Population response of eastern wild turkeys and white-tailed deer to removal of wild pigs

by

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Abstract

Recently, wild pigs *(Sus scrofa)* have expanded their range and have the potential to greatly impact ecosystems in North America. Wild pig's generalist diets and high fecundity make them a strong competitor with native species in areas that they invade. We studied how wild pigs may be affecting two native species in the United States, white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallopavo silvestris*). We used camera trapping and N-mixture models to determine if there were any population level effects of wild pig removals on these species. We found there to be a significant change in both detection and abundance of wild turkey and a significant change in detection of white-tailed deer as wild pigs were removed. We suggest that removal of wild pigs could benefit declining turkey populations in the Southeast and benefit the efficiency of white-tailed deer camera surveys and hunter satisfaction.

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Chapter I: The impact of wild pig removals on eastern wild turkey

Abstract:

Much of the research relating to wild pigs (*Sus scrofa*) is focused on monetary values of anthropogenic damage, such as crop depredation, and are lacking in the understanding of interspecific interactions with sympatric species like eastern wild turkey (*Meleagris gallopavo*). Wild pigs have been shown to affect wild turkey through competition, nest depredation, and some predation of adults. However, no research has examined population-level effects on wild turkey. Using camera trapping, we assessed responses of wild turkey populations to wild pig removal in central Alabama from 2018-20121. We compared wild turkey abundance and occupancy on three pig-removal treatment sites relative to a control site during one pre-treatment year and 2 post-treatment years. We removed 1,851 wild pigs from the 3 treatment sites over a 22-month period. Based on N-mixture modeling, when the number of pigs removed was equal to our baseline population estimates there were 1.496 (1.005-2.226; 95% CL) times as many wild turkeys, and detection of wild turkey was 2.01 (1.489-2.703; 95% CL) times as likely. These data suggest that long term reduction of wild pig populations may lead to an increase in populations of wild turkeys.

Introduction:

Wild pigs (*Sus scrofa*) are a well-established invasive species that have been of increasing concern in North America. Wild pigs are native to Eurasia, where they were domesticated for agricultural purposes, and were first brought to the United States in the 16th century as free ranging livestock (Mayer and Brisbin 2009). Until recently, wild pigs had been isolated in the United States to a few areas occurring mostly in the Southeast. In the past 50 years, however, the range of wild pigs has expanded considerably, and this has been largely facilitated by their popularity as a hunted species (Mayer 2009, Beasley et al. 2018). This recent range expansion brought attention to a number of negative economic, anthropogenic, and ecosystem impacts that wild pigs can have in their nonnative range (Pimental 2007, McDonough et al. 2022). Wild pigs have been estimated to cause $1.5 billion in agricultural damage annually in the United States (Pimental 2007). In more recent studies, McKee et al. (2020) estimated $272 million annual crop damage across 12 states with an established wild pig population and Anderson et al. (2019) estimated an additional $40 million lost each year to livestock predation and disease exposure by wild pigs in 13 states with established wild pig populations. While we have begun to understand the economic impacts of wild pigs in the United States, this is only a portion of the damages that wild pigs cause. The impacts of wild pigs to ecosystems in their invasive range have been understudied, specifically their impact on fauna (Bengsen et al. 2017, Beasley et al. 2018, McDonough et al. 2022).

Wild pigs, being generalist omnivores and efficient foragers (Ditchkoff and Mayer 2009), can successfully compete with native animals in the ecosystems they invade, such as the eastern wild turkey (*Meleagris gallopavo silvestris*; McDonough et al. 2022). Wild pigs and eastern wild turkey show some dietary overlap and a major source of dietary competition between wild pigs and wild turkey is competition for hard mast such as acorns (Scott 1973, Barnett and Barnett 2008, Elston and Hewitt 2010). When consumed in mass, energy rich acorns can help satisfy basic metabolic energy requirements, allowing animals to allocate more energy towards growth and reproduction (Kirkpatrick and Pekins 2002). However, acorns are a pulse resource that is limited spatially and temporally (Ostfeld and Keesing 2000), and are highly sought after by both species, composing up to 65% of the wild pigs diet and over 20% of the wild turkeys diet at times (Dalke et al. 1942, Henry and Conley 1972). Due to the high dietary overlap and constrained availability of this resource, wild pigs directly compete with wild turkey as mast consumers (Elston and Hewitt 2010), and this competition is likely to be exacerbated during years of low acorn availability (Henry and Conley 1972, Barnett and Barnett 2008).

Though much of a wild pig's diet consists of plant matter, there have been many documented events in which wild pigs behave as predators of both nests and individuals of all age classes of wild turkey (Ditchkoff and Mayer 2009, McDonough et al. 2022). The same generalist omnivorous food habits that make wild pigs successful competitors also leads to the consumption of animal matter as a protein source, and this occurs at a greater rate in their invasive range than their native range (Wilcox and Van Vuren 2009, Ballari and Barrios-García 2014). Eggs of ground nesting birds and other species are particularly susceptible to predation by wild pigs. For example, Sanders et al. (2020) reported that the probability of a turkey nest being depredated by wild pigs was 29%. In addition to nest depredation, predation events of larger species such as white-tailed deer fawns (*Odocoileus virginianus*; Taylor and Hellgren 1997) and eastern wild turkey (Miller and Leopold 1992, Ditchkoff and Mayer 2009) have been observed, although most animal matter consumed by wild pigs is usually comprised of insects, herpetofauna, and small mammals (McDonough et al. 2022).

Although wild pigs undoubtedly have negative impacts on wild turkeys, the cumulative effect of these impacts on turkey populations is poorly understood. For this reason, the goal of this study was to assess the impacts of invasive wild pigs on eastern wild turkey populations using camera trap surveys to compare population metrics of wild turkey before and after intensive wild pig removals. Following wild pig removals, we expected the abundance of wild turkey of all sex and age classes to increase on the treatment sites after we began removing wild pigs because of reduced competition and predation We specifically expected poult occupancy to increase after wild pig removals during the summer surveys due to less nest depredation.

Study Area:

We conducted the study on four privately owned sites in Alabama's upper coastal plains region. The upper coastal plains is a region classified by sandy soil intermixed with ferrous clay in the higher elevations (De Steven and Toner 2004). Forests in the upper coastal plains are pine dominated with intermixed hardwood and mixed forests (De Steven and Toner 2004). This region typically receives approximately 131 cm of annual rainfall and has an average annual temperature of around 19°C (Cope et al. 1962, Outcalt and Brockway 2010). The study sites were privately owned and managed primarily for game species such as white-tailed deer, eastern wild turkey, and northern bobwhite (*Colinus virginiana*), and for pine (*Pinus* spp.) timber production. We selected the study sites based on their well-established wild pig populations. These properties did have active control programs for wild pigs; however, they consisted primarily of opportunistic shooting and a few permanently placed traps in areas that were historically occupied by pigs.

Treatment Site 1: Treatment Site 1 was a 3407-ha plantation that was managed for both game species and timber. This treatment site was the most forested treatment site having 61% of the site being either hardwood (20.1%), pine (17.5%), or mixed pine-hardwood forest (23.3%). Water on this site was isolated to ponds, a creek, and a large wetland that made up 30.9% of the treatment site. Of the ponds, there was one 8.4-ha pond and two smaller ponds approximately 0.4 ha. There was also a medium-sized (1st order stream) tributary of the Tallapoosa River that bisected the site and passed through the large wetland.

Treatment Site 2: Treatment site 2 was a 4515-ha plantation that was primarily managed for white-tailed deer with some active forest management. This site was 59.5% forested with interspersed wetlands that total 15.9% of the site. Of the forested areas, hardwood bottoms were the predominant forest type (31.9%), followed by pine (15.6%) and mixed pine-hardwood forests (12%). Treatment Site 2 was unique in that there was a 188-ha lake in the center of the site that was fed by creek (1^{st} order). There were also numerous ephemeral creeks throughout the site.

Treatment Site 3: Treatment Site 3 was the largest of the sites at 5531 ha. This property was largely managed for northern bobwhite with some supplementary deer and turkey management. There were two ponds on the site (40.5 and 8.5 ha), and three creeks (1^{st} order). This site was the least forested with total forest cover of only 45.2%. Most of the forest was pine (23.5%), followed by mixed pine-hardwood (11.3%), and hardwood (10.5%). This site also had a large proportion of early successional habitat (19.5%) and cultivated fields (18.5%).

Control Site: The control site was 2510 ha and was managed mainly for timber production with some turkey, northern bobwhite, and white-tailed deer management. The site was bisected by a creek (2^{nd} order) and wetlands made up 14% of the site. There was also a heavily wooded 53-ha lake that was fed by ephemeral creeks. This site was 59.5% forested (32.4% hardwood, 10.8% pine, and 16.3% mixed pine-hardwood), and approximately 14% of the site was comprised of early successional unforested habitats.

Methods:

Camera surveys: We used camera surveys to assess the impact of wild pig removals on eastern wild turkey populations, conducting surveys for one year prior to the beginning of wild pig removals, and for two years during removals. We conducted camera surveys during the summer (July and August) from 2018-2020 to maximize poult detection. We again conducted camera surveys in the spring (February and March) from 2019-2021 to measure the population prior to the spring hunting season. The survey design consisted of establishing a 1-km^2 grid over each study site using the fishnet tool in ArcMap™ (Esri, Redlands, CA, USA) and placing a camera within a 100m buffer zone around the center of each grid cell, with camera station locations constant throughout the study. Grids were sized at 1 km^2 to reflect the home range of wild turkey broods at the time of the summer surveys (Healy 1992). The summer surveys consisted of surveying every grid cell that fell at minimum 75% within the study area. We conducted spring surveys using a random subset of 20 of the grid cells selected at the beginning of the study. We placed 11.3kg of cracked corn for bait at the camera location seven days prior to the camera being deployed, then repeated the baiting 3-4 days later. After 7 days from the initial baiting, we set up the camera (ReconyxTM PC800 Hyperfire Professional IR Cameras, Reconyx Inc., Holmen, WI, USA) and placed another 11.3kg of bait and repeated the previous baiting cycle until the end of the 7-day survey period. We set cameras on trees at a height of 1 m, faced them north or south to minimize overexposure at sunrise and sunset, and placed bait 4 m in front of the camera. Cameras were programmed to take a time-lapse image on a 4-minute interval, and to also take motion-triggered images in sets of 3, each with a delay of 2 seconds apart with a 1-minute rest period where the camera could not be triggered. We removed the camera from the bait site at the end of the seventh day

Initial wild pig population estimates: We used additional camera surveys in April 2019 to assess the initial population of wild pigs priori to removals. We determined the location of the cameras by overlaying a grid with 1-km^2 cells over the sites in the same manner as the wild turkey surveys. We then selected areas with the most pig sign in each grid cell for the camera location. Each camera location received four bait iterations of 11.3kg of whole kernel corn every 3-4 days apart. The first two bait iterations of whole kernel corn began 7 days prior to camera deployment to habituation pigs to feeding at the location. After 7 days, a Reconyx™ PC800 Hyperfire Professional IR Camera was placed on the camera location and the baiting cycle was repeated for two more bait iterations. The cameras were programmed to take a time-lapse image every 4 minutes and 3 consecutive images at the detection of motion and a minimum of 30 seconds between motion triggers.

Wild pig removal: We began wild pig removals in May 2019 and ended removal efforts in March 2021, following completion of the last turkey survey. We removed wild pigs primarily by trapping given its efficiency and effectiveness (Garcelon et al. 2005), with additional removals accomplished with helicopter gunning. We used corral style traps with a guillotine style door and a combination of animal-activated and manual trigger mechanisms to capture wild pigs . We built traps in areas where wild pig sign was present (i.e., rubs, rooting, tracks) or pigs were visually observed. Animal-activated traps were constructed similarly to Garcelon et al. (2005) and Lewis et al. (2022) while employing a wooden guillotine style door inside a metal frame attached to a trip line, rather than the swing door described by Garcelon et al. (2005). Manual triggers followed the procedure of Lewis et al. (2022). We employed helicopter gunning 3 times on Treatment Site 1, 5 times on Treatment Site 2, and twice on Treatment Site 3. Gunning occurred between November to March when the leaves in the canopy had fallen. All helicopter gunning was performed by USDA APHIS Wildlife Services trained employees and pilots. Animal handling, capture, and euthanasia were conducted following the procedures approves by the Auburn University Institutional Animal Care and Use Committee (PRN 2017-3143; PRN 2020-3779).

Image analysis: Using the program TimeLapse2 V2.2.3.9 (University of Calgary, Calgary, Canada), we used physical characteristics to classify all turkeys observed in images into 5 categories: adult male (>1.5 years old), juvenile male (0.5-1.5 years old), female (>=0.5 years old), poult (<0.5 years old of either sex), and unknown (sex and age indistinguishable due to visual obstruction or distance), with age classed described in Pelham and Dickson (1992). For wild pig surveys, we used sounder size, demographics, and unique individual characteristics to identify each sounder on camera and therefore a produce an assumed census of wild pigs on the study areas similarly to Lewis et al. (2022).

Statistical analysis: For wild turkeys, we binned the detections from these images into one-hour bins using the maximum count for each age and sex class in a single image in each hour bin to create an encounter history for each camera in the survey. Due to low detections, the male age classes were analyzed together. To model the populations of eastern wild turkey from the camera surveys we used N-mixture models to determine the relative abundance around each camera (Royle 2004) with package 'unmarked' (Fiske and Chandler 2011) in R (The R Foundation for Statistical Computing, 2009). Relative abundance was used because the effective sampling area around the camera is unknown (Gilbert et al. 2021), though cameras were evenly spaced on the landscape. We first created a global model using year, study site, season, and number of pigs removed as covariates for both detection and abundance. Our wild pig removal variable was the number of wild pigs removed on each treatment site at the time of each survey that was standardized using the estimated wild pig baseline population numbers prior to removal efforts. Based on Akaike Information Criteria adjusted for small sample sizes (AICc; Sugiura 1978), we ranked all models in the model list created from our universal models and considered models that had an AICc within 2 from the best model. The model with the lowest AICc score was considered to be our best model and evaluated for identifiability by the convergence of the beta estimates at varying levels of K. This process was repeated for each age and sex class of turkey and for a comprehensive total population model.

Due to the sparsity of detections, we used occupancy modeling (Ward et al. 2017, MacKenzie and Nichols 2004) with package 'unmarked' (Fiske and Chandler 2011) to assess poult occurrence. As the global model used for N-mixture modeling was too complex for the poult occupancy data, we used a bottom-up modeling approach and created models by adding variables to the null model to test for significance of the variable and lack of singularities from our data to create a model set. Our top model was then selected as having the lowest AIC score. We used the same variables to create occupancy models as was used in the N-mixture models.

Results:

We initially estimated 1,270 pigs across the treatment sites: 291 pigs (9 pig/km^2) on Treatment Site 1, 701 (16 pig/km^2) on Treatment Site 2, 278 (6 pig/km^2) on Treatment Site 3 and 235 (9 pig/km^2) on the control. We removed 1,851 pigs total across the treatment sites during 22 months: 657 on Treatment Site 1, 879 pigs on Treatment Site 2, and 315 on Treatment Site 3 (Table 1.1). Of those pigs removed, 70 pigs on Treatment Site 1, 298 pigs on Treatment Site 2, and 78 pigs on Treatment Site 3 were removed by helicopter gunning.

In N-mixture modeling, the top models for both detection and relative abundance of total turkeys (all age and sex classes combined), males, and females all included effects of site, year, season. Effects of pig removal on detection were also included in top models for total turkeys for females and for overall relative abundance (Table 1.2; Figures 1.1-1.3; Appendixes 1.1-1.3). Based on the analysis of total turkey detections, wild turkeys were 2.01 (1.489-2.703; 95% CL) times as likely to be detected when the number of pigs removed was equal to our baseline population estimates (Figure 1.2). We found that there were 1.496 (1.005-2.226; 95% CL) times as many wild turkeys when the number of pigs removed was equal to our baseline population estimates (Figure 1.3). Female wild turkeys were 4.061 (2.775-5.943; 95% CL) times as likely to be detected when the number of pigs removed was equal to our baseline population estimates.

From the model selection (Appendix 1.4), the top occupancy model for poults included effects of site on detection and, for poult occupancy, percent of the initial population of wild pigs that was removed ($P = 0.031$; Table 1.5). Poults were 3.49 (1.12-10.89; 95% CL) times as likely to occupy an area when the number of pigs removed was equal to our baseline population estimates.

Discussion:

The positive relationship between removal of wild pigs and abundance of wild turkey suggests that wild pigs negatively affect wild turkey at a population level. As described earlier, although the manner in which wild pigs negatively impact wild turkeys has been studied, no previous studies have examined the effects of wild pigs on population parameters of wild turkeys. These results are similar to those reported for the Lord Howe Island woodhen (*Tricholimnas sylvestris*; Miller and Mullette 1985) and the Galapagos rail (*Laterallus spilonotus*; Donlan et al. 2007). These two species experienced similar interspecific impacts from wild pigs prior to removals and population recoveries after removals, similar to how wild turkey populations responded. However, while the populations of these species that were studied were island populations, the study took place on an open landscape where immigration by wild pigs was possible.

We believe that increases in the turkey population during the first year of wild pig removals was likely due to adult birds emigrating from surrounding areas, as we did not detect an increase in number of poults after the first year of wild pig removals. Previous studies have reported that wild turkeys select for areas with lesser amounts of predatory pressure, whether that pressure be on adults or nests (Wood et al. 2019, Wakefield et al. 2020), and while documentation of predation of adult wild turkeys by wild pigs is minimal (Miller and Leopold 1992, Ditchkoff and Mayer 2009), they are likely perceived as a predator. We also speculate that hens would select for nesting areas with less perceived threat of predation (Fontaine and Martin 2006), as has been found with white-tailed deer when selecting fawning sites (Cherry et al. 2017). The increase in wild turkeys could also be a result of competitive release. These species have high dietary overlap with pulse resource such as acorns (Dalke et al. 1942, Henry and Conley 1972). While this would not account for the initial increases prior to masting in the first fall after removals, consumption of acorns by wild pigs is significant (A. S. Fay, Auburn University, unpublished data), and reductions in wild pigs would have increased availability of acorns on the treatment sites.

Poults were not present on camera surveys of the treatment sites until the third year of summer surveys (two years post pig removal). This was likely due to wild pig removals beginning after the peak of nesting season for wild turkey during the first year. Therefore, any impacts that pig removals may have had would have come too late in the breeding cycle to have an impact on reproduction until the second year. Most research that has examined impacts of wild pigs on reproduction of other species has been focused on reproductive loss, typically in the form of nest depredation, and not an increase in reproduction (McDonough et al. 2022). Increased poult occupancy after wild pig removals may be evidence of increased reproductive success. However, we did not directly measure nest or poult survival. Sanders et al. (2020) stated that nest depredation by wild pigs was a function of both nest density and wild pig density due to opportunistic feeding rather than searching behaviors. It is feasible that following removal of wild pigs, the likelihood of a pig randomly finding a nest decreased. This would allow more nests to continue to be occupied and poults to hatch and grow to adulthood. Though there have been no studies to document predation of poults by wild pigs, another potential cause of the increase in poult occupancy after wild pig removal could be reduced poult predation. Wild pigs are known to prey on adult turkey, and ground birds similar in size to turkey poults (Miller and Mullette 1985, Ditchkoff and Mayer 2009, Wilcox 2015, McDonough et al. 2022), therefore it is feasible that predation on poults may occur on some scale even though it has not been studied.

In the model for the total population, we documented an increase in detection of wild turkeys at baited sites following wild pig removal. These findings are similar to those reported by Walters and Osborne (2021) and Lewis (2021), who both theorized this to be a function of temporary displacement of wild turkeys by wild pigs. Temporary displacement by wild pigs has been previously documented in wild turkeys (Sanders 2017), and other ground birds such as the Lord Howe Island woodhen (Miller and Mullette 1985). This phenomenon has also been well documented in mammals (Taylor and Hellgren 1997, Ferretti et al. 2011, Galetti et al. 2015, Perez Carusi et al. 2017). Displacement of wild turkeys by wild pigs could impact space and resource use of wild turkeys, particularly at feeding areas. In other species, avoidance of wild pigs resulted in feeding being constrained to those times that wild pigs were less active at feeding sites (Galetti et al. 2015). Lewis (2021) found similar shifts in bait site use by wild turkeys when wild pigs were removed from a site. We speculate that similar impacts could occur with resources that are spatially and temporally limited such as acorns or other masting species, food plots, and feeders (Ostfeld and Keesing 2000).

We detected an increase in detection of female turkey following wild pig removals, but not of male turkey. Multiple studies have shown that hens are more susceptible than males to predation due to their solitary behavior during nesting (Speake 1980, Miller and Leopold 1992, Vangilder 1995). Hens are most vulnerable to predation when nesting, and 95% of hen mortality occurs during nesting or brood rearing, when hens are alone (Palmer et al. 1993). Additionally, nesting hens experience greater rates of predation than non-breeding hens (Miller et al. 1998). Males commonly exist in familial groups or large flocks for most of their life (Watts and Stokes 1971), whereas females actively avoid other turkey during the pre-nesting and nesting seasons. Flock size is positively associated with group vigilance (Spears et al. 2003, Williams et al. 2003). Therefore, it is not surprising that females, who have a greater predation risk due to nesting, are more susceptible than males to displacement by wild pigs, which was found by Sanders (2017) and suggested by Walters and Osborne (2021).

Wild turkeys have recently been on the decline in the eastern united states (Byrne et al. 2015, Robinson et al. 2017, Crawford et al. 2021, Bakner et al. 2022). This has largely been attributed to declines in reproductive parameters (Byrne et al. 2015), although it has been established that decreased reproductive output is the driving cause, the reasons for this are still unclear (Byrne et al. 2015, Crawford et al. 2021). Recent research has pointed to loss of nesting and brooding habitat, harvest regulations, nest failure, and nest depredation as some of the potential causes (Little et al. 2014, Byrne et al. 2015, Robinson et al. 2017, Bakner et al. 2022). While the interspecific interactions between wild turkey and wild pigs may not be the sole reason for the recent decline in turkey populations, the increases in both total turkey abundance and poult occupancy after wild pig removals suggests that removing wild pigs could benefit the declining turkey populations where these species co-occur. Wild pigs are nest predators and competitors of wild turkey (Tolleson et al. 1995, Elston and Hewitt 2010, Sanders et al. 2020), therefor removing wild pigs could create more favorable conditions for wild turkey and increase reproductive output.

Management Implications:

These results suggest that the current decline in wild turkey populations in the southeastern U.S. may be helped by removing wild pigs from the landscape. These results also suggest that timing of intensive removal of wild pigs is important, and removal prior to nesting season should increase poult production. We suggest that the increase in wild turkeys that we detected was driven by 1) adult turkeys moving into areas from which wild pigs were removed, and 2) potentially by improved nesting and brood rearing following removal of wild pigs. We believe the potential exists for at least some of the positive impacts we detected with turkey populations following pig removal to occur with other species that occupy similar niches or follow similar life-history patterns.

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Table 1.1. Initial population estimates of wild pigs on four sites in south-central Alabama in April 2019, and total number of wild pigs removed from each site during the study (2019-2021).

Site	Initial estimate	Density (pig/km^2)	Total removed	Proportion of the initial population removed
Treatment Site 1	291	9	657	226%
Treatment Site 2	701	16	879	125%
Treatment Site 3	278	6	325	113%
Control	235	9	0	0%

Table 1.2. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for all sex and age classes of eastern wild turkeys on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-3.123	0.119	<0.001	-0.828	0.203	<0.001
Treatment Site 1	-0.973	0.252	<0.001	-0.053	0.362	0.883
Treatment Site 2	-0.273	0.151	0.700	-0.316	0.231	0.170
Treatment Site 3	-0.032	0.127	0.804	0.350	0.201	0.081
Year 2	-0.748	0.124	<0.001	0.339	0.181	0.062
Year 3	-0.790	0.196	<0.001	0.605	0.257	0.019
Summer	0.351	0.103	0.001	-0.437	0.13	<0.001
Pig removal	0.696	0.152	<0.001	0.403	0.203	0.047

Table 1.3. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for male eastern wild turkeys on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-8.063	0.310	<0.001	3.608	0.298	<0.001
Treatment Site 1	0.347	0.487	0.475	-0.125	0.475	0.791
Treatment Site 2	-0.032	0.165	0.848	0.002	1.449	0.987
Treatment Site 3	1.573	0.301	<0.001	-1.439	0.294	<0.001
Year 2	0.835	0.078	<0.001	-	-	-
Year 3	1.253	0.074	<0.001	-	-	-
Summer	-1.664	0.286	<0.001	1.481	0.283	<0.001
Pig removal	-	-	-	-	-	-

Table 1.4. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for female eastern wild turkey on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-2.826	0.165	<0.001	-1.229	0.242	<0.001
Treatment Site 1	-1.963	0.295	<0.001	0.438	0.252	0.083
Treatment Site 2	-0.442	0.186	0.017	-0.435	0.283	0.124
Treatment Site 3	-0.200	0.167	0.231	0.721	0.233	0.002
Year 2	-1.188	0.151	<0.001	0.341	0.204	0.094
Year 3	-1.652	0.245	<0.001	0.687	0.191	<0.001
Summer	0.527	0.135	<0.001	-0.879	0.151	<0.001
Pig removal	1.401	0.194	<0.001	-	-	-

Table 1.5. Beta estimates, standard error, and p-values of detection (p) and occupancy (Ψ) from the top N-mixture model fitted to the data for eastern wild turkey poults on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (Ψ)	Standard error (Ψ)	P (Ψ)
Intercept	-1.179	0.233	<0.001	-5.110	0.834	<0.001
Treatment Site 1	-1.389	0.356	<0.001	-	-	-
Treatment Site 2	-0.208	0.338	0.539	-	-	-
Treatment Site 3	-3.989	1.228	0.002	-	-	-
Pig removal	-	-	-	1.250	0.580	0.031

Figure 1.1. Beta estimates (95% confidence intervals) for detection (p; logit scale) and relative abundance (λ; log scale) from top N-mixture model for wild turkey (all turkeys) on 4 sites in Alabama between 2018-2021.

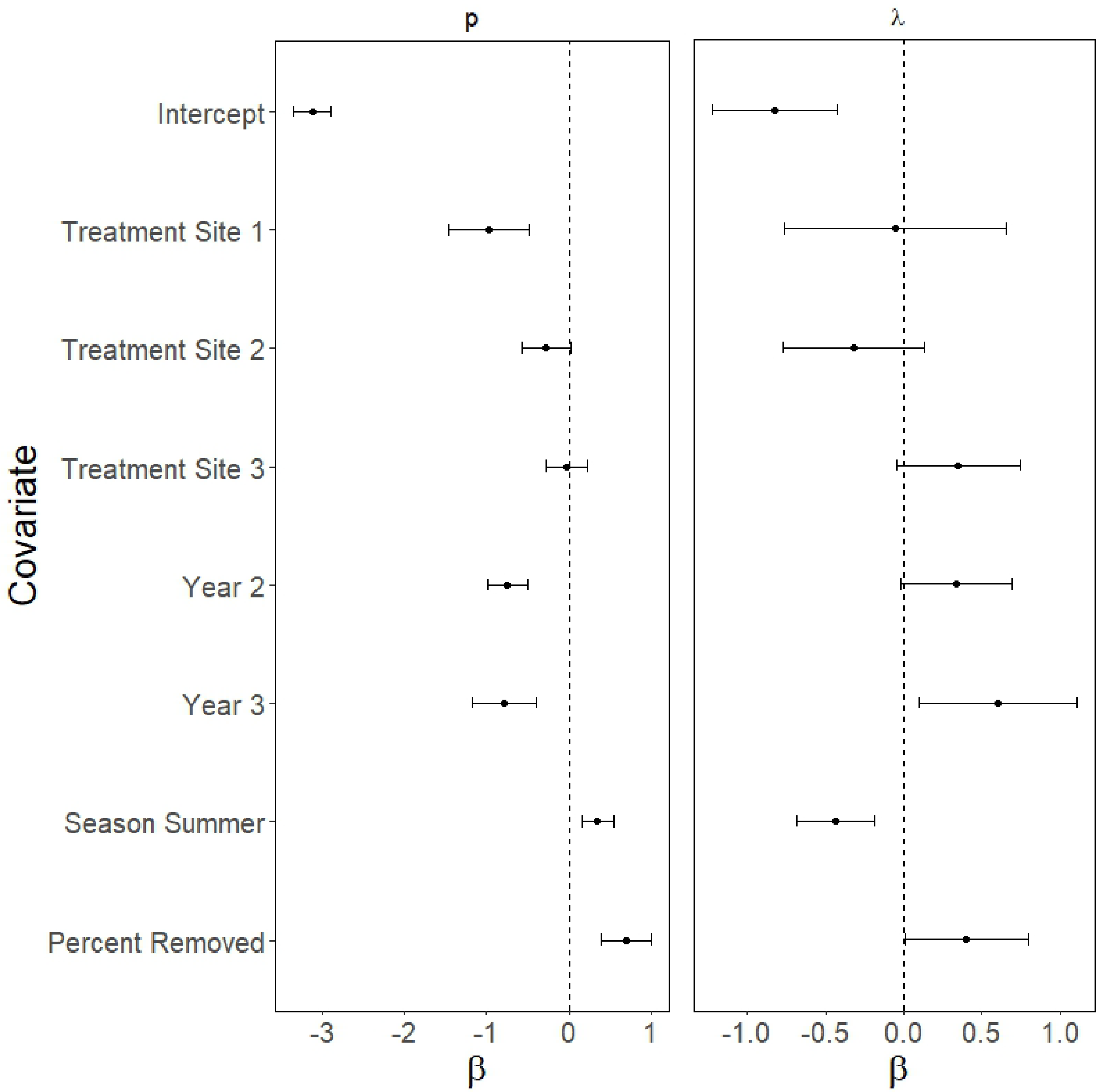


Figure 1.2. Effect size of wild pig removals, expressed as a percent of the initial population estimate that had been removed, on the detection of wild turkeys of all sex and age classes o on 4 sites in Alabama between 2018-2021.

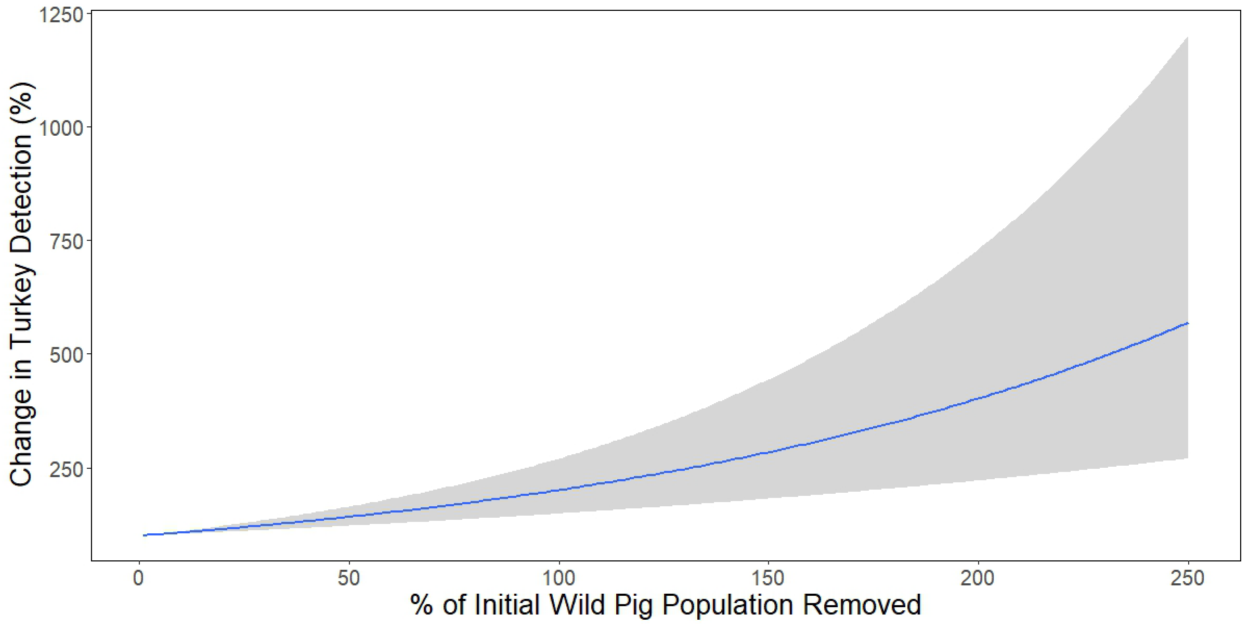
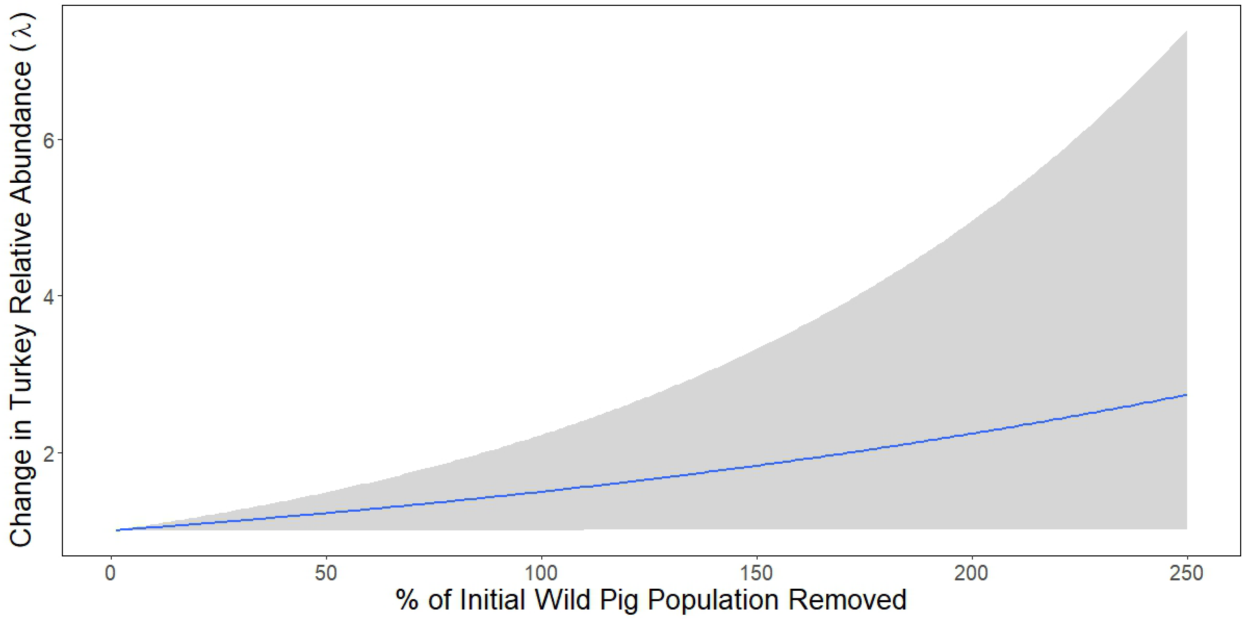


Figure 1.3. The effect size of wild pig removals, expressed as a percent of the initial population estimate that had been removed, on the total relative abundance (λ) of wild turkeys of all sex and age classes on 4 sites in Alabama between 2018-2021.



Chapter II: The effect of wild pig removals on white-tailed deer

Abstract:

With the recent range expansion of wild pigs (*Sus scrofa*), there has been an increasing concern with how wild pigs affect native species in the ecosystems that they invade. An abundance of research on the impacts of wild pigs has been through the lens of damage to anthropogenic resources and plant communities. However, quantitative research on how wild pigs affect native animal species is a relatively new topic. The goal of this study was to assess how wild pigs affect white-tailed deer (*Odocoileus virginianus*) at a population level. We used N-mixture models to compare data from camera trap surveys before and after wild pigs were removed from treatment areas. We removed 1,851 pigs from May of 2019 - March 2021. We found that wild pigs did not significantly affect white-tailed deer abundance, but that white-tailed deer were 1.12 (1.02-1.23; 95% CL) times as likely to be detected when the number of pigs removed was equal to our baseline population estimates. These results are congruent with other research that suggests wild pigs affect white-tailed deer behavior at a local scale.

Introduction:

Wild pigs (*Sus scrofa*), native to Eurasia, are considered one of the most destructive invasive mammals in the world, and now exist on every continent besides Antarctica (McClure et al. 2018). In North America, they have experienced a large, human-induced range expansion within the last century (Mayer and Brisbin 2009), and the implications of this are now beginning to be understood . A large proportion of wild pig research has focused on management of populations and mitigation of anthropogenic damages; however, understanding of how wild pigs affect the ecosystems they invade is lacking (Beasley et al. 2018). Understanding the impacts of wild pigs on native ecosystems is of great importance as wild pigs continue to become established in new areas.

Wild pigs can impact ecosystems in multiple ways, from altering soil and water chemistry, polluting running waters with bacteria (Bevins et al. 2014, Bradley and Lockaby 2021), to negatively impacting native flora and fauna (Strickland et al. 2020). More recently the impacts of wild pigs on the biota have begun to be examined more closely, and the breadth of ecological impacts that wild pigs can have is a relatively unexplored area of research (McDonough et al. 2022). Some of the main ways in which wild pigs negatively affect native fauna are through predation, competition, and aggressively excluding native species from resources (McDonough et al. 2022).

As dietary generalists, wild pigs frequently consume animal matter to satisfy protein requirements, and several studies suggest that animal matter is a greater component of the diet in their invasive range than their native range (Loggins et al. 2002, Ballari et al. 2015). Species commonly consumed include arthropods, herpetofauna, and eggs of ground-nesting birds (Tolleson et al. 1993, Ditchkoff and Mayer 2009, Jolley et al. 2010, McDonough et al. 2022), but also include species such as white-tailed deer (*Odocoileus virginianus*; Ditchkoff and Mayer 2009). In addition to predation, wild pigs also indirectly affect native species via competition for resources. Most research on wild pigs competing with native species to date involves consumption of mast, specifically mesquite (*Prosopis* spp*.)* and acorns (*Quercus* spp.; McDonough et al. 2022). Wild pigs consume mast in high quantities when available (Taylor and Hellgren 1997, Elston and Hewitt 2010), resulting in competition with native mast consumers such as rodents (*Rodentia*), peccaries (*Tayassuidae*), wild turkey (*Meleagris gallopavo*), white-tailed deer , and others (Ilse and Hellgren 1995, Kirkpatrick and Pekins 2002, Elston and Hewitt

2010, Sanguinetti and Kitzberger 2010). Wild pigs have been documented to defend resources against competitors and conspecifics through aggressive exclusion (Taylor and Hellgren 1997, Hegel et al. 2019). This phenomenon is believed to occur with species of similar size (Galetti et al. 2015), as wild pigs have been found to displace collared peccaries (*Pecari tajacu*; Galetti et al. 2015), pampas deer (*Ozotoceros bezoarticus*; Perez Carusi et al. 2017), and white-tailed deer (Keever 2014).

Aggressive exclusion of white-tailed deer by wild pigs is not well studied, and the belief of its existence is based largely upon implications of spatial avoidance from only a few studies (Taylor and Hellgren 1997, Keever 2014, Lewis 2021). This phenomenon has, however, been demonstrated in other ungulate species (Pérez Carusi et al. 2009, Ferretti et al. 2011, Galetti et al. 2015, Perez Carusi et al. 2017), and is an exploitation of spatially limited resources by wild pigs that results in decreased availability for the subdominant species (Case and Gilpin 1974, Ostfeld and Keesing 2000). Aggressive exclusion of white-tailed deer from feeding areas by wild pigs exacerbates the competition between these two species.

With the ability to both compete dietarily with and aggressively exclude deer, competitive interactions between wild pigs and white-tailed deer have the potential to have population level impacts. The goal of this study was to evaluate the degree to which wild pigs negatively affect populations of white-tailed deer by using camera surveys to assess the effect of removing wild pigs on white-tailed deer populations. We expected to see an increase in abundance of all sex and age classes of white-tailed deer due to decreased competition and exclusion from food resources on our sites as wild pigs are removed. We also expected to see an increase in detection of white-tailed deer at baited camera sites after wild pigs were removed due to less localized exclusion of white-tailed deer from bait sites by wild pigs.

Study Area:

We selected four sites within the upper coastal plains in south-central Alabama for the study. The upper coastal plains were characterized by pine (*Pinus* spp.) forests situated in ferrous clay in the upland areas, while the lowland riparian areas were characterized by closed canopy hardwood forests and sandy soils (De Steven and Toner 2004). This region of Alabama had an average temperature of 19° C and 131 cm of rainfall each year (Cope et al. 1962, Outcalt and Brockway 2010). These properties were all primarily managed for game species such as northern bobwhite (*Colinus virginiana*), eastern wild turkey, and white-tailed deer, while also managing for revenue from commercial timber.

Treatment Site 1: Treatment Site 1 was a heavily forested site intermixed with large wetlands. This site totaled 3,407 ha and was comprised of 61% forested ground cover. Of the forested areas, 23% were mixed pine-hardwood forest, 20% hardwood forests, and 18% pine forests. The hardwoods on this site consisted of mature, closed canopy forests surrounding the wetland areas and small creeks that made up 31% of the site. The pine forests existed as open canopy commercial pines that were burned annually to maintain their early successional understory.

Treatment Site 2: Treatment Site 2 (4,515 ha) was characterized by large expanses of closed canopy bottomland hardwood forests that made up 32% of the site, intersected by pine savannah upland areas that were burned annually, totaling 12%. This site also consisted of 16% mixed forests that were interspersed randomly within the site. On this site, open water consisted of 16% wetlands, and a 188-ha man-made lake in the center of the study area.

Treatment Site 3: Treatment Site 3 was the least forested of the four study areas. This 5,531-ha site was 45% forested, most of which was upland pine savannah (24%) with early successional understory. The remaining forested portions of the study area consisted of mixed (11%) and bottomland hardwood forests (10%). The hardwood bottoms existed solely along the three creeks on the study area, and the mixed forest was the gradient between the hardwoods and pine savannah. In addition to the three creeks, there were two ponds totaling 20 ha. This site was unique in that 20% of this study area was early successional habitat and 19% was cultivated cropland.

Control Site: The Control Site was a 2,510-ha property that was dominated by hardwood forests, totaling 32% of the site. Additionally, this site was comprised of 16% mixed forests and 11% pine forests that were heavily managed for timber production. The unforested areas of this site were composed of 14% early successional areas and 14% wetlands. These wetlands mostly existed as a floodplain surrounding the creek that bisected the property. In addition to the creek, there was a 53-ha man-made lake in the southern portion of the property.

Methods:

Camera Surveys: We used camera surveys to collect detection and abundance data of white-tailed deer for one year before wild pig removals and two years after wild pig removals began. To do so, we conducted two annual surveys: one during October and another survey in February/March between 2018-2021. The final camera survey was concluded in March of 2021.

To determine where we placed cameras, we created a grid array across the study areas with grid cells at a size of 2.4 km^2 similar to previous studies (Keever 2014, Price Tack 2019). At the center of each grid cell, which was at minimum 75% within the study area, we established a camera location that was used consistently throughout the study. We baited each camera location with four iterations of 11.3kg of whole kernel corn kernels every 3-4 days, with 7 days prior to camera deployment being the first iteration of bait. This pre-baiting period served as an acclimation period in which animals became accustomed to feeding in the area (Holtfreter et al.

2008). We then placed a Reconyx™ PC800 Hyperfire Professional IR Camera (Reconyx Inc., Holmen, WI, USA) at each location after 7 days and reapplied bait. This baiting cycle was repeated once more until the camera was removed from the location after being deployed for 7 days. Each camera was set to take a time lapse image on a 4-minute interval, coupled with a set of three consecutive motion pictures triggered by motion with a 5-minute dead-period between triggers, similar to Keever et al. (2017). During this dead-period the camera would take time-lapse images but could not be triggered by motion. We placed cameras so they were pointed either north or south to minimize overexposure at sunrise and sunset. Cameras were placed at a height of 1m and set approximately 3-4m from the bait pile. For each survey we had 28 total camera locations, 23 of which were on treatment sites and 5 in the control area.

Initial wild pig population estimates: We estimated the initial density of wild pigs on the study sites in April of 2019, prior to wild pig removals, using camera surveys and the simple count method (Lewis et al. 2022). We overlayed a grid on the study areas using the same methodology as the white-tailed deer survey and used a grid size of 1km^2. In every grid cell we picked the area with the greatest amount of wild pig sign to establish a camera location. At each camera location we placed 11.3kg of whole kernel corn 7 days prior to the camera deployment to acclimate wild pigs to feeding in the area, then placed more bait 3-4 days later. The camera was then deployed, and the baiting cycle was repeated and cameras were removed after 7 days of deployment. We used Reconyx™ PC800 Hyperfire Professional IR Cameras (Reconyx Inc., Holmen, WI, USA) that were programmed to take a time-lapse image every 4 minutes and 3 consecutive images triggered by motion with a 30-second period where the camera could not be triggered by motion.

To determine the population size of wild pigs on the study areas, we used sounder size, demographic information, proportion of age classes, and uniquely identifiable pelage characteristics to identify every sounder detected on camera, as described by Lewis et al. (2022). Unique identification (sounder size and composition, and unique pelage characteristics) was used to minimize repeated counts of sounders that would result in overestimation of population size. Once every sounder was identified, all individuals were summed for the population size.

Wild pig removals: Wild pig removals began in May of 2019, after the baseline camera surveys, and continued until March of 2021, when the final survey was completed. We used 4-m wide corral style traps with guillotine doors to remove wild pigs like those described by Ditchkoff and Bodenchuk (2020). We determined trap placement based on the presence of wild pig sign or visual detection of wild pigs in the area. Traps were placed in shaded areas to minimize thermoregulatory stress to trapped animals. Trapping sites were baited with whole kernel corn prior to construction of the trap to allow pigs to become accustomed to feeding in the area, after which we began to construct the traps in successional steps, allowing for pigs to adjust to a novel item being placed in the feeding area. We only set traps when every pig in the sounder was accustomed to feeding in the trap. Once the traps were set, they were checked at a maximum interval of 24 hours. Trigger styles consisted of cellular trigger mechanisms and animal-activated triggers. For cellular trigger systems, we trapped following the protocol of Lewis et al. (2022). The use of these traps was limited and only available for use where cellular signal was available. Animal-activated triggers were trip lines that were triggered by pigs in the trap similar to the approach described by Garcelon et al. (2005). As a supplement to trapping efforts, we occasionally used helicopter gunning to remove wild pigs, conducted by USDA APHIS Wildlife Services. Gunning was conducted in a manner similar to that described by Ditchkoff and

Bodenchuk (2020). During the 22-month removal period, Treatment Site 1 was gunned for 3 days, Treatment Site 2 was gunned for 5 days, and Treatment Site 3 was gunned for 2 days. Helicopter gunning was used between late fall and early spring when visibility through the canopy was at its greatest. Animal handling, capture, and euthanasia were conducted following the procedures approves by the Auburn University Institutional Animal Care and Use Committee (PRN 2017-3143; PRN 2020-3779).

Image analysis: We manually classified images for presence and absence of white-tailed deer and documented sex and age-class (mature male, immature male, adult female, fawn, and unknown) of all deer in the images using the TimeLapse2 V2.2.3.9 (University of Calgary, Calgary, Canada) image processing program. Mature males were those determined to be older than 3.5 years of age based on body and antler characteristics of the area. Immature males were classified as males that were 0.5 to 3.5 years of age. Females were classified as any member of the female sex that was older than 0.5 years of age. Fawns were considered to be either sex up to 0.5 years of age (DeYoung 2011). We applied the unknown classification to individuals that were unidentifiable from the camera images. The most common occurrences of this were due to distinguishable sex characteristics not being captured on camera or distance from the camera being too great to allow for classification.

Statistical analysis: For statistical analysis we first created an encounter history that was binned by hour for the entire survey period. Within each bin we recorded the maximum number of individuals within a single image of each sex and age class per 1-hour bin. We then modelled the effect of the wild pig removals on populations of white-tailed deer using N-mixture models (Royle 2004, Keever et al. 2017) in package ‘unmarked’ (Fiske and Chandler 2011) in program R (The R Foundation for Statistical Computing, 2009). We analyzed each sex and age class together as a total population and examined each sex/age category separately. For the total population models, the maximum of each sex and age class per one hour bin was summed to create an overall encounter history.

We conducted top-down model building where we started with a universal model using the covariates of year, study site, season, and the total number of pigs removed at the time of the survey that was standardized by the initial estimate of wild pigs prior to removal activities for both the abundance and detection portions of the N-mixture model. We also included an additional covariate of whether the site was rebaited while the camera was deployed. This was due to a missed baiting iteration during the spring baseline surveys which could affect detection of individuals but not overall abundance at that time. From the universal models, we performed model selection on all potential models within the subset from the top model using Akaike Information Criterion adjusted for small sample sizes (AICc; Sugiura 1978). We considered models that had an AICc score within 2 of the top model. The top model was considered to be the model with the lowest AICc score. This model was then tested for identifiability by observing converging parameter estimates at varying levels of K. If we had multiple models of similar model weights, we averaged the parameters of these models using the function 'modavgShrink' in package AICcmodavg (Mazerolle 2020). Models for fawns only included spring surveys as fawn detection is generally unreliable during fall surveys (Mckinley 2002).

Results:

Using simple counts, we estimated there were 1,270 pigs among the treatment sites and 235 pigs (9 pig/km^2) on the control site at the beginning of the study. We had removed 1,851 wild pigs from the treatment sites after 22 months of wild pig removals. On Treatment Site 1, we estimated 291 wild pigs (9 pig/km^2) and removed 657. On Treatment Site 2, we estimated 701 wild pigs (16 pig/km^2) and removed 879 wild pigs. On Treatment Site 3 we estimated 278 wild pigs (6 pig/km^2) and removed 315. Of the pigs that we removed, a total of 446 were removed by helicopter gunning. Helicopter gunning accounted for 70 pigs on Treatment Site 1, 298 on treatment Site 2, and 78 on Treatment Site 3. No pigs were removed from the control site during the course of the study.

The top models for detection of the total population of white-tailed deer (all sex and age classes combined), females, and immature males included the variables of site, year, season, and whether the site was rebaited. These models also included the wild pig removal variable. When the number of pigs removed was equal to our baseline population estimates, deer were 1.12 (1.02-1.23; 95% CL) times as likely to be detected ($p = 0.015$; Figure 2.2). We had two competitive models with similar model weights ($w = 0.42$; $w = 0.34$) for females (Appendix 2.2). Though wild pig removals were included in the averaged covariates, it was not statistically significant. When the number of pigs removed was equal to our baseline population estimates, immature males were 2.76 (1.81-4.20; 95% CL) times as likely to be detected ($p < 0.001$). The top detection model for mature males included the site and rebait variables. The top model for the detection of fawns included the site and year variables.

The top models for abundance of the total population of white-tailed deer (all sex and age classes combined), females, and mature males included the variables of site, year, and season. The top models for females ($w = 0.42$; $w = 0.34$) also included the variable of wild pig removals, this variable was however not significant. The top model for immature males included the variables of site, season, and wild pig removals. When the number of pigs removed was equal to our baseline population estimates, there were 0.50 (0.36-0.70; 95% CL) times as many immature bucks in the population ($p < 0.001$). The top model for fawn abundance included the variables of site and year.

Discussion:

We did not detect an effect of wild pig removals on relative abundance of white-tailed deer. While we had originally hypothesized we would detect an increase in deer numbers, previous research examining the interspecific relationship between wild pigs and white-tailed deer has reported mixed results regarding impacts on abundance. Keever (2014) found that abundance of all sex and age classes of white-tailed deer was negatively associated with wild pig visitation to baited camera sites. However, this study did not include wild pig site visitation as a variable. It is possible the effect of wild pigs on abundance of white-tailed deer is dictated locally by co-occurrence, lending itself to temporal partitioning that would not have been detectable at the scale in which we were measuring our wild pig removal variable but which Keever (2014) was able to account for. The models in this study were based on wild pig removal that was measured at a larger scale than individual bait piles, as one of the goals of this study was complete removal of wild pigs from the treatment areas. Similarly, Ilse and Hellgren (1995) suggested that cohabitation of wild pigs and collared peccaries occurred even though there was a high level of spatial segregation between the species.

We found wild pigs negatively impacted the detection of deer, and this is similar to other studies with white-tailed deer (Keever 2014, O'Brien et al. 2019) and other ungulates (Galetti et al. 2015, Perez Carusi et al. 2017). When confronted by more dominant species, white-tailed deer have previously been found to be excluded by that species or to actively avoid that species. Faas and Weckerly (2010) found, after identifying axis deer (*Axis axis*) as the dominant species, that white-tailed deer either avoided or were actively excluded from feeding areas by axis deer.

Wild pigs have been reported to exhibit dominant behaviors with other ungulates (Barrett 2007, Pérez Carusi et al. 2009), and this would explain why detection of white-tailed deer increased after wild pig removals. This is similar to the observation of Taylor and Hellgren (1997) that wild pigs aggressively excluded white-tailed deer from feeding areas. Barrett (2007) reported that black-tailed deer (*Odocoileus hemionus columbianus*) are subordinate to wild pigs when in the same area. We observed in the camera trap images several instances of active aggression from wild pigs towards deer at bait piles, where one or more wild pigs appeared to aggressively charge an approaching deer before returning to feed. In these interactions, the white-tailed deer fled with their tail up, indicating a threat (DeYoung and Miller 2011). More commonly, we observed avoidance, where white-tailed deer could be seen approaching a bait pile where wild pigs were feeding and either leaving the view of the camera or maintaining distance and vigilance in the background until the wild pigs were gone from the bait pile. We speculate that temporal segregation at food sources occurs between white-tailed deer and wild pigs and is due to active avoidance by deer and/or aggressive exclusion by wild pigs.

Although we did not find an increase in detection of mature males, females, and fawns at bait sites following pig removal, we did see an increase in detection of immature males. In other species, different age classes have been shown to respond differently to invasive species (D’amore et al. 2009, Freed and Cann 2009, Eaton et al. 2016). The life history and behavioral differences of immature male white-tailed deer relative to other age/sex categories could explain this unique finding. The majority of immature male white-tailed deer disperse at approximately 1.0-1.5 years of age (DeYoung 2011). This stage of life consists of unpredictable space use due to this dispersion. For example, Webb et al. (2007) found that properties that were, at minimum, 4,000 ha were needed to keep 50% of yearling bucks on a property. This age class has regular exchange of individuals with the surrounding populations, resulting in unpredictability in their distributions, use of space, and use of food sources. Additionally, immature males are typically inexperienced and reckless compared to other age classes (Miller and Marchinton 1995, Ditchkoff et al. 2001). Therefore, it is possible that immature male deer may be reacting differently from a behavioral standpoint than other age classes when faced with the stressors of competition and aggressive exclusion from wild pigs. The relationship between detection and abundance in an N-mixture model is inherently inverse (Royle 2004), and given that detection increased when wild pigs were removed, immature bucks were likely using the bait piles more frequently but potentially using a larger space than the other age classes. This would effectively dilute the estimate of the effect of wild pig removals on the abundance of immature males.

Management Implications:

It is unlikely that removal of wild pigs is an effective tool to increase the population of white-tailed deer in the 2-year time frame that this study was conducted. However, given the increase in detection from the data, findings in previous research on the displacement of white-tailed deer (Keever 2014, Lewis 2021), and accounts of aggressive exclusion at food resources (Taylor and Hellgren 1997), wild pigs seem to affect deer at a local scale. It is therefore possible that long term removal of wild pigs may benefit relative abundance of deer populations over a longer time scale than we were able to examine in this study. Additionally, since wild pigs affect the detection of white-tailed deer, removing wild pigs may improve the efficiency of camera surveys for white-tailed deer.

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Table 2.1. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for all sex and age classes of white-tailed deer on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-4.66	0.15	< 0.001	3.49	0.14	< 0.001
Treatment Site 1	-0.53	0.15	< 0.001	1.04	0.14	< 0.001
Treatment Site 2	0.93	0.14	< 0.001	-0.52	0.14	< 0.001
Treatment Site 3	-0.61	0.16	< 0.001	0.82	0.16	< 0.001
Year 2	-0.27	0.12	0.0216	0.06	0.11	0.620
Year 3	0.95	0.13	< 0.001	-1.31	0.11	< 0.001
Spring	-0.30	0.09	< 0.001	0.22	0.09	0.014
Rebaited	0.67	0.06	< 0.001	-	-	-
Pig removal	0.12	0.05	0.015	-	-	-

Table 2.2. Model averaged beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model (w = 0.42) and the second top model (w=0.34) fitted to the data for female white-tailed deer on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	CL Lower (p)	CL Upper (p)	β (λ)	Standard error (λ)	CL Lower (λ)	CL Upper (λ)
Intercept	-4.47	0.22	-4.90	-4.04	2.95	0.21	2.55	3.35
Treatment Site 1	0.57	0.33	-0.08	1.22	-0.44	0.33	-1.09	0.21
Treatment Site 2	1.46	0.21	1.06	1.87	-1.42	0.21	-1.8	-0.10
Treatment Site 3	0.47	0.20	0.08	0.86	-0.50	0.20	-0.89	-0.11
Year 2	-0.70	0.17	-1.04	-0.36	0.48	0.18	0.13	0.83
Year 3	0.44	0.25	-0.04	0.93	-0.86	0.25	-1.35	-0.37
Spring	-0.70	0.12	-0.93	-0.47	0.56	0.12	0.33	0.79
Rebaited	0.67	0.098	0.48	0.87	-	-	-	-
Pig removal	-0.13	0.20	-0.52	0.26	0.29	0.20	-0.10	0.69

Table 2.3. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for mature male white-tailed deer on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-3.87	0.18	< 0.001	0.61	0.21	0.004
Treatment Site 1	0.02	0.18	0.894	1.19	0.25	< 0.001
Treatment Site 2	0.22	0.16	0.181	0.46	0.25	0.067
Treatment Site 3	-0.33	0.15	0.031	1.36	0.23	< 0.001
Year 2	-	-	-	-0.57	0.13	< 0.001
Year 3	-	-	-	-0.64	0.14	< 0.001
Spring	-	-	-	0.39	0.12	0.001
Rebaited	0.58	0.15	< 0.001	-	-	-
Pig removal	-	-	-	-	-	-

Table 2.4. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for immature male white-tailed deer on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-3.59	0.23	< 0.01	0.04	0.21	0.86
Treatment Site 1	-1.27	0.39	0.001	2.64	0.38	< 0.001
Treatment Site 2	-0.24	0.19	0.210	1.02	0.26	< 0.001
Treatment Site 3	-0.73	0.19	< 0.001	1.46	0.24	< 0.001
Year 2	-0.40	0.14	0.003	-	-	-
Year 3	-0.93	0.21	< 0.001	-	-	-
Spring	-0.32	0.13	0.017	0.39	0.15	0.009
Rebaited	0.99	0.16	< 0.001	-	-	-
Pig removal	1.01	0.22	< 0.001	-0.70	0.17	< 0.001

Table 2.5. Beta estimates, standard error, and p-values of detection (p) and relative abundance (λ) from the top N-mixture model fitted to the data for white-tailed deer fawns on the study areas in south-central Alabama from summer of 2018 to spring of 2022.

Variable	β (p)	Standard error (p)	P(p)	β (λ)	Standard error (λ)	P (λ)
Intercept	-6.42	0.48	<0.001	2.88	0.55	<0.001
Treatment Site 1	-0.72	0.54	0.182	1.19	0.64	0.063
Treatment Site 2	1.08	0.58	0.062	-0.60	0.63	0.337
Treatment Site 3	-1.20	0.40	0.003	1.23	0.51	0.016
Year 2	0.39	0.0.46	0.386	-0.003	0.50	0.994
Year 3	3.57	0.43	< 0.001	-2.95	0.47	<0.001
Pig removal	-	--	--	--	--	--

Figure 2.1. The betas from the top model for detection of the total population of white-tailed deer and confidence intervals at the 95% confidence level surrounding those estimates on 4 sites in Alabama between 2018-2021.

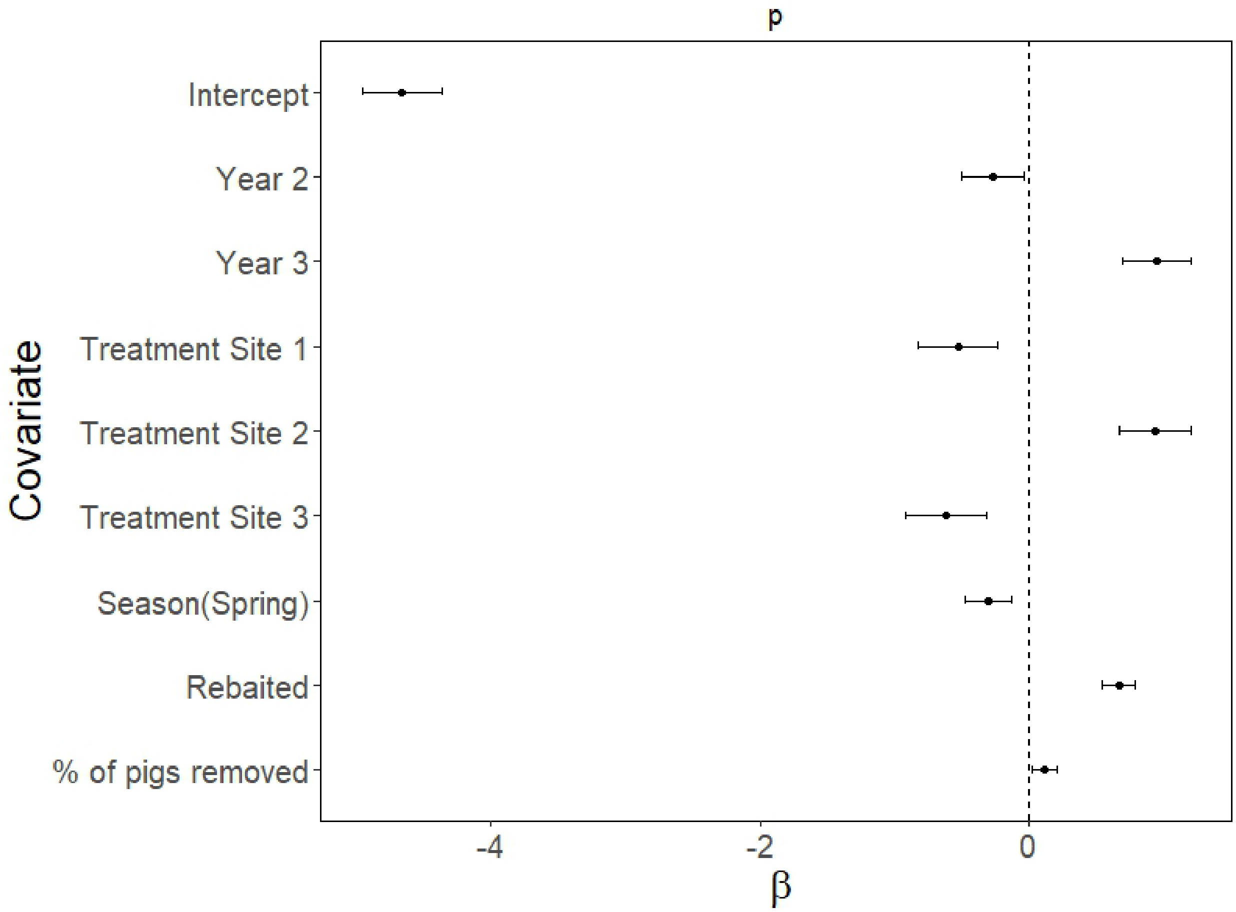
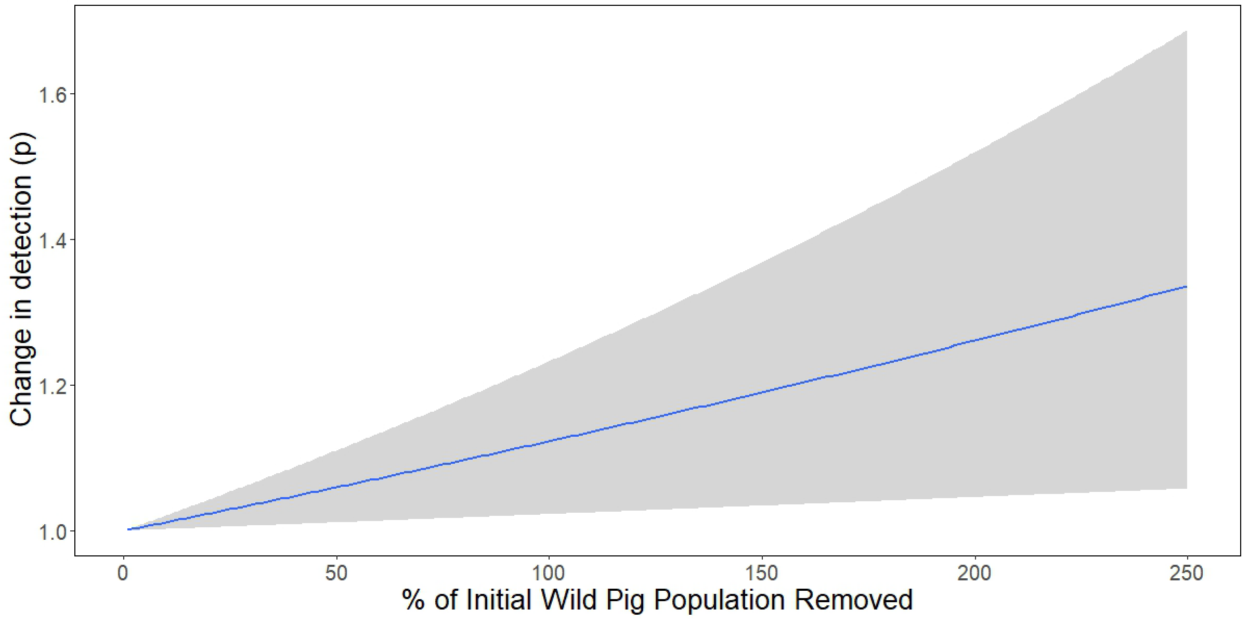


Figure 2.2. The effect size of wild pig removals on detection of the total population of white-tailed deer on 4 sites in Alabama between 2018-2021.



Appendix 1.1. Total turkey model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the summer of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year+Pig Removal	~Season+Site+Year+Pig Removal	16	-5565.30	11163.49	0.00	0.53
~Season+Site+Year+Pig Removal	~Season+Site+Pig Removal	14	-5568.17	11165.02	1.54	0.25
~Season+Site+Year+Pig Removal	~Season+Site+Year	15	-5567.32	11165.43	1.94	0.20
~Season+Site+Year+Pig Removal	~Site+Pig Removal	13	-5572.34	11171.27	7.78	0.01
~1	~1	2	-5665.64	11335.30	171.82	0.00
~Season	~1	3	-5665.62	11337.29	173.80	0.00

Appendix 1.2. Male turkey model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the summer of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year	~Season+Site	12	-8180.56	16385.60	0.00	0.38
~Season+Site+Year	~Season+Site+Pig Removal	13	-8180.50	16387.58	1.97	0.14
~Season+Site+Year+Pig removal	~Season+Site	13	-8180.55	16387.68	2.08	0.14
~Season+Site+Year	~Season+Site+Year	14	-8180.29	16389.24	3.64	0.06
~Season+Site+Year+Pig removal	~Season+Site+Pig Removal	14	-8180.32	16389.31	3.71	0.06
~Season+Site	~Season+Site+Year	12	-8182.72	16389.94	4.33	0.04
~Season+Site+Year	~Season+Site+Year+Pig Removal	15	-8180.28	16391.32	5.72	0.02
~Season+Site+Year+Pig removal	~Season+Site+Year	15	-8180.29	16391.34	5.73	0.02
~Season+Site+Pig removal	~Season+Site+Year+Pig Removal	14	-8181.41	16391.49	5.88	0.02
~Season+Site+Pig removal	~Season+Site+Year	13	-8182.54	16391.65	6.05	0.02
~Season+Site	~Season+Site+Year+Pig Removal	13	-8182.71	16392.00	6.40	0.02
~Season+Site+Year	~Site	11	-8184.83	16392.08	6.47	0.02
~Season+Site+Year+Pig removal	~Season+Site+Year+Pig Removal	16	-8180.23	16393.34	7.73	0.01
~Season+Site	~Site+Year	11	-8185.74	16393.90	8.30	0.01
~Season+Site+Year	~Site+Pig Removal	12	-8184.82	16394.12	8.52	0.01
~Season+Site+Year+Pig removal	~Site	12	-8184.83	16394.15	8.55	0.01
~1	~1	2	-8377.70	16759.41	373.80	0.00

Appendix 1.3. Female turkey model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the summer of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year+Pig removal	~Season+Site+Year	15	-3180.42	6391.62	0.00	0.64
~Season+Site+Year+Pig removal	~Season+Site+Year+Pig Removal	16	-3180.31	6393.50	1.88	0.25
~Season+Site+Year+Pig removal	~Season+Site+Pig Removal	14	-3183.29	6395.26	3.64	0.10
~Season+Site+Year+Pig removal	~Season+Site	13	-3187.31	6401.20	9.59	0.01
~1	~1	2	-3271.49	6547.01	155.39	0.00
~Season	~1	3	-3270.80	6547.63	156.02	0.00

Appendix 1.4. Poult turkey model selection table from occupancy models using data collected using camera trap surveys beginning in the summer of 2018 until the summer of 2020. Variables included were the site of the camera survey, and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*).

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Site	~Pig removal	6	-191.27	394.74	0.00	0.77
~Site	~1	5	-193.57	397.29	2.54	0.22
~Site	~Site	8	-192.95	402.26	7.52	0.02
~Pig Removal	~Pig Removal	4	-205.87	419.83	25.09	0.00
~Pig Removal	~1	3	-208.71	423.49	28.74	0.00
~Pig Removal	~Site	6	-208.03	428.26	33.52	0.00
~1	~Pig Removal	3	-211.92	429.90	35.16	0.00
~1	~1	2	-214.76	433.54	38.8	0.00
~1	~Site	5	-214.07	438.30	43.55	0.00

Appendix 2.1. Total deer model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the fall of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year	16	-27472.87	54981.46	0.00	0.38
~Season+Site+Year+Rebait	~Season+Site+Year+Pig Removal	16	-27473.13	54981.99	0.53	0.29
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	17	-27472.85	54983.93	2.47	0.11
~Season+Site+Year+Rebait	~Season+Site+Year	15	-27475.61	54984.49	3.03	0.08
~Season+Site+Year+Pig Removal+Rebait	~Site+Year	15	-27476.25	54985.76	4.30	0.04
~Season+Site+Year+Rebait	~Site+Year+Pig Removal	15	-27476.44	54986.15	4.69	0.04
~Season+Site+Year+Pig Removal+Rebait	~Site+Year+Pig Removal	16	-27476.22	54988.17	6.71	0.01
~Season+Site+Year+Rebait	~Site+Year	14	-27479.16	54989.17	7.71	0.01
~Site+Year+Pig Removal+Rebait	~Site+Year	14	-27479.44	54989.72	8.26	0.01
~Site+Year+Rebait	~Site+Year+Pig Removal	14	-27479.49	54989.82	8.36	0.01
~1	~1	2	-27847.53	55699.14	717.68	0.00

Appendix 2.2. Female deer model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the fall of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year+Rebait	~Season+Site+Year+Pig Removal	16	-17867.54	35770.81	0.00	0.41
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	17	-17866.50	35771.21	0.40	0.34
~Season+Site+Year+Rebait	~Season+Site+Year	15	-17869.99	35773.25	2.43	0.12
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year	16	-17868.76	35773.25	2.44	0.12
~1	~1	2	-18046.42	36096.91	326.10	0.00

Appendix 2.3. Mature male deer model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the fall of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Site+Rebait	~Season+Site+Year	12	-6486.73	12999.54	0.00	0.24
~Site+Pig Removal+Rebait	~Season+Site+Year	13	-6486.23	13000.90	1.36	0.12
~Season+Site+Rebait	~Season+Site+Year	13	-6486.33	13001.10	1.56	0.11
~Site+Rebait	~Season+Site+Year+Pig Removal	13	-6486.51	13001.45	1.92	0.09
~Season+Site+Pig Removal+Rebait	~Season+Site+Year	14	-6485.40	13001.63	2.09	0.09
~Season+Site+Rebait	~Season+Site+Year+Pig Removal	14	-6486.13	13003.09	3.55	0.04
~Site+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	14	-6486.21	13003.25	3.72	0.04
~Site+Year+Rebait	~Season+Site+Year	14	-6486.22	13003.28	3.74	0.04
~Season+Site+Rebait	~Site+Year	12	-6488.81	13003.69	4.16	0.03
~Season+Site+Pig Removal+Rebait	~Site+Year	13	-6487.75	13003.94	4.40	0.03
~Season+Site+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	15	-6485.39	13004.04	4.51	0.03
~Site+Year+Pig Removal+Rebait	~Season+Site+Year	15	-6485.72	13004.71	5.17	0.02
~Season+Site+Year+Rebait	~Season+Site+Year	15	-6485.81	13004.89	5.35	0.02
~Site+Year+Rebait	~Season+Site+Year+Pig Removal	15	-6486.02	13005.31	5.77	0.01
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year	16	-6485.09	13005.90	6.36	0.01
~Season+Site+Pig Removal+Rebait	~Site+Year+Pig Removal	14	-6487.55	13005.95	6.41	0.01
~Season+Site+Rebait	~Site+Year+Pig Removal	13	-6488.79	13006.02	6.48	0.01
~Season+Site+Year+Rebait	~Season+Site+Year+Pig Removal	16	-6485.64	13007.00	7.46	0.01
~Site+Year+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	16	-6485.72	13007.16	7.62	0.01
~1	~1	2	-6553.03	13110.14	110.60	0.00

Appendix 2.4. Immature male deer model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the fall of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Pig Removal	15	-8325.50	16684.27	0.00	0.24
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	17	-8323.69	16685.61	1.33	0.12
~Season+Site+Pig Removal+Rebait	~Season+Site+Year	14	-8327.99	16686.82	2.55	0.07
~Site+Year+Pig Removal+Rebait	~Site+Pig Removal	13	-8329.37	16687.18	2.90	0.06
~Site+Year+Pig Removal+Rebait	~Season+Site+Pig Removal	14	-8328.28	16687.41	3.13	0.05
~Site+Pig Removal+Rebait	~Site+Year	12	-8330.80	16687.68	3.40	0.04
~Season+Site+Year+Pig Removal+Rebait	~Season+Site+Year	16	-8326.16	16688.05	3.77	0.04
~Site+Pig Removal+Rebait	~Season+Site+Year	13	-8330.07	16688.59	4.32	0.03
~Site+Year+Pig Removal+Rebait	~Site+Year+Pig Removal	15	-8327.73	16688.73	4.45	0.03
~Site+Rebait	~Season+Site+Year	12	-8331.35	16688.78	4.51	0.02
~Season+Site+Year+Pig Removal+Rebait	~Site+Pig Removal	14	-8329.00	16688.84	4.56	0.02
~Site+Year+Pig Removal+Rebait	~Site+Year	14	-8329.05	16688.93	4.66	0.02
~Site+Year+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	16	-8326.61	16688.95	4.67	0.02
~Season+Site+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	15	-8327.85	16688.96	4.68	0.02
~Site+Rebait	~Site+Year	11	-8332.74	16689.23	4.95	0.02
~Season+Site+Rebait	~Season+Site+Year	13	-8330.40	16689.25	4.98	0.02
~Season+Site+Pig Removal+Rebait	~Site+Year	13	-8330.44	16689.33	5.05	0.02
~Site+Year+Pig Removal+Rebait	~Season+Site+Year	15	-8328.15	16689.56	5.28	0.02
~Site+Rebait	~Site+Year+Pig Removal	12	-8331.78	16689.65	5.37	0.02
~Site+Rebait	~Season+Site+Year+Pig Removal	13	-8330.78	16689.99	5.72	0.01
~Site+Pig Removal+Rebait	~Site+Year+Pig Removal	13	-8330.79	16690.02	5.75	0.01
~Season+Site+Year+Pig Removal+Rebait	~Site+Year+Pig Removal	16	-8327.35	16690.43	6.16	0.01
~Season+Site+Rebait	~Season+Site+Year+Pig Removal	14	-8329.81	16690.45	6.18	0.01
~Season+Site+Year+Pig Removal+Rebait	~Site+Year	15	-8328.85	16690.96	6.69	0.01
~Site+Pig Removal+Rebait	~Season+Site+Year+Pig Removal	14	-8330.08	16690.99	6.71	0.01
~Season+Site+Rebait	~Site+Year	12	-8332.74	16691.56	7.28	0.01
~Year+Pig Removal+Rebait	~Site+Year	11	-8333.91	16691.56	7.29	0.01
~Season+Site+Pig Removal+Rebait	~Site+Year+Pig Removal	14	-8330.44	16691.72	7.44	0.01
~1	~1	2	-8439.55	16883.17	198.90	0.00

Appendix 2.5. Fawn deer model selection table from N-mixture models using data collected using biannual camera trap surveys beginning in the fall of 2018 until the spring of 2021. Variables included were the season of the camera survey, the site of the camera survey, the year of the camera survey and the percent of the initial population of wild pigs that was removed. We selected models based on the AICc, change in AICc (Δ), and the weight of the model (*w*). Only models with weight >= 0.01 and the intercepts-only model are listed.

Detection	Abundance	df	Log Likelihood	AICc	Δ	*w*
~Site+Year	~Site+Year	13	-2376.00	4783.52	0.00	0.23
~Site+Year+Pig Removal	~Site+Year	14	-2374.97	4784.40	0.88	0.15
~Site+Year	~Site+Year+Pig Removal	14	-2375.24	4784.95	1.43	0.11
~Year	~Year	7	-2384.76	4785.08	1.57	0.10
~1	~1	3	-2390.25	4786.82	3.31	0.04
~Site+Year+Pig Removal	~Year	11	-2380.63	4787.15	3.64	0.04
~Site+Year+Pig Removal	~Site+Year+Pig Removal	15	-2374.90	4787.29	3.78	0.03
~Site+Year	~Year	10	-2382.09	4787.37	3.86	0.03
~Year	~Year+Pig Removal	8	-2384.76	4787.55	4.04	0.03
~Year+Pig Removal	~Year	8	-2384.76	4787.56	4.04	0.03
~Pig Removal	~Pig Removal	5	-2388.49	4787.80	4.28	0.03
~Pig Removal	~1	4	-2389.90	4788.34	4.82	0.02
~Year+Pig Removal	~Year+Pig Removal	9	-2383.92	4788.42	4.90	0.02
~1	~Pig Removal	4	-2390.03	4788.60	5.08	0.02
~Site+Year+Pig Removal	~Year+Pig Removal	12	-2380.11	4788.87	5.35	0.02
~Site+Year	~Year+Pig Removal	11	-2381.59	4789.07	5.55	0.01
~Year	~1	5	-2389.35	4789.52	6.00	0.01
~1	~Year	5	-2389.54	4789.89	6.37	0.01
~Year	~Site+Year	10	-2383.91	4791.00	7.48	0.01
~Year+Pig Removal	~Pig Removal	7	-2387.74	4791.03	7.51	0.01