Impact of Invasive Wild Pig on White-Tailed Deer and Eastern Wild Turkeys in Southwest Georgia

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Abstract: Wild pigs (*Sus scrofa*) are a highly destructive invasive species and reported to be present in 77% of counties in the southeastern U.S. Wild pigs may negatively affect white-tailed deer (*Odocoileus virginianus*; hereinafter, deer) and eastern wild turkeys (*Meleagris gallopavo silvestris*; hereinafter, turkey) via competition over forage or exclusion from preferred areas. To explore effects of wild pigs on spatial distribution of these species within a mixed agriculture-forest landscape, we developed models predicting camera trap detections of deer and turkeys as a function of landcover, calendar season, and wild pig presence. We deployed 147 passive camera traps and collected data for one month during each calendar season during 2020 to 2022 in southwestern Georgia (32,760 camera nights). We observed a negative association between turkeys and wild pigs during summer and within mixed forests, and a negative association between deer and wild pigs in pecan (*Carya illinoinensis*) orchards during summer, fall and winter. However, there was a positive association between deer and wild pigs in forested wetlands and mixed forests during fall and winter. The negative relationships between turkeys and wild pigs or deer and wild pigs may be from adverse interactions or simply species-specific landcover preferences. Similarly, the positive correlations with deer are likely the result of common landcover preferences, as it seems highly unlikely that deer benefit from wild pigs. Our results highlight how the relationship between invasive species and native species may be confounded by differences in land cover preferences and suggest further, manipulative experiments, may be necessary to better assess the effects of wild pigs on native wildlife.

Keywords: camera traps, habitat selection, invasive species, *Meleagris gallopavo, Odocoileus virginianus, Sus scrofa*

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Introduced (i.e., non-native) species can compete aggressively with native species, prey on native species, and alter natural disturbance regimes resulting in altered community composition and, in some cases, native species extinction (Mack and D'Antonio 1998, Wilcove et al. 1998, Gurevitch and Padilla 2004, Kass et al. 2020). Characteristics of successful invasive species that allow them to compete with native species include high fertility and fecundity, generalist and opportunistic diets, early reproductive maturity, and the ability to quickly exploit vacant niches via range expansion and competitive behavior (Wilcove et al. 1998, Sakai et al. 2001). Native species often avoid invasive species and exhibit behavioral changes more frequently than the invasive species (Ruland and Jeschke 2020).

Wild pigs (*Sus scrofa;* also known as wild boar, feral swine, wild hog, feral hog, and feral pig; hereinafter referred to as wild pig; Keiter et al. 2016) are globally invasive and particularly damaging outside of their native range. Invasive wild pigs are linked with the extinction of 14 species and are considered a threat to 672 endangered or critically endangered species worldwide (345 flora and 327 fauna; Risch et al. 2021). An estimated 6.9 million wild pigs are now found in 31 states in the U.S., with the greatest concentrations in the southeastern U.S. where wild pigs occupy approximately 77% of counties in Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia (Lewis et al. 2019, USDA APHIS 2020, USDA APHIS 2022). While there is extensive literature available on wild pig economic costs (Pimentel 2007, Mengak 2016, Anderson et al. 2019, McKee et al. 2020), diet (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010, Ballari and Barrios-Garcia 2014), and population expansion (Wood and Barrett 1979, Graves 1984, McClure et al. 2018, Lewis et al. 2019), there is less empirical evidence of their effects on native species, especially economically valuable game species (McDonough et al. 2022, Walters and Osborne 2022).

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Existing research of effects of wild pigs on native species is largely observational (McDonough et al. 2022). Studies of wild pig interactions with native wildlife has focused on potential competition by quantifying dietary overlap (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010) or nest depredation by wild pigs (Tolleson et al. 1993, Sanders et al. 2020). However, there is recent research on effects of wild pigs on the spatial distribution of white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallapovo*; Keever 2014, O'Brien et al. 2019, Lewis 2020, Garabedian et al. 2022, Walters and Osborne 2022, Dykstra et al. 2023, McDonough 2023), and these studies have generally found negative or neutral associations. White-tailed deer and eastern wild turkey (hereinafter deer and turkey, respectively) are the most popular game animals in the U.S., pursued by 8.1 and 2.0 million hunters, respectively (USFWS and USCB 2018), and deer hunting is the most important source of funds for state wildlife agencies in the Southeast (Duda et al. 2022). Although evidence suggests wild pigs may compete with and prey upon turkey and deer, there is little evidence of population-level effects of wild pigs on these species. However, given the importance of deer and turkeys, it is imperative to understand how wild pigs may affect these game species.

In this study, we explored effects of wild pig relative abundance on detection rates of deer and turkey across a mixed agricultural-forest landscape in southwestern Georgia. To examine potential effects, we collected passive camera trapping data for one month during each calendar season from 2020 to 2022. We predicted that the relative abundance of wild pigs, accounting for the interaction of season and landcover types, would have a negative effect on both deer and turkey detection rates.

Methods

Study Area

Our study occurred on private property in Calhoun County, Georgia (Figure 1) with an historically abundant wild pig population. The 92.44-km^2 study area consisted of row crops (39%), wetlands (32%), pine forests comprised of longleaf (*Pinus palustris*) and loblolly pine (*P. taeda*; 13%), pecan (*Carya illinoinensis*) orchards (10%), and mixed hardwood-pine interspersed with live oak (*Quercus virginiana*; 3%), with the remaining 3% consisting of wildlife food plots and narrow riparian areas. Row crops were planted in late spring and harvested in late summer or early fall, with crops consisting of corn (*Zea mays*), cotton (*Gossypium* spp.), and peanuts (*Arachis hypogaea*). Daily temperatures average 34 C and 17 C in summer and winter months, respectively (U.S. Climate Data 2020). Monthly precipitation averages 150.6 mm in summer and 100.8 mm in winter (U.S. Climate Data 2020).

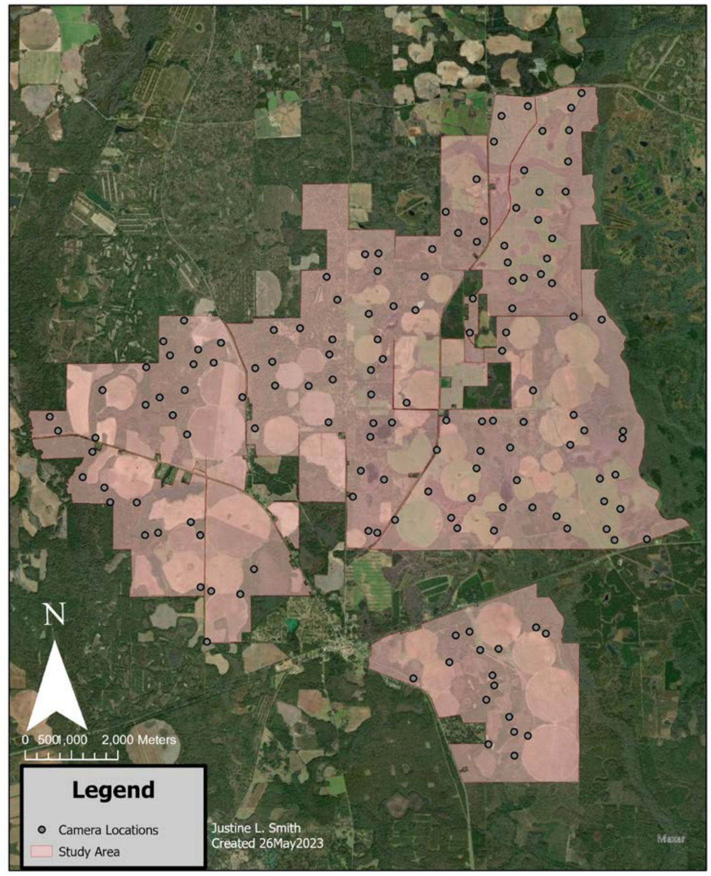

Figure 1. Study area in Calhoun County, Georgia with gray circles indicate camera locations (n = 147) used for assessing game species response to wild pig presence.

Data Collection

We used Browning Strike Force HD Pro X (Browning Trail Cameras, Morgan, Utah) trail cameras for passive camera trapping surveys. We used ArcGIS 10.8.1 (ESRI 2020) to determine locations by overlaying 40-ha grid cells over the study area. We placed one camera trap within each cell approximately 1.5 m away from a wildlife trail and 1.0 m above the ground. We used the 2019 National Land Cover Data (NLCD, 30-m resolution; Dewitz and U.S. Geological Survey 2021) to determine landcover at each camera trap location. We excluded cells that fell entirely within row crops to avoid camera damage associated with farming activity. Overall, we deployed 60 cameras in evergreen forests, 49 cameras in forested wetlands, 23 cameras in pecan orchards, and 15 cameras in mixed forests. Of the cover types included in sampling (i.e., excluding row crops), evergreen forests, pecan orchards, and mixed forests were over-sampled relative to their availability. Forested wetlands were under-sampled relative to their availability due to accessibility, as we avoided placing cameras in areas that were prone to flooding. When able, we placed cameras in forested wetlands above the flood line.

We programmed cameras to capture one image upon motion trigger with a 30 sec delay between photos. We conducted camera surveys for one month each calendar season for two years, using months with solstices or equinoxes (i.e., March = spring, June = summer, September = fall, December = winter). We sampled two seasons in 2020 (fall and winter), all four seasons in 2021, and two seasons in 2022 (spring and summer) for a total of eight seasons.

We partitioned detections for each species (deer, turkey, and wild pig) within each season quantified as detections camera^{-1} day^{-1}. We avoided double counting individuals by withholding detections occurring within 15 min of a prior detection at a given camera when group size remained the same or decreased. However, if the group size of a detection event increased relative to the detection event immediately preceding, and within the 15-min window, we retained the detections of the larger group size.

Statistical Analysis

We estimated deer, turkey, and wild pig detections camera^{-1} day^{-1} from spatiotemporal predictors using a zero-inflated Poisson regression (ZIPR) model and the pscl package (Zeileis et al. 2008) in R (R Core Team 2021). We used a ZIPR model because deer, turkey, and wild pig detections camera^{-1} day^{-1} primarily consisted of zeroes (66.4%, 98.2%, and 93.3% respectively). We included landcover data (evergreen forests, mixed forests, pecan orchards, forested wetlands) and season (spring, summer, fall, winter) as predictor variables. For each species, we developed a null model, models for each predictor, and a global model including the two-way interaction of predictors. We calculated the Akaike Information Criteria (AIC) and delta AIC (ΔAIC) using the 'AICmodavg' package (Mazerolle 2023) in R and identified the most parsimonious spatiotemporal model using an information-theoretic approach. We considered models within 2 ΔAIC as competing models and used model averaging for parameter estimates if presented with competing models (Burnham and Anderson 2002). We identified the most parsimonious spatiotemporal model to understand how each species (deer, turkey, and wild pigs) used different landcover types throughout calendar seasons. Upon identifying the most parsimonious spatiotemporal model for deer and turkeys, we included the original wild pig detections camera^{-1} day^{-1} as a main effect and associated interactions as predictor variables to determine if adding wild pig detection rates improved model predictions using an information-theoretic approach (i.e., reduced AIC score). We considered any predictors informative when their 95% confidence intervals did not overlap zero.

Results

We monitored 147 camera traps across eight seasons for 32,760 camera days. We detected deer at all camera locations ($n = 147$), wild pigs at 86% ($n = 126$), and turkey at 63% of locations ($n = 93$). We detected deer most (1.07 deer detections camera^{-1} day^{-1}) during winter 2020 and least (0.48 deer detections camera^{-1} day^{-1}) during spring 2021. Wild pigs were detected most (0.20 wild pig detections camera^{-1} day^{-1}) during fall 2021 and least (0.07 wild pig detections camera^{-1} day^{-1}) during spring 2022. Turkey detection rates were greatest during spring 2021 (0.06 turkey detections camera^{-1} day^{-1}) and least during summer 2021 (0.03 turkey detections camera^{-1} day^{-1}).

For wild pigs, turkeys, and deer, our global spatiotemporal model received the most support. There were no competing models (i.e., second-best models had ΔAIC = 282.84, 137.99, and 266.48 for wild pigs, turkey, and deer, respectively). The pig model suggested that their detection rates increased in pecan orchards during fall and winter and forested wetlands during winter but declined in mixed forests during summer (Table 1).

Including wild pig detections camera^{-1} day^{-1} and associated interactions reduced AIC for the turkey model by 25.22 and the deer model by 126.99, markedly improving both deer and turkey models. Models that only considered wild pig detections camera^{-1} day^{-1} as an additive predictor (i.e., no predictors interacting with wild pig detections) were not competitive with models including

Table 1. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict wild pig detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	*β*	SE	*P*
Reference Condition	0.639	0.070	<0.01***
Summer	–0.067	0.098	0.50
Fall	–0.026	0.088	0.77
Winter	–0.258	0.095	<0.01**
Forested Wetlands	–0.081	0.097	0.41
Mixed Forests	–0.240	0.128	0.06
Pecan Orchards	–0.637	0.260	0.01*
Summer × Forested Wetlands	–0.001	0.138	0.99
Fall × Forested Wetlands	–0.179	0.121	0.14
Winter × Forested Wetlands	0.527	0.124	<0.01***
Summer × Mixed Forests	–0.486	0.241	0.04*
Fall × Mixed Forests	–0.198	0.160	0.21
Winter × Mixed Forests	0.211	0.166	0.20
Summer × Pecan Orchards	0.310	0.323	0.33
Fall × Pecan Orchards	0.753	0.283	0.01**
Winter × Pecan Orchards	0.837	0.305	0.01**

interactions ΔAIC = 113.84 for the deer model and 6.73 for the turkey model. The three-way interaction in the deer model was informative (Table 2). In the presence of wild pigs, deer detection rates declined in pecan orchards during summer, fall, and winter but increased in forested wetlands and mixed forests during fall and winter (Figure 2). The three-way interaction associated with the turkey model was not estimable. Therefore, we only included two-way interactions in our modeling efforts for turkeys (Table 3). Relative to the reference condition, turkey detection rates declined in forested wetlands during summer, mixed forests during fall and winter, and pecan orchards during winter and increased in pecan orchards during summer (Table 3). Turkey detections showed a significant negative association with wild pigs during summer (Figure 3A) and in mixed forests (Figure 3B).

Table 2. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict white-tailed deer detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	β	SE	P
Reference Condition	0.603	0.026	<0.01***
Pig	0.117	0.024	<0.01***
Summer	–0.296	0.040	<0.01***
Fall	0.077	0.036	0.03*
Winter	–0.089	0.036	0.01*
Forested Wetlands	–0.100	0.043	0.03*
Mixed Forests	0.142	0.057	0.01*
Pecan Orchards	0.052	0.049	0.29
Pig × Summer	–0.023	0.044	0.60
Pig × Fall	–0.020	0.055	<0.01***
Pig × Winter	–0.019	0.047	<0.01***
Pig × Forested Wetlands	–0.138	0.072	0.05*
Pig × Mixed Forests	–0.609	0.213	<0.01***
Pig × Pecan Orchards	0.591	0.182	<0.01**
Summer × Forested Wetlands	0.090	0.063	0.16
Fall × Forested Wetlands	–0.899	0.059	0.13
Winter × Forested Wetlands	0.020	0.057	0.72
Summer × Mixed Forests	0.048	0.083	0.56
Fall × Mixed Forests	–0.185	0.080	0.02*
Winter × Mixed Forests	–0.252	0.080	<0.01**
Summer × Pecan Orchards	–0.293	0.090	<0.01**
Fall × Pecan Orchards	–0.110	0.072	0.13
Winter × Pecan Orchards	–0.025	0.065	0.70
Pig × Summer × Forested Wetlands	–0.083	0.103	0.42
Pig × Fall × Forested Wetlands	0.220	0.096	0.02*
Pig × Winter × Forested Wetlands	0.226	0.083	<0.01**
Pig × Summer × Mixed Forests	–0.881	0.731	0.23
Pig × Fall × Mixed Forests	0.863	0.220	<0.01***
Pig × Winter × Mixed Forests	0.528	0.236	0.03*
Pig × Summer × Pecan Orchards	–1.602	0.489	<0.01**
Pig × Fall × Pecan Orchards	–0.553	0.193	<0.01**
Pig × Winter × Pecan Orchards	–0.535	0.190	<0.01**

Table 3. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict eastern wild turkey detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	β	SE	P
Reference Condition	0.488	0.091	<0.01***
Pig	–0.169	0.163	0.30
Summer	–0.046	0.166	0.78
Fall	0.404	0.155	0.01*
Winter	1.435	0.120	<0.01***
Forested Wetlands	0.204	0.125	0.10
Mixed Forests	0.453	0.186	0.01*
Pecan Orchards	–0.169	0.221	0.44
Pig × Summer	–0.967	0.327	<0.01**
Pig × Fall	0.085	0.154	0.58
Pig × Winter	–0.160	0.099	0.10
Pig × Forested Wetlands	0.221	0.135	0.10
Pig × Mixed Forests	–0.897	0.360	0.01*
Pig × Pecan Orchards	0.192	0.138	0.16
Summer × Forested Wetlands	–0.579	0.260	0.03*
Fall × Forested Wetlands	–0.185	0.206	0.37
Winter × Forested Wetlands	0.062	0.160	0.70
Summer × Mixed Forests	–1.001	0.452	0.03*
Fall × Mixed Forests	–1.751	0.606	<0.01**
Winter × Mixed Forests	–1.010	0.396	0.01*
Summer × Pecan Orchards	0.748	0.283	0.01*
Fall × Pecan Orchards	0.224	0.269	0.41
Winter × Pecan Orchards	–0.624	0.274	0.02*

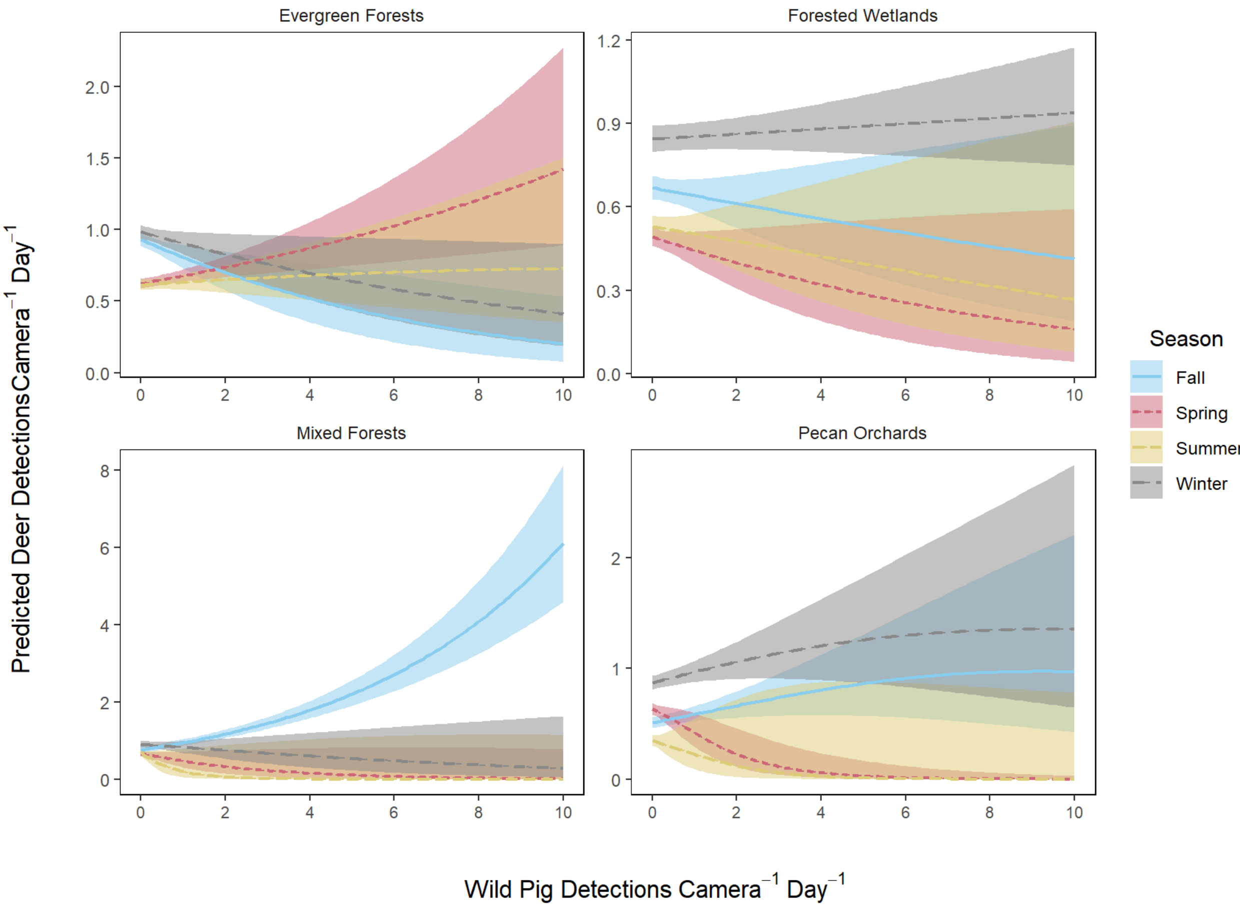

Figure 2. Predicted deer detections camera^{-1} day^{-1} across landcover types (evergreen forests, forested wetlands, mixed forests, and pecan orchards) during spring (pink), summer (yellow), fall (blue), and winter (gray) as wild pig detections camera^{-1} day^{-1} increases from a zero-inflated Poisson regression (ZIPR) model. Color lines indicate the predicted relationship paired with 95% confidence intervals (shaded ribbon).

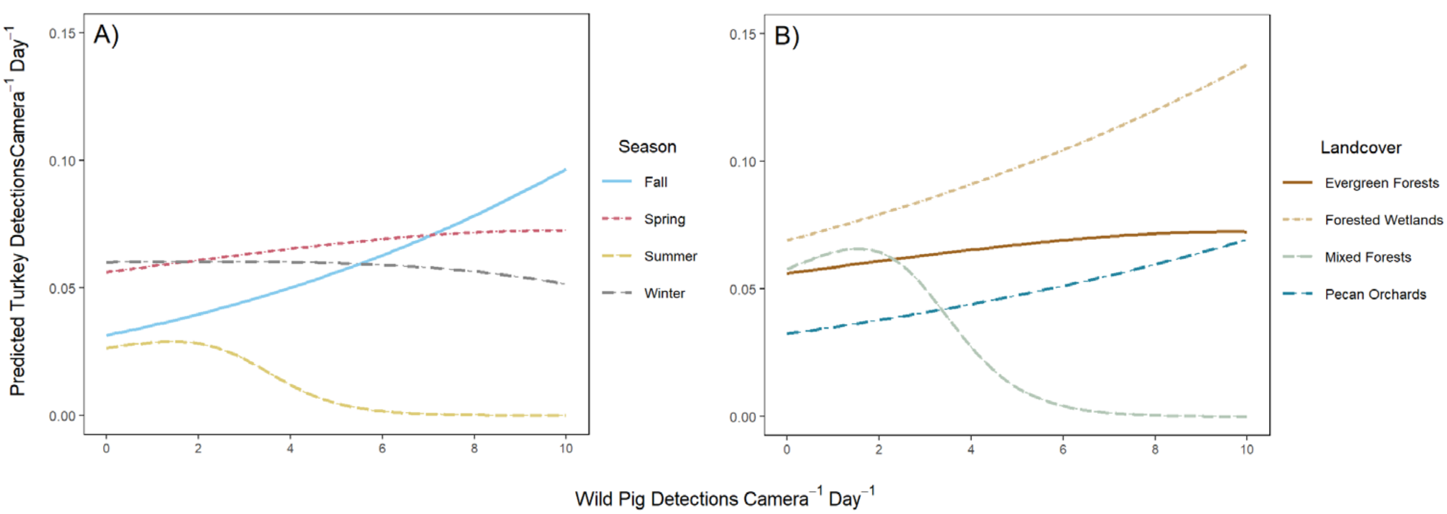

Figure 3. A) Predicted wild turkey detections camera^{-1} day^{-1} during spring (pink), summer (yellow), fall (blue), and winter (gray) as wild pig detections camera^{-1} day^{-1} increases from a zero-inflated Poisson regression (ZIPR) model. B) Predicted wild turkey detections camera^{-1} day^{-1} in evergreen forests (brown), forested wetlands (yellow), mixed forests (gray), and pecan orchards (blue) as wild pig detections camera^{-1} day^{-1} increases from a ZIPR model.

Discussion

Wild pigs are highly adaptable and thrive in heterogeneous landscapes (Morelle and Lejeune 2015, Lewis et al. 2017, Boyce et al. 2020). Previous studies have evaluated spatiotemporal associations between wild pigs and deer and/or turkey, so we interpret our findings in light of past empirical evidence. We did not anticipate a positive association between deer and wild pigs, as this does not align with previous research (Keever 2014, O'Brien et al. 2019, Lewis 2020, Garabedian et al. 2022, Dykstra et al. 2023, McDonough 2023). However, like earlier work (Lewis 2020, McDonough 2023), we found a negative association between wild pigs and turkeys.

Contrary to our prediction, we found a positive association between wild pig and deer detection rates. Nonetheless, there are studies indicating no association (Garabedian et al. 2022, Dykstra et al. 2023) or a negative association (Keever 2014, O'Brien et al. 2019, Lewis 2020, McDonough 2023) between wild pigs and deer. Deer and wild pig preference for forested areas is greater in fall and winter months associated with acorn production (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010, Rose et al. 2011, Touzot et al. 2018) and is reflected in our modeling results. Because we cannot envision a scenario for increased wild pig detection rates causing increased deer detection rates, we suggest species-specific habitat preferences are responsible for the observed positive association.

Based on anecdotal observations, pigs exhibit aggressive behavior toward deer at baited sites (Tolleson et al. 1995, McDonough 2023) and we suspect a similar relationship may occur between pigs and deer in pecan orchards. Wild pig aggression is primarily exhibited in the presence of food (Vargas et al. 1987). We used passive camera trapping (i.e., without bait) and observed no aggressive encounters between wild pigs and deer as we did not observe either species within the same photo. Other research using passive camera trapping did not report aggressive behaviors of pigs toward deer (O'Brien et al. 2019, Dykstra et al. 2023), suggesting that baited camera surveys may trigger competition for pulse resources (Ozoga 1972, Vargas et al. 1987, Pimm et al. 1985, Theimer et al. 2015, Payne et al. 2017, Johnson et al. 2021). Pecans can be considered a pulse resource as harvesting occurs in the fall (Wells and Conner 2009) and pecans are consumed by some wildlife due to pecan's high fat and protein content (Shimada and Saitoh 2006, Atanasov et al. 2018). We propose aggressive behavior by wild pigs toward deer is a foraging-specific behavior, as there are no reports of active aggression at camera locations without bait (O'Brien et al. 2019, Dykstra et al. 2023). We suggest that passive camera trapping studies that record wild pig foraging behavior may provide additional information regarding the importance of available forage in mediating wild pig aggression toward other animals.

Predicted turkey detection rates declined when more than two wild pigs were detected per camera per day and approached zero when wild pig detections exceeded 6 detections camera^{-1} day^{-1} in mixed forests (Figure 3B). In contrast to our observations of negative associations between turkeys and pigs in mixed forest, Walters and Osborne (2022) found that turkeys were more likely to occupy camera sites where wild pigs were detected (59.4% occupancy when compared to 45.5% occupancy at sites with no wild pig detections). We suggest the negative association between wild pigs and turkeys within mixed forests is due to wild pigs temporarily displacing turkey from these areas (Taylor and Hellgren 1997, Elston and Hewitt 2010) and turkeys return to these locations when wild pigs are not present.

In southwest Georgia, turkey nesting typically begins mid-April with poults hatching after a 28-day incubation period (Little et al. 2014). Our first captured image of an adult female turkey with poults was recorded on 6 June 2021. Poult survival (i.e., nesting survival) strongly influences population reproductive success as poult mortality rate averages 48% with mammalian predators as the primary cause of mortality (Hubbard et al. 1999). Turkey populations respond behaviorally to predation risk (Wright 1914, Wynveen et al. 2005, Hughes and Lee 2015) and likely avoid areas with wild pigs to reduce exposing poults to potential predation, especially during nesting and when poults are young (Healy 1992, Bakner et al. 2022) as wild pigs are known nest predators (Tolleson et al. 1993, Sanders et al. 2020). Thus, we suggest the negative association between wild pig relative abundance and turkey detections during summer may be a mechanism to increase poult survival, but we cannot rule out differential species-specific habitat associations as an alternative explanation for our observations.

Our research, and that of others, indicate habitat overlap between wild pigs and deer (Lewis 2020, Garabedian et al. 2022, Dykstra et al. 2023) and wild pigs and turkeys (Lewis 2020, Walters and Osborne 2022). Dietary overlap among the three species (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010), competition between wild pigs and deer (Lewis 2020, Garabedian et al. 2022, McDonough et al. 2022, Dykstra et al. 2023) and aggressive behavior exhibited by wild pigs toward deer have been observed (Tolleson et al. 1995, McDonough 2023). Furthermore, artificial nest studies indicate wild pigs may be a significant nest predator (Tolleson et al. 1993, Sanders et al. 2020). Our results support previous findings that there is a negative association between wild pigs and turkeys (Lewis 2020, McDonough 2023). However, we observed both positive and negative associations between deer and wild pig detections, depending on landcover and season. In contrast, prior studies observed either no association (Garabedian et al. 2022, Dykstra et al. 2023) or a negative association (Keever 2014, O'Brien et al. 2019, Lewis 2020, McDonough 2023) between deer and wild pigs. Our research contributes to the growing number of studies detecting negative impacts associated with wild pigs and suggests a need for better understanding factors that contribute to hypothesized interactions, i.e., competition and predation, between wild pigs and native wildlife.

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