camera-monitoring surveys on the SRS (USDA Forest Service-Savannah River, unpublished data) and based on the home range radii of wild pigs and white-tailed deer on SRS (Kilgo et al., 2021; J. C. Kilgo, unpublished data). We set cameras to capture a single image per trigger with no delay between consecutive triggers and did not use bait or lures to increase the detection rates of deer and wild pigs. From the images, we assigned

individual identities to as many wild pigs as possible based on pelage color, pattern, natural markings, and/or uniquely numbered ear tags.

We used spatial capture–recapture models for partially marked populations (Royle et al., 2014) and data augmentation (Tanner & Wong, 1987) to estimate wild pig density using data on both marked (i.e., individually identifiable) and unmarked wild pigs. We augmented the observed dataset of marked pigs by adding M all-zero detection histories to account for individuals that were present but went undetected in the study area (Royle et al., 2007; Royle & Dorazio, 2012). Following Royle et al. (2007), we set M to three times the number of marked pigs (m) identified in camera images during each month, such that $m + M$ was larger than the total number of pigs in the study area. We fit models using a 1-km buffer around the camera grid (Appendix S1: Figure S1). For each month, we ran models with three chains for 500,000 iterations and a burn-in of 100,000 using an Markov chain Monte Carlo algorithm from the contributed *scrbook* R package (Royle et al., 2020) in the R statistical environment (v. 4.2.0; R Core Team, 2021).

Deer space use

We obtained GPS data from 29 individuals captured by darting (Pneu-Dart Models 389 and XCal) from vehicles on roads that bisected the camera grid ($n = 26$) or from stands over bait in the study area ($n = 3$). We targeted equal numbers of each sex and adult instead of yearling males to minimize the likelihood that captured males would disperse from the study area. To anesthetize deer for capture, we used either a Telazol (250 mg)/xylazine hydrochloride (150 mg) mix or BAM (butorphanol tartrate [54.6 mg]/azaperone tartrate [18.2 mg]/medetomidine hydrochloride [21.8 mg]; ZooPharm) in 2-cc darts equipped with a radio transmitter to facilitate the location of darted deer. We equipped captured deer with satellite radio collars (Model G5-2D Iridium, 700 g, Advanced Telemetry Systems, Inc., Isanti, MN) programmed to record GPS location fixes at 6-h intervals; collars were equipped with a drop-off mechanism programmed to release after 2 years. After collaring, we reversed anesthesia for deer anesthetized with Telazol/xylazine with tolazoline hydrochloride (160–180 mg), and for deer anesthetized with BAM, we reversed anesthesia with atipamezole (100 mg) and naltrexone hydrochloride (25 mg). Because Telazol is not reversible, we remained with anesthetized deer until they were fully recovered and ambulatory to prevent predation. Capture and handling procedures were approved under USDA Forest Service Institutional Animal Care and Use Committee protocol 2017-010.

We used fixed-kernel density methods and the reference bandwidth to estimate utilization distributions (UD; Worton, 1989) from deer GPS data during the same time periods for which we obtained wild pig density estimates. We used only three-dimensional fixes with a horizontal dilution of precision <10 and visually examined maps of these locations using the *sp* R package (Bivand et al., 2013; Pebesma & Bivand, 2005) to ensure there were no erroneous locations. We estimated separate UD for each deer on a 90-m spatial grid using the *adehabitatHR* R package (Calenge, 2006) and considered all 90-m pixels within 99% UD contours as available to a given deer.

Vegetation and weather covariates

We used high-resolution light detection and ranging (LiDAR)-derived estimates of percent hardwood canopy cover to account for shared use of a preferred vegetation cover type. Discrete-return airborne LiDAR used in this study was acquired with an average of 8 returns/m² across SRS in March 2018 from a fixed-wing aircraft using a Leica ALS70-HP LiDAR system and the FUSION program was used to process and summarize LiDAR sensor data (McGaughey, 2019). Regression methods were then used to relate LiDAR sensor data to forest inventory plots ($n = 477$) distributed across the entire SRS. The resulting regressions were used to predict forest structural attributes and populate raster layers at 30-m resolution across the entire SRS (McGaughey et al., 2019). Following Garabedian et al. (2014), we aggregated 30-m rasters of LiDAR-derived hardwood canopy cover to 90 m to reduce prediction error and match the resolution of the wild pig density covariate and deer UD. Finally, we obtained temperature and barometric pressure measurements collected at 15-min intervals from weather stations located in Aiken, SC (USC00380072; www.ncdc.noaa.gov).

Data analysis

We evaluated spatiotemporal relationships between deer and wild pigs using three complementary techniques. First, we used quantile regression to estimate the effects of wild pig density on the intensity of deer space use (i.e., UD volume) within high-, moderate-, low-, and very-low use areas we defined using 90%, 70%, 50%, and 30% quantiles of cell-specific deer UD volume, respectively. We fit quantile regression models using the *quantreg* R package (Koenker, 2022) where cell-specific deer UD volume was the response variable and

interactions among deer sex, month, and a quadratic term for cell-specific wild pig density were explanatory variables.

Second, we used the coefficient of overlap, Δ^4 (Ridout & Linkie, 2009), to compare the overlap of diel activity patterns of deer and wild pigs, where values of Δ^4 range from 0 to 1, with 0 representing no overlap and 1 representing complete overlap in diel activity (Ridout & Linkie, 2009). We calculated coefficients of overlap using the overlap R package (Meredith & Ridout, 2021) and used 10,000 bootstrap samples to estimate 95% confidence intervals for overlap coefficient estimates. We considered overlap in diel activity to be low if the estimated coefficient of overlap was <0.5 with a bootstrapped confidence interval that did not overlap 0.5 and vice versa for a high estimate; overlap was neutral (i.e., neither avoidance nor aggregation) if the bootstrapped confidence interval overlapped 0.5 (Farmer et al., 2021).

Finally, we developed single-season multispecies occupancy models (Rota et al., 2016) using the unmarked R package (Fiske & Chandler, 2011) to characterize the co-occurrence of deer and wild pigs while accounting for the effects of shared resources and wild pig density. We measured the detection and nondetection (i.e., presence and absence) of deer and wild pigs as a binary variable (“1” for detection and “0” for nondetection), regardless of the number of individuals detected (Davis, McCreary, et al., 2018), at individual camera stations during each sampling occasion. We created 200-m nonoverlapping circular buffers centered on camera locations (based on 225-m minimum distance between cameras) to extract wild pig density and hardwood canopy cover covariates for each month. Then, for each month, we fit percent

hardwood canopy cover and a quadratic term for wild pig density as covariates on marginal deer occupancy (i.e., occupancy probability of deer irrespective of wild pig detection or nondetection; Rota et al., 2016). We fit percent hardwood canopy cover and a linear term for wild pig density as covariates on deer detection probability; we could not fit wild pig density as a quadratic term due to model convergence issues. We fit percent hardwood canopy cover as a covariate on marginal wild pig occupancy. We also fit quadratic terms for daily mean temperature and pressure as covariates on detection of both species given the SRS is characterized by hot and humid climate, and thermal cover is important to deer and wild pigs, particularly during the summer (Dexter, 1998; Webb et al., 2010; Wiemers et al., 2014). Finally, we fit hardwood canopy cover and a quadratic term for wild pig density as covariates on conditional occupancy (i.e., occupancy probability of one species conditional on the detection or nondetection of another; Rota et al., 2016). We extracted covariates for multispecies occupancy models using the Spatial Analyst Toolbox provided in ArcGIS Pro v. 2.8.1 (ESRI, 2021).

RESULTS

Wild pig density

Across a total of 156,238 remote camera images providing 19,519 wild pig detections, we identified 32–98 individual wild pigs based on natural markings from 432 to 4749 detections, with 401–2297 detections of unidentifiable wild pigs across sampling periods (Table 1). We did not observe

TABLE 1 Total remote camera images, detections of marked and unmarked wild pigs (*Sus scrofa*), number of marked wild pigs assigned individual identification (number of pigs identified), and estimates of abundance and density (pigs per square kilometer) from spatial capture–recapture models for partially marked populations based on remote camera images collected between March 2018 and August 2019 in Savannah River Site, SC, USA.

Month	Total images	No. wild pig detections		No. pigs identified	Pig abundance	Pig density (no./km ²)
		Unmarked	Marked			
March 2018	24,671	2297	4749	98	128 (123–146)	2.71 (2.60–3.09)
May 2018	22,170	466	867	86	156 (139–175)	3.30 (2.94–3.70)
July 2018	12,036	892	1759	91	152 (140–167)	3.21 (2.96–3.53)
October 2018	28,841	401	811	60	103 (92–118)	2.18 (1.94–2.49)
December 2018	21,124	918	576	32	107 (92–125)	2.26 (1.94–2.64)
February 2019	14,339	947	1416	69	129 (114–151)	2.73 (2.41–3.19)
April 2019	16,132	663	585	46	110 (96–128)	2.32 (2.03–2.71)
June 2019	8523	811	494	42	131 (113–153)	2.77 (2.39–3.23)
August 2019	8402	435	432	46	124 (108–142)	2.62 (2.28–3.00)

Note: Values in parentheses are 95% CIs.

deer and pigs together in any remote camera images. Estimated wild pig density ranged from 2.2 to 3.3 pigs/km², was highest in May 2018 and lowest in October 2018, and varied spatially across months (Appendix S1: Figure S2).

Wild pig effects on deer space use

We obtained a total of 19,511 locations for 29 deer ($n_{\text{male}} = 14$ and $n_{\text{female}} = 15$; Appendix S1: Figure S3) and estimated deer UD for each month using 67–123 locations per deer. While deer space use differed between males and females across months, wild pig density affected space use by both sexes to a larger degree (Appendix S1: Table S1). Overall, wild pig density effects on deer space use were strongest within high- and moderate-use areas (i.e., 90% and 70% quantiles of cell-specific deer UD volume, respectively), with negligible effects in low- and very-low-use areas (i.e., 50% and 30% cell-specific UD volume, respectively; Appendix S1: Table S1). Wild pig density had positive effects on female deer space use during December

2018 and August 2019, but negative effects during March, June, July, and October 2018 and April 2019 (Figure 1; Appendix S1: Table S1). For male deer, wild pig density had positive effects on space use during July 2018 and June 2019, but negative effects during March, October, and December 2018 (Figure 2; Appendix S1: Table S1). In May 2018 and April, June, and August 2019, male deer space use increased at relatively low wild pig density but decreased at relatively high wild pig density (Figure 2; Appendix S1: Table S1).

Temporal overlap

Across all months, deer and wild pigs tended to be active during the same periods of the day (Figure 3). Overlap in diel activity between deer and wild pigs was generally high (i.e., overlap coefficients ranging between 0.74 and 0.86 and lower confidence bounds >0.5; Table 2). However, there was some evidence for divergence in the diel activity of wild pigs and male and female deer ($\Delta^4_{\text{male}} = 0.68$, 95% CI = 0.67–0.71; $\Delta^4_{\text{female}} = 0.71$;

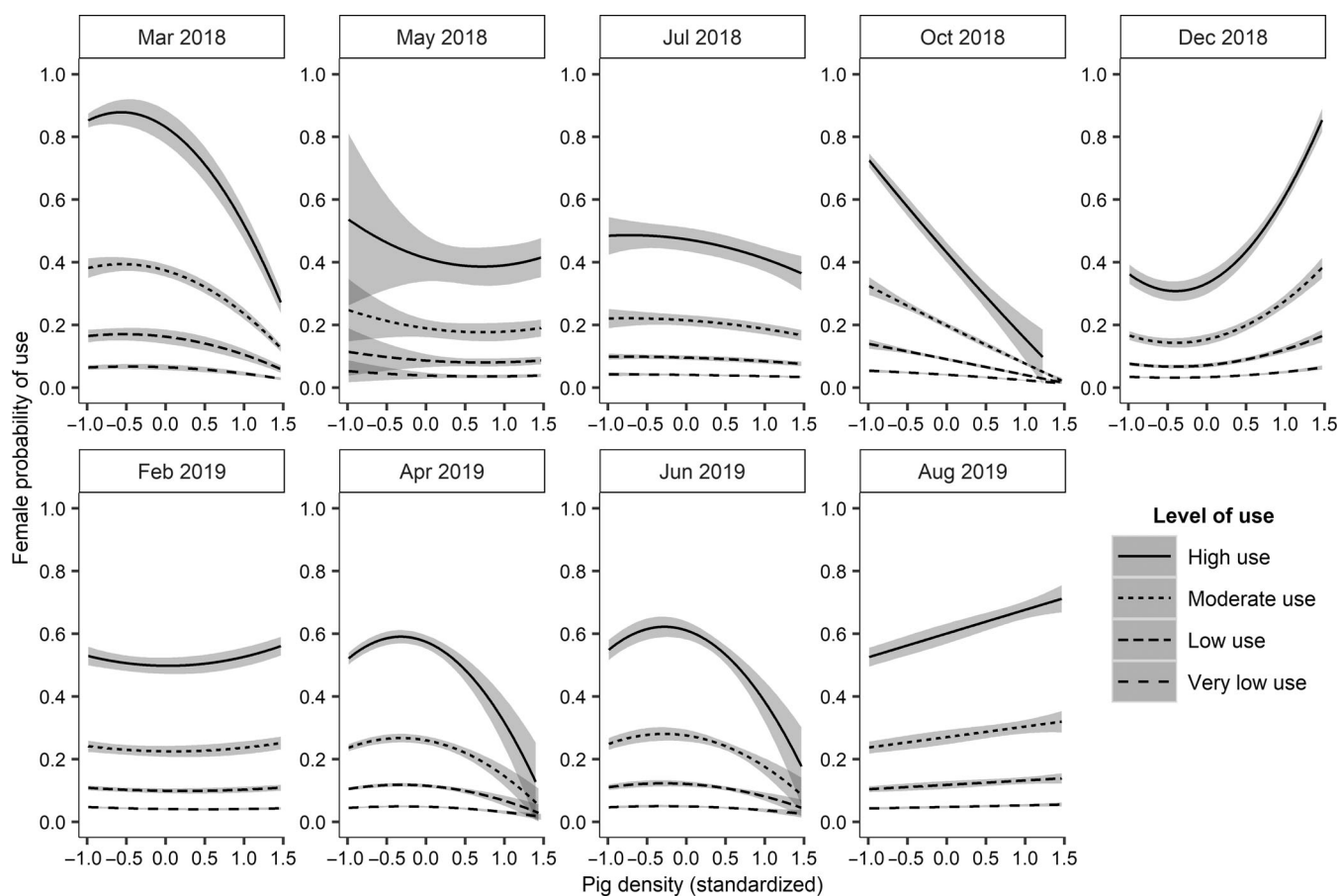


FIGURE 1 Effects of wild pig (*Sus scrofa*) density on space use by female white-tailed deer (*Odocoileus virginianus*) within high-, moderate-, low-, and very-low-use areas (defined as 90%, 70%, 50%, and 30% quantiles of cell-specific utilization distribution volume estimates, respectively) of female deer (level of use) between March 2018 and August 2019 in Savannah River Site, SC, USA.

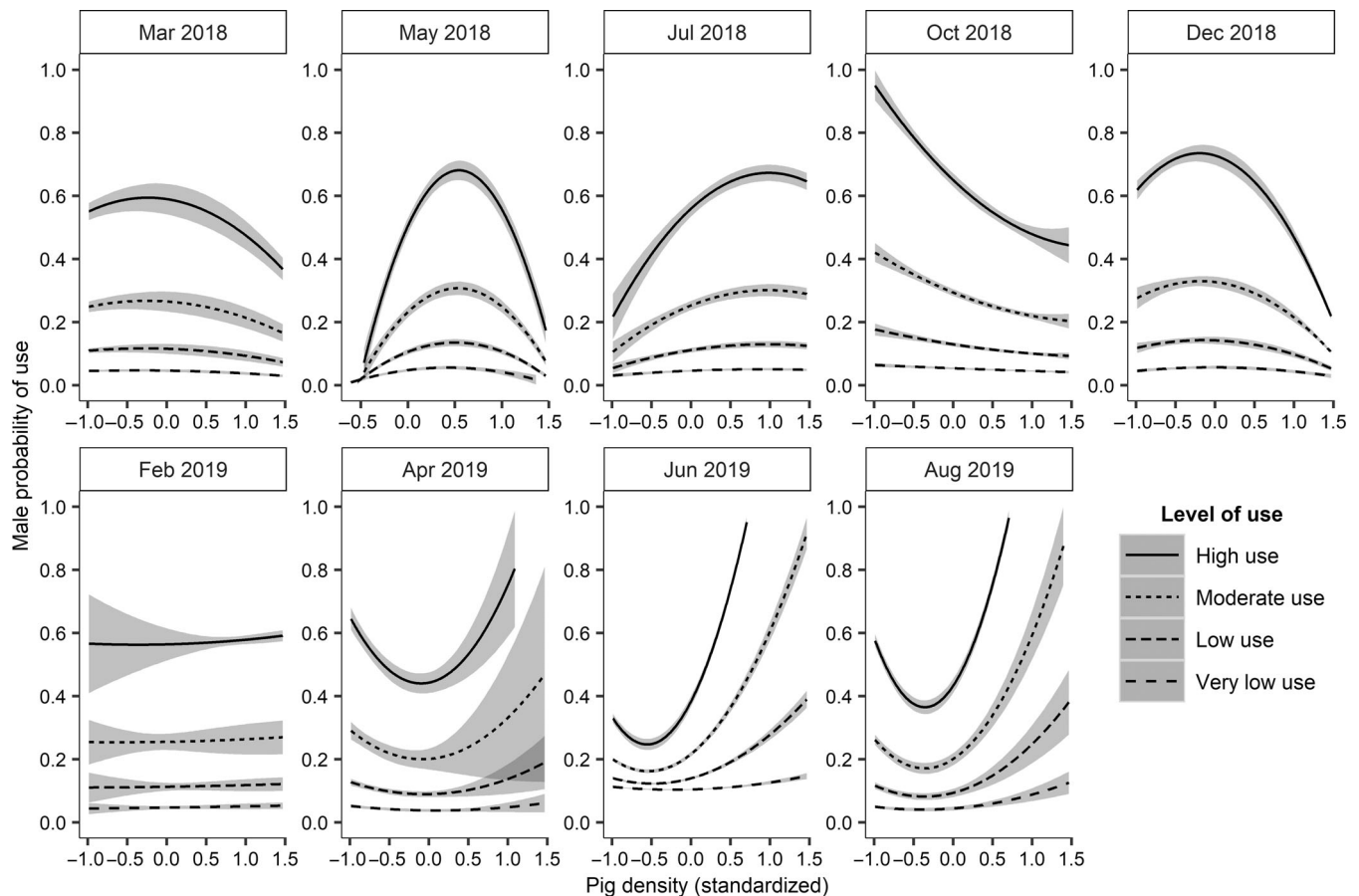


FIGURE 2 Effects of wild pig (*Sus scrofa*) density on space use by male white-tailed deer (*Odocoileus virginianus*) within high-, moderate-, low-, and very-low-use areas (defined as 90%, 70%, 50%, and 30% quantiles of cell-specific utilization distribution volume estimates, respectively) of male deer (level of use) between March 2018 and August 2019 in Savannah River Site, SC, USA.

95% CI = 0.69–0.73) during October 2018, when male and female deer activity peaked between midnight and dawn, whereas wild pig activity peaked between dusk and midnight (Figure 4). Additionally, wild pigs exhibited much more diurnal activity than male and female deer during October 2018 (Figure 4).

Multispecies occupancy models

Across months, deer were detected at 78%–99% of camera sites, whereas wild pigs were detected at 33%–62% of camera sites (Appendix S1: Table S2 and Figure S4). Marginal deer occupancy increased in response to hardwood canopy cover in July 2018 but decreased in August 2019 (Figure 5; Appendix S1: Table S3). Wild pig density had negative effects on marginal deer occupancy during May and October 2018 but positive effects during July 2018 and February and April 2019 (Figure 5; Appendix S1: Table S3). Effects of hardwood canopy cover on deer detection probability mirrored the effects of wild pig density on

deer detection probability (Appendix S1: Table S3, Figure S5). Hardwood canopy cover had a positive effect on marginal wild pig occupancy during October 2018 and August 2019, but no effect during all other months (Appendix S1: Table S3).

Deer and wild pigs co-occurred at 30%–59% of camera sites across all months (Appendix S1: Table S2, Figure S4). Conditional deer occupancy was affected by wild pig density and hardwood canopy cover across all months (Appendix S1: Table S3). Conditional on wild pig detection, deer occupancy increased with wild pig density during March, July, and December 2018 and February, April, and August 2019, but decreased during May and October 2018 (Appendix S1: Figure S6). Importantly, deer occupancy across the range of hardwood canopy cover differed between sites where wild pigs were detected and not detected during certain months. Conditional on detection of wild pigs at a site, deer occupancy increased in response to hardwood canopy cover during July 2018, but decreased during August 2019 (Figure 6). Conditional on nondetection of wild pigs at a site, deer occupancy

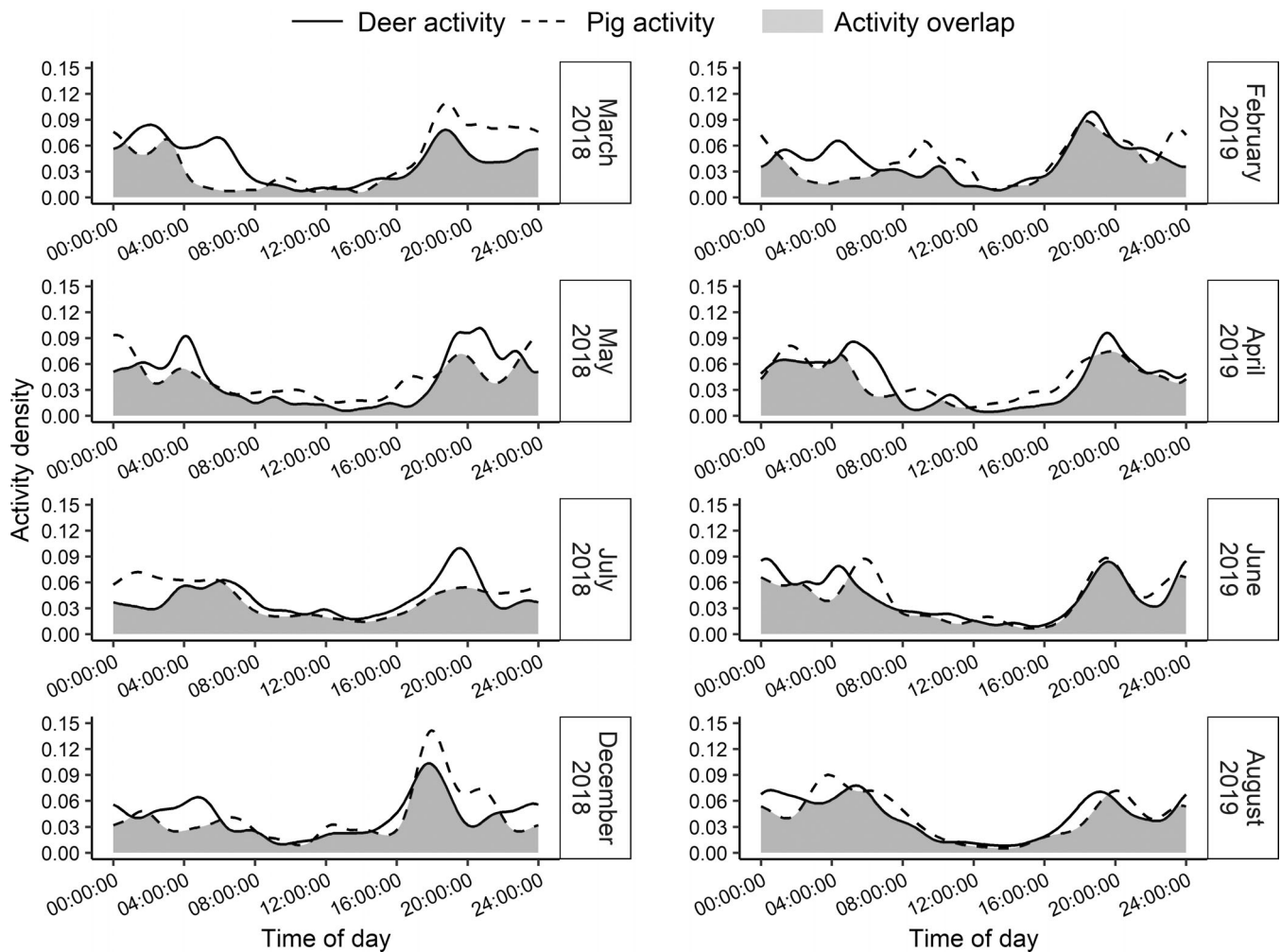


FIGURE 3 Overlap in diel activity between white-tailed deer (*Odocoileus virginianus*) and wild pigs (*Sus scrofa*) during March, May, July, and December of 2018 and February, April, June, and August of 2019 in Savannah River Site, SC, USA.

TABLE 2 Coefficient of overlap (Δ_4) and 95% bootstrapped confidence intervals (95% CI, in parentheses) of diel activity of white-tailed deer (*Odocoileus virginianus*) and wild pigs (*Sus scrofa*) between March 2018 and August 2019 in Savannah River Site, SC, USA.

Month	Δ_4
March 2018	0.744 (0.729–0.760)
May 2018	0.777 (0.754–0.800)
July 2018	0.823 (0.797–0.848)
October 2018	0.766 (0.746–0.785)
December 2018	0.796 (0.773–0.820)
February 2019	0.796 (0.774–0.818)
April 2019	0.833 (0.809–0.856)
June 2019	0.866 (0.842–0.890)
August 2019	0.862 (0.829–0.895)

decreased in response to hardwood canopy cover during February and August 2019 (Figure 6). In contrast, wild

pig occupancy response to hardwood canopy cover was unaffected by or increased regardless of whether deer were detected (Appendix S1: Figure S7).

DISCUSSION

Our results indicate that fine-scale shifts in space use are the primary strategy deer use to minimize the costs of competition with wild pigs. In many cases, native species shift diel activity to avoid direct encounters with invasive competitors (Kass et al., 2020). In the case of deer and wild pigs, deer did not extensively shift diel activity patterns nor large-scale occupancy patterns, but rather deer exhibited increasingly stronger fine-scale responses to wild pig density in high- and moderate-use areas. It has been shown that high- and moderate-use areas likely are where competition for resources is greatest given that body mass, age, and sex of deer have a minimal effect on changes in space use compared with competition (Lesage et al., 2000).

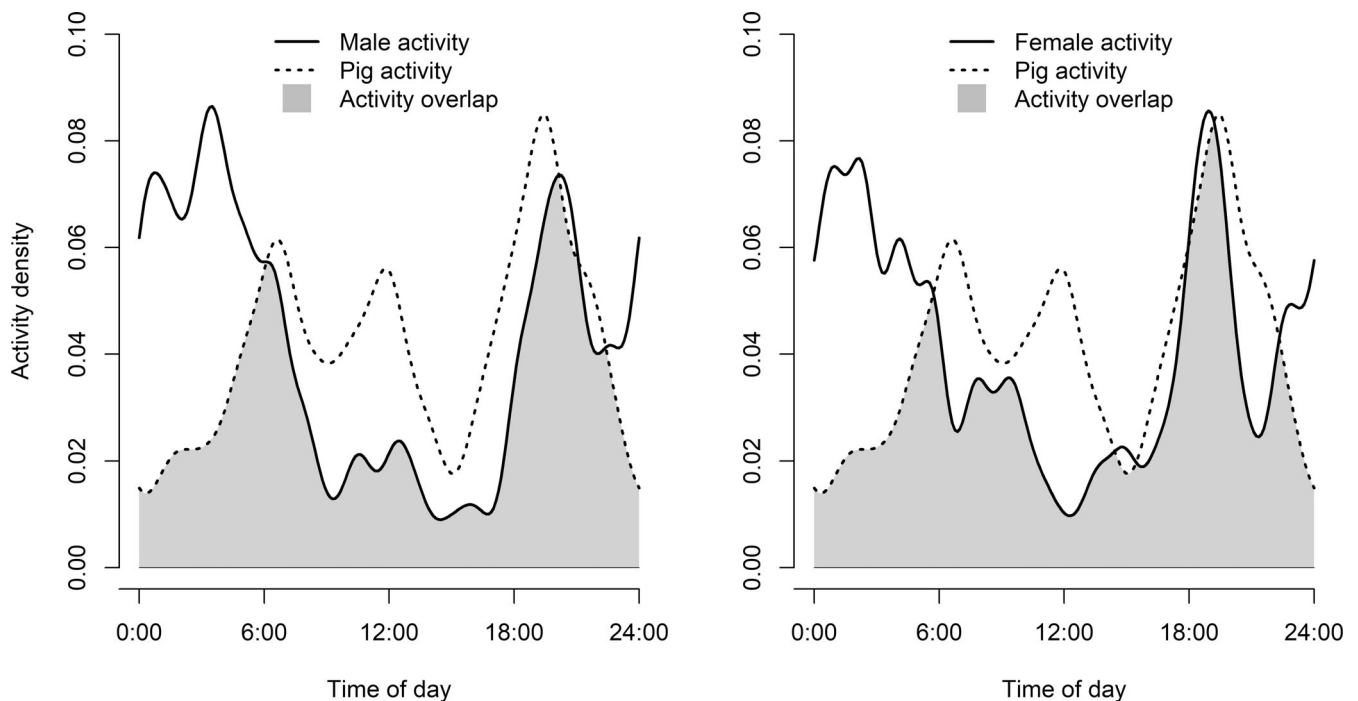


FIGURE 4 Overlap in diel activity between wild pigs (*Sus scrofa*) and male (left panel) and female (right panel) white-tailed deer (*Odocoileus virginianus*) during October 2018 in Savannah River Site, SC, USA.

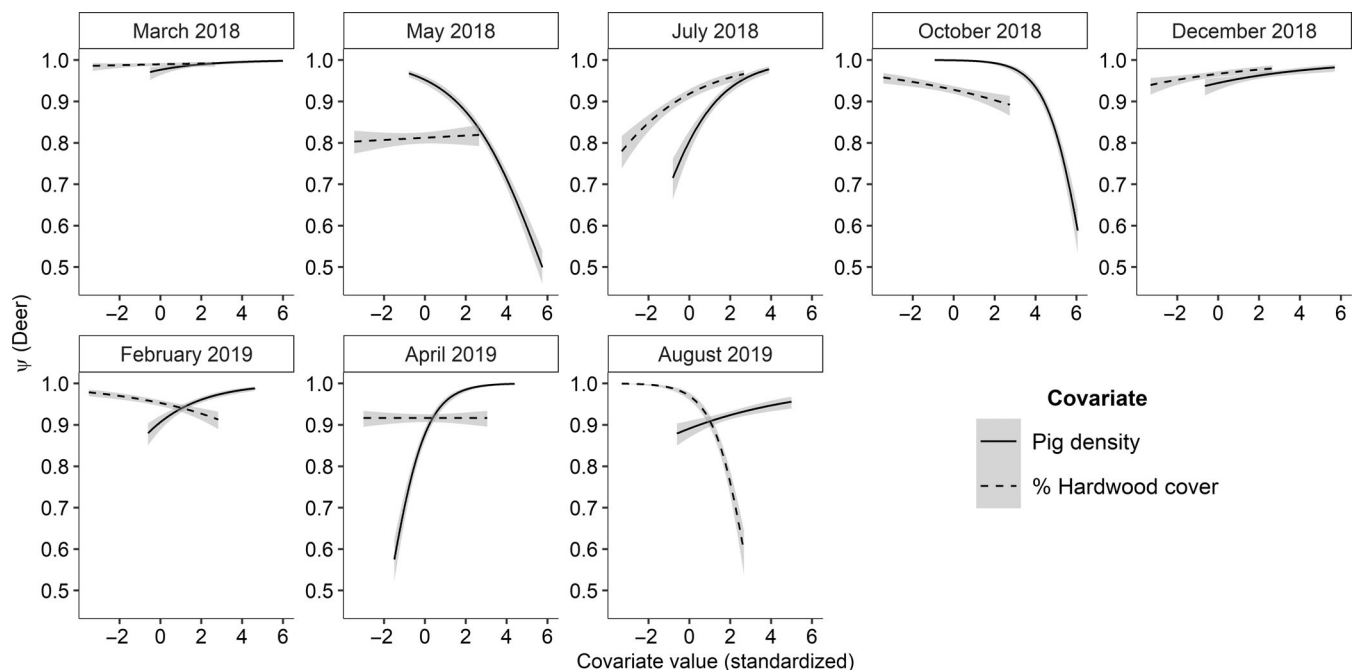


FIGURE 5 Predicted white-tailed deer (*Odocoileus virginianus*) occupancy and 90% confidence bands (gray shaded areas) in response to wild pig (*Sus scrofa*) density (pig density) and percent hardwood canopy cover (% hardwood cover) within 200 m of remote cameras between March 2018 and August 2019 in Savannah River Site, SC, USA.

The steeper declines in deer space use in response to increased wild pig density in high- and moderate-use areas are also consistent with interference competition theory (Case & Gilpin, 1974). While interpreting co-occurrence as

a direct proxy for interactions without direct behavioral observations runs the risk of assuming negative responses reflect interspecific competition, there is some evidence from this work that deer might experience interference

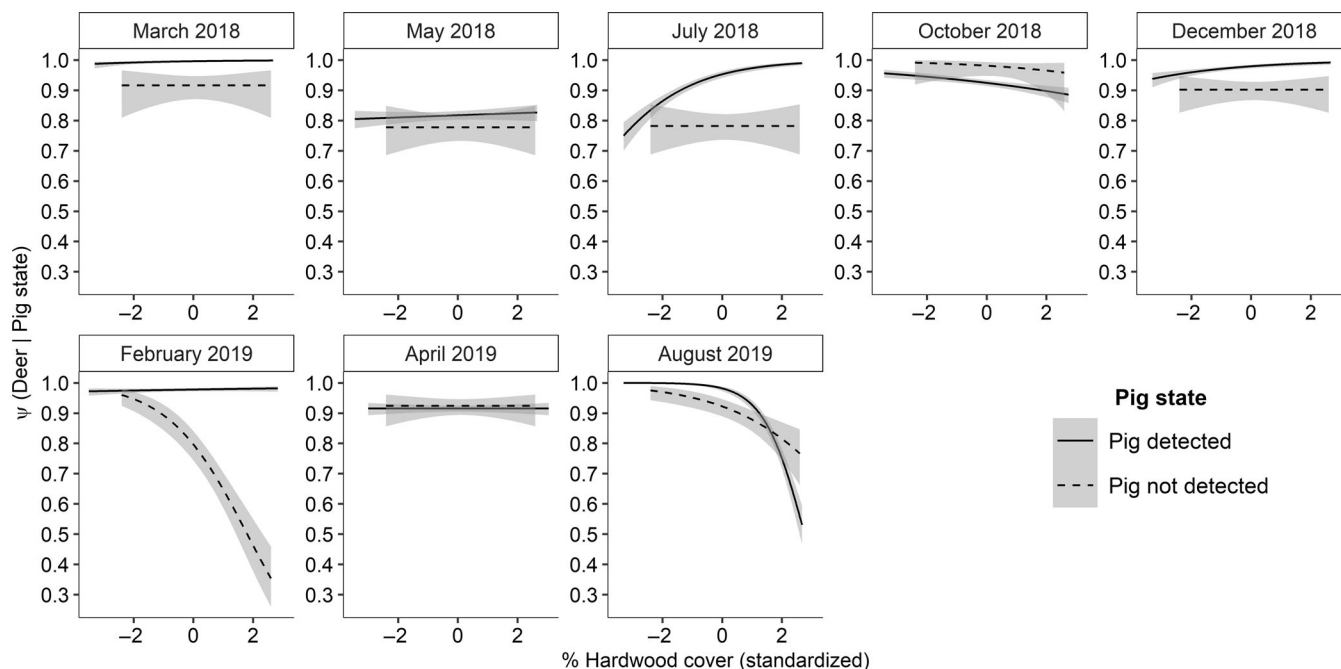


FIGURE 6 Predicted white-tailed deer (*Odocoileus virginianus*) occupancy and 90% confidence bands (gray shaded areas) in response to percent hardwood canopy cover (% hardwood cover [standardized]) within 200 m of cameras, conditional on wild pig (*Sus scrofa*) detection and nondetection between March 2018 and August 2019 in Savannah River Site, SC, USA.

competition from wild pigs at a fine scale. However, we found no evidence that wild pigs broadly displace deer from using an area, and fine-scale spatial adjustments may be the mechanism enabling long-term co-existence of deer and wild pigs, as observed in other native species (e.g., blue tit, *Cyanistes caeruleus*, and great tit, *Parus major*, Peck et al., 2014; green anole lizard, *Anolis carolinensis*, Bush et al., 2021; black garden ant, *Lasius niger*, Gippet et al., 2021; wild turkeys, *Meleagris gallopavo*, Walters & Osborne, 2022).

Our results also suggest that increased density of wild pigs exacerbates negative indirect effects on deer. Displacement of native species by invasive competitors often occurs through aggressive direct interactions, but in some cases, native species leave an area even before aggressive direct interactions (Huntingford & Turner, 1987; Perez Carusi et al., 2017; Polo-Cavia et al., 2009). Similarly, native competitors may increase vigilance, thereby reducing foraging efficiency and fitness, due to the perceived risk of competition where density of an invasive competitor is increased (Kodric-Brown & Mazzolini, 1992; Thornhill, 1987). Considering we did not observe deer and wild pigs together in any remote camera images, and that deer space use declined where wild pigs occurred at high density, it is possible that noise, olfactory cues, and movement of wild pigs where they occur at high density may be an indirect mechanism driving fine-scale spatial avoidance of wild pigs by deer. Additionally, modifications to habitat by wild pigs

where they occur at high density could degrade forage and cover resources to the extent these resources are less suitable to deer, thus leading to deer avoidance during seasons when forage or vegetation cover resources are most limiting (e.g., understory cover during fawning [May 2018], hard mast accessibility during peak rut [October 2018], and cover for thermoregulation during warmer months [August 2019]).

It is also notable that the effects of wild pig density on deer were not consistent throughout the year. Spatial partitioning alone by deer may not be sufficient to minimize the costs of competing with wild pigs (if this is indeed occurring) during periods of increased nutritional demands or physiological stress. Several species partition resources in both space and time, such that resources are partitioned temporally when spatial partitioning is not sufficient to minimize the costs of competition (Ji et al., 2022; Li, Li, et al., 2022; Li, Xue, et al., 2022; Mori et al., 2020). Similarly, we observed fine-scale spatial avoidance of wild pigs and clear differences in times of peak deer and wild pig activity during October, which coincides with peak rut when deer activity and sensitivity to olfactory cues increase. Additionally, female deer may be more sensitive to wild pigs in October as they prepare for and enter gestation, an energetically demanding time of the year. Thus, spatiotemporal partitioning may be beneficial during times when life history needs are particularly demanding and minimizing costly interactions

with competitors is paramount. This has been observed in other studies on white-tailed deer (Saldo, 2022) and species such as Asiatic black bears (*Ursus thibetanus*) and brown bears (*Ursus arctos*; Ji et al., 2022), and blue tits and great tits (Gustafsson, 1987), as well as assemblages of suiforms (Gabor et al., 2001). On the other hand, the observed shift in peak activity time of males during October was likely because males are actively searching for females at this time, rather than due to direct effects of wild pig density. During other months of the year, fine-scale spatial partitioning by deer may have been sufficient to avoid wild pigs to the extent that temporal partitioning was not necessary. However, we cannot rule out the possibility that deer temporal responses to wild pigs occurred at finer temporal scales than we could detect in our analysis (Davis, Rich, et al., 2018).

Many factors we were unable to account for in our study may affect spatiotemporal relationships between deer and wild pigs. Importantly, we lacked a metric reflecting the availability of shared food resources, which may be a primary driver of competition between these species throughout the year, but especially during autumn. Considering the importance of mast and acorns to both deer and wild pigs in autumn, and that wild pigs can monopolize entire mast crops (Mikulka et al., 2018), poor mast years could increase competition and the extent to which deer avoid areas if wild pig density is high. Additionally, hunting activities can change peak activity times of deer (Kilgo et al., 1998), which could negate any benefits deer gain by shifting activity times to periods of low pig activity during October, as we observed in this study. Predators may further complicate understanding the nature of interactions between deer and wild pigs (Gurevitch et al., 2000). Eastern coyotes (*Canis latrans*) are an invasive predator that can influence deer neonate survival on the SRS (Kilgo et al., 2012) and may exacerbate the impacts of wild pigs on deer (MacKenzie et al., 2021; Petroelje et al., 2021). For example, the onset of deer parturition provides an influx of fawns that are vulnerable to coyote predation, and the associated costs of increased vigilance in deer could be additive to the costs of competition with wild pigs. Moreover, other vegetation cover types may also interact with coyote occurrence, particularly dense understory vegetation that is selected for cover by both deer and wild pigs. Dense understory vegetation provides hiding cover that may facilitate co-occurrence of deer and wild pigs where coyotes also occur and could explain the observed positive fine-grained spatial responses of female deer to wild pigs during fawning (Kittle et al., 2008; Van Moorter et al., 2009). Thus, positive associations between deer and wild pigs during certain months are likely driven by selection for shared cover by both species (e.g., selection for hardwood areas during July 2018 and

August 2019), rather than any benefits wild pigs may confer on deer.

That deer occupancy was affected to a large extent by wild pig density within the vicinity of cameras, rather than simply detection or nondetection of wild pigs at a camera, suggests ongoing control efforts to keep wild pig density low may better facilitate co-existence of native wildlife and this invasive competitor. This finding has important implications for wild pig control programs given the nonlinear nature of wild pig effects that increased with wild pig density. Previous studies clearly demonstrated negative effects of invasive competitors on native species are exacerbated under high densities (Gurnell et al., 2004; Mazzamuto et al., 2017; Wauters et al., 2001). However, wild pig density within our study area was relatively low (2–3 pigs/km²) compared with other areas on SRS, where wild pig density can be as high as 20 pigs/km² (Kilgo et al., 2021). While the low-density condition we studied could explain why we did not observe clear avoidance of wild pigs by deer across months, our results suggest deer could still be impacted at even our low observed wild pig densities. However, sharp declines in deer occupancy in response to wild pig density during May and October suggest relatively small increases in wild pig density can have measurable negative impacts on deer during energetically demanding times of the year.

In conclusion, we determined that deer responses to wild pigs are perhaps more complex than previously recognized due to their fine-scale nature and the nonlinear effect of wild pig density. The nonlinear response of deer to wild pig density suggests even relatively small increases in density of invasive competitors can have measurable effects on native species. Deer likely face a trade-off between resource acquisition and avoiding interactions where they co-occur with wild pigs (Peck et al., 2014), particularly when deer life history needs are especially demanding. Thus, fine-scale behavioral plasticity enables deer to minimize costly interactions and avoid broadscale displacement by wild pigs. Our study reinforces the importance of considering spatial and temporal responses of native species to occurrence and density of invasive competitors and shared resources at various scales.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Garabedian et al., 2022) are available from Figshare: <https://doi.org/10.6084/m9.figshare.17219432.v3>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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