Pigs by the Sounder: Wild Pigs, Whole Sounder Removal, and their Effects on Deer and Turkey

by

Alexandra Anne Lewis

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Approved by

Stephen S. Ditchkoff, Chair, Ireland Professor of Wildlife Sciences
Mark D. Smith, Co-chair, Mosley Environmental Professor of Wildlife Sciences
Christopher A. Lepczyk, Professor of Wildlife Sciences
Robert A. Gitzen, Associate Professor of Wildlife Sciences

Abstract

Wild pigs (*Sus scrofa*) are an invasive species in North America with known negative impacts on agricultural lands and native ecosystems. To explore one commonly used, but ill-described management strategy, we implemented whole sounder removal on Lowndes Wildlife Management Area in Alabama and were able to successfully remove wild pig sounders from our removal area. We also explored competition between wild pigs and two important native species, white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallopavo silvestris*) using occupancy and activity analyses. We found that wild pigs negatively affected probability of use and detection of deer and turkey at baited camera sites and found that turkey activity at baited camera sites may be positively impacted by sounder removals. Our results suggest that wild pigs compete with deer and turkey, so removing wild pigs with whole sounder removal will likely have a positive impact on deer and turkey populations.

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LWMA – Lowndes Wildlife Management Area

WSR – Whole sounder removal

NW – Northwest section of Lowndes Wildlife Management Area

SE – Southeast section of Lowndes Wildlife Management Area

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Shifting to Sounders: Whole Sounder Removal Eliminates Wild Pigs

ALEXANDRA A. LEWIS,[1,2] *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

BRIAN L. WILLIAMS, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

MARK D. SMITH, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

STEPHEN S. DITCHKOFF, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

ABSTRACT Wild pig (*Sus scrofa*) eradication in demographically open populations has seemed an impossible feat for managers. This daunting task likely stems from management philosophies grounded in focusing on total wild pigs removed versus investing resources to initially identify the sounders and individuals in a population, and then maintaining removal efforts until all sounders are removed (i.e. whole sounder removal; hereafter WSR). Our objective was to implement and describe wild pig management using WSR. We established a 27-km^2 area (northwest section) where sounders were removed using WSR and a 29-km^2 area (southeast section) where GPS collars were deployed on Lowndes Wildlife Management Area in Alabama. Prior to implementing WSR, we used game cameras over bait at a density of 1 camera/km^2 in November 2014 and counted 65 and 100 individuals in our northwest and southeast sections,

[1] Email: Alex.Lewis@alaska.gov
[2] Current affiliation: Alaska Department of Fish and Game, PO Box 110024 Juneau, AK 99811-0024, USA

respectively. We began WSR July 2015 and by May 2016, we reduced the population by 90%. However, due to births and seasonal movements of pigs in the periphery of the study area, the population fluctuated between 10-20 individuals from May 2016 to December 2017. In December 2017, we removed the last remaining sounder and using game cameras, observed no sounders in the northwest section for the following 7 months, the remaining length of the study. We determined that using the WSR approach can lead to a drastic delay before inevitable recolonization. Therefore, WSR can be a successful tool to significantly reduce a wild pig population and provide managers a clean slate to start a monitoring program.

KEY WORDS invasive species, management techniques, *Sus scrofa*, trapping, whole sounder removal, wild pig

Biological invasions are the introduction, establishment, and spread of non-native organisms (Mack et al. 2000, Kolar and Lodge 2001, Clout and Russell 2007), and wild pigs (*Sus scrofa*) are a prime example of a biological invader in North America. In the United States, wild pigs cost producers and landowners an estimated $1.5 billion in yearly agricultural damage and control (Pimentel 2007). In addition, wild pigs carry and transmit parasites and diseases such as pseudorabies and swine brucellosis, which are transmissible to native fauna and humans, an issue made more problematic as wild pigs reach greater population densities (Seward et al. 2004, Engeman et al. 2007, Muller et al. 2019). Wild pigs also compete with native wildlife for resources, depredate herpetofauna, small mammals, and neonates of large mammals, and destroy nests of ground-nesting birds (Mayer 2009, Wilcox and Van Vuren 2009, Jolley et al. 2010, Suselbeek et al. 2014). Because wild pigs have a wide-reaching impact on native species, a primary focus of management has been to maximize the number of individuals removed (Campbell and Long 2009).

Wildlife professionals generally recommend using a variety of control techniques when managing wild pigs, such as corral traps and ground shooting, (Campbell and Long 2009, Pepin et al. 2017). Using this variety of approaches allows managers to avoid habituation to traps (e.g. trap shyness) and to mitigate the ability of wild pigs to readily adapt to changing environments (Campbell and Long 2009, Pepin et al. 2017). Further, managers often employ trapping as their primary management tool because it is efficient and economically available to most managers (Williams et al. 2011). However, trapping programs have never documented success in eradicating wild pigs in a demographically open population. The typical measure of success for wild pig control is usually a final or total annual kill count that neglects the number of pigs or sounders left on the landscape. Therefore, pieces of sounders -breeding adults or juveniles that quickly rebuild population numbers due to their high rate of reproduction- are left on the landscape (Mayer and Brisbin 2009).

Eradication of wild pigs is often considered infeasible in open populations, though their social nature and site fidelity cause wild pig populations to encroach slowly across the landscape (Gabor et al. 1999). Wild pigs travel in tight-knit matriarchal social groups (sounders) that may contain several generations of females and their offspring (Graves 1984, Boitani et al. 1994). The ranges and movements of entire sounders vary depending on resources, but wild pigs generally do not move great distances (Gabor et al. 1999, Kay et al. 2017). In fact, several researchers have reported that sounders maintain exclusive home ranges (Ilse and Hellgren 1995, Gabor et al. 1999, Sparklin et al. 2009). This high site fidelity suggests that wild pig populations could be vulnerable to control programs that focus on removing entire sounders. However, most control programs focus on the need to overcome the prolific rate of reproduction rather than exploiting potential vulnerabilities in their biology, such as high site fidelity or tight-knit social groups.

Current management approaches have resulted in documented successful eradications, such as on Santa Rosa and Santa Cruz Islands, but these have mostly been in closed populations (Lombardo and Faulkner 2000, Parkes et al. 2010). The wild pig population that occupied Pinnacles National Monument was eradicated after fences surrounding the monument were built (McCann and Garcelon 2008). Complete local eradication implies that there is no threat of immigration from neighboring populations, but local elimination of wild pigs (i.e. the removal of local populations with consideration for immigrating wild pigs) is plausible in demographically open populations. Removing entire sounders and ensuring that no individuals remain behind to repopulate the area will facilitate effective management of wild pig populations and maintain pig free areas for longer.

The whole sounder removal (WSR) management strategy was originally founded on the premise that individual and groups of wild pigs could be identified and tracked. Thus, managers are able to develop intimate knowledge of a population, enhancing their ability to eliminate that population (McCann and Garcelon 2008). This premise is facilitated by wild pigs' high site fidelity and slow recolonizing rates (Gabor et al. 1999). WSR has been used with wild pigs in a number of areas including on Fort Benning, Georgia (Ditchkoff and Bodenchuk 2020). However, while this strategy has become popular in name, it has yet to be described in peer-reviewed literature. We examined the biological (e.g. social and spatial) and logistical aspects of a WSR program and provide evidence that this approach to wild pig management can effectively eliminate wild pigs existing in open populations.

STUDY AREA

We conducted our study between November 2014 and June 2018 on Lowndes Wildlife Management Area (LWMA) in central Alabama (32º21'46"N 86º44'48"W, elevation 44.5 m).

Between 2015 and 2018, average annual temperature was 19°C and average annual rainfall for LWMA was 146 cm (NCEI 2019). Summer temperatures in the region reached an average temperature of 8°C in January and 27°C in July (NCEI 2019). LWMA was a 67-km^2 property located near White Hall, Alabama was managed by the Alabama Department of Conservation and Natural Resources (ADCNR), Division of Wildlife and Freshwater Fisheries for game animals such as white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallopavo silvestris*). Land cover classes and vegetation of the area were planted pines (*Pinus* spp.), planted hardwoods (*Quercus* spp.), mixed pine and hardwood forest, wildlife openings, and bottomland hardwoods (Gaston et al. 2008).

We divided LWMA into two areas, the northwest section and the southeast section (Figure 1). The northwest section where we removed pigs was approximately 27 km^2 and was bounded by the Alabama River on its western, northern, and northeastern sides. Our southeast section of the study area was 29 km^2 bordered by Alabama state highways and some agricultural land. Additionally, the two sections were separated by approximately 2.5 km of mixed private and state land composed of agricultural lands, residential area, a gravel mine, and mixed pine and hardwood forests. No removal operations were conducted on the southeast section of the study area; however, wild pigs were monitored with trail cameras, and some wild pigs from this section were captured and fitted with a GPS (Geospatial Positioning Satellite)/VHF (Very High Frequency) collar. Both sections of the study area had wild pigs that were not naïve to traps. Since their introduction to LWMA by a private citizen in the 1990s, Alabama Department of Conservation and Natural Resources (ADCNR) personnel have used corral traps, box traps, night shooting, and hunting to manage the population (C. Jawarowski, ADCNR, personal communication). Across LWMA, special hunting seasons for wild pigs occurred for two weeks in August and one week in March annually. Outside of these special seasons, wild pigs could be hunted during any other hunting season using the approved weapons and ammunition for those hunts. Removal efforts by adjacent landowners varied, but there were some management efforts on adjacent land to the northwest section using corral and box traps, and night shooting at the gravel mine adjacent to the southeast section.

METHODS

Our WSR strategy was founded on an adaptive four step process (Figure 2). Step one was to survey the population. We used trail cameras to systematically survey the study area to locate individuals and sounders prior to removal. Step two was to identify individual wild pigs and unique sounders based on pelage characteristics and sounder composition (Sweitzer et al. 2000). We used the images from our camera surveys to identify sounders and optimize our removal locations based on which camera sites were visited most. In step three, we constructed traps and conditioned sounders to the trap using whole corn. Step four was removal and inventory, accounting for which pigs had been removed and which remained.

A preliminary wild pig survey was conducted in late November to early December 2014. This survey provided an initial count of wild pigs in our study area. Camera densities were approximately 1.25 cameras/km^2, and each site was chosen based on a grid system and either existing pig sign (rooting, tracks, and tree rubs) or a site where we were likely to detect pigs based on proximity to a water source, cover, and food availability (Kay et al. 2017). These sites were pre-baited with 12 kg of whole corn and left undisturbed for 7 days prior to camera deployment. After 7 days, 12 kg of whole corn was used to replenish the site and a Reconyx HC500 (Reconyx, Inc., Holmen, WI, USA) trail camera was deployed 1 m high on trees at least 15 cm diameter at breast height. Cameras were set to a 5-minute time lapse interval, and cameras were collected at the end of 7 days. Sites occupied by a sounder were baited continually to keep the sounder in the area until a trap was built and removal or radio collaring efforts could be executed. We defined a sounder as any group of wild pigs with at least one adult female (Graves 1984).

Following our initial survey, we began a continual monitoring effort that lasted until June 2018. This effort was conducted using trail cameras to monitor individual wild pigs and sounders. During this phase of monitoring, cameras were sited at locations where initial surveys had documented sounders, where physical sign was present, and at locations where there was a high probability of pig presence (based on water, food, and cover availability; Kay et al. 2017). We deployed and maintained an average of 10 cameras across LWMA with 7 kg of whole corn until June 2018.

Surveying for wild pig sounders was disrupted 3 times each year when trail cameras were required for other surveys each February/March, July, and September. We used these surveys as an additional opportunity to monitor and track wild pigs across the WMA. Each February and September, we deployed cameras at a density of 1 camera/7 km^2. Each March, we deployed cameras at a density of 1 camera/4 km^2, and each July, we deployed cameras at a density of 1 camera/1 km^2. Outside of these other surveys, we had an average of 13 cameras (SD = 9.52) in the northwest section per month, yielding an average density of 1 camera/2 km^2, a density greater than 1 per average home range size for the region (Sparklin et al. 2009). All trail camera surveys were baited with whole corn. When cameras were deployed to monitor wild pigs, they were re-baited every 7 to 10 days and rotated throughout the removal area to target sounders.

We counted the wild pig population in the northwest section once per month between November 2014 and June 2018. We identified wild pigs by sex, juvenile or adult age class, pelage characteristics, and group composition (Sweitzer et al. 2000). Although our focus was sounders, we counted all wild pigs (adult males, adult females, and juveniles). Juveniles were estimated to be <6 months old while adults were ≥6 months old. Juveniles were distinguished from adults based on relative size. If pigs with the same characteristics and sounders with the same composition were observed at different camera stations, they were assumed to be the same pigs. If we did not see an individual or sounder for greater than 6 months, we considered those pigs as either dead or emigrated.

We removed sounders between June 2015 and November 2017. When a sounder was targeted for removal, we constructed a corral trap to capture and remove the sounder. We used whole kernel corn to condition sounders to an area and condition them to enter the trap once it was built. The trap consisted of 5, 4.9-m panels attached to 1.6-m t-posts driven into the ground on the outside of the panel. Panels were arranged with a 0.5-m overlap between panels and attached to t-posts with baling wire. In addition, a 2.4-m guillotine-style M.I.N.E.™ Gate (Jager Pro, Fortson, GA, USA) was used as a door and was also attached to t-posts on both sides with baling wire. After traps were constructed, we monitored each trap remotely between 1700 hours and 0600 hours with a Jager Pro M.I.N.E. ™ Cam (Jager Pro, Fortson, GA, USA). Wild pigs were habituated to the trap with whole corn until the entire sounder consistently entered. When an entire sounder appeared to enter the trap, an observer closed the gate remotely and traveled to the trap to euthanize the trapped pigs. If some pigs escaped, those pigs were found and targeted by the same trapping protocol.

We defined three periods to calculate trapping and monitoring effort: pre-removal monitoring, post-removal monitoring, and no-removal monitoring. Pre-removal monitoring effort was counted from the first night a trap was set and ready to be triggered (i.e. active) to the first night a sounder was removed. This pre-removal monitoring included identifying individuals within a sounder to target for removals. Post-removal monitoring was counted as the nights following an initial removal to when the trap was no longer active. No removal monitoring was when a trap was active, but no removal event occurred at that trap site. When a trigger system or trap failed (i.e. the door closed because of interference with the door mechanism) and the interval between active trapping was <7 days, we considered it part of the same effort sequence. If the interval between active trapping was ≥ 7 days, we considered it a new effort. We did not quantify our effort into hours because of the remote trigger, nor did we document how many hours were spent constructing or moving traps because of our ability to trigger and monitor traps remotely. Our calculations of trapping effort were only associated with removals and not in efforts to deploy GPS collars.

We deployed GPS collars on individual wild pigs prior to and during WSR to monitor space use on our study area. Specifically, we thought it was important to understand if sounders quickly recolonized areas where wild pigs had been removed or made long excursions to areas such as local agricultural resources. We deployed G2110D GPS/VHF (Advanced Telemetry Systems, Isanti, MN) collars on reproductively mature female pigs (>6 months of age or approximately 40 kg). Adult females in the northwest section were collared in April and May 2015. Once removals began in the northwest, we no longer deployed collars in that section. We deployed GPS collars in the southeast section from May 2015 to November 2017. We targeted 1-2 adult females in each sounder in case one collar failed, to explore space use within and between sounders, and to monitor potential emigration. We trapped adult females using the same trapping method as removals. An observer remotely closed the gate, and then immediately traveled to the trap to restrain and immobilize the adult females. We immobilized wild pigs using an intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA; 11 mg/ml given at a rate of 2 mg/kg) diluted with sterile water. We fitted adult females with collars such that the collar could not slip over the sagittal crest. We programmed collars to acquire fixes every 30 minutes, and we monitored collars at least once per month via VHF for mortality or collar failure. The information from these collars was imported into ArcGIS 10.3.1 to determine the spatial structure of sounders.

We assumed that data from collars on adult females were representative of the entire sounder based on previous literature (Sparklin et al. 2009) and our own observations. We calculated kernel density home ranges from collars that collected at least 30 days of data with at least 60 locations (Sparklin et al. 2009) using a plug-in bandwidth in adehabitatHR and ks libraries in R (R Core Team 2019, Calenge 2006, Duong 2019). Kernel density home ranges were defined as the 95% probability utilization distributions (UD) and the core area as the 50% UD (Gabor et al. 1999). When multiple individuals were collared simultaneously within the same sounder, we used the data for the individual that collected the most data (Sparklin et al. 2009). We also used the adehabitatHR package to calculate home range overlap of individuals within and between sounders. We used the volume of intersection statistic (VI) to determine overlap between individuals within a single sounder and individuals between sounders (Fieberg and Kochanny 2005) 100% of the available GPS points. The VI was calculated using the full length of a collar's time on an individual and using a truncated version of the data, restricting the data used in the analysis to only when the GPS collars were collecting data at the same time. All animal handling for captures and euthanasia procedures were approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2014-2555; PRN 2017-3164).

RESULTS

We counted 65 and 120 wild pigs on the northwest and southeast sections, respectively, prior to initiating removal efforts in June 2015. We continued counts with trail cameras until June 2018, tracking the impact of removals on the population (Figure 3). We removed 96 individual wild pigs from eight sounders during 22 removal events (adult females n = 15; adult males n = 9; juvenile females n = 36; juvenile males n = 36). One sounder was removed by a local landowner when it had wandered outside of the LWMA boundaries. There were four sounders removed in a single removal event (i.e. one night), two sounders were removed in two removal events, one sounder was removed in three removal events, and one sounder was removed over four removal events. There were 10 individual pigs removed during the study that were not associated with a sounder. After May 2016, the sounders found on camera were those that moved in and out of the LWMA boundary. Between July and October 2015, 69 percent of individuals were removed in two main pulses (Figure 4). Subsequent efforts removed fewer total individuals. The final sounder was removed in December 2017, which consisted of two adult females, two adult males, and five juveniles. Any adult males that were removed were either captured in a trap with a sounder or were consistent visitors to a trap that was prepared for a sounder. Incidentally, we found behavioral changes between pigs that were trapped at night and then removed the following morning and pigs that were trapped and removed during the night. In general, trapped pigs responded less to human presence at a trap when approached at night whereas pigs that were approached in the morning were more alert to approaching humans and made more efforts to jump or climb over the trap fence.

Cumulatively, we used 15 different trapping locations across the northwest section. We spent 644 total nights (mean = 24.8 nights per effort, SD = 29.6) monitoring a trap that was ready to be triggered. There were a total of 211 pre-removal nights (mean = 8.12 nights per effort, SD

= 19.6), 203 post-removal nights (mean = 7.81 nights per effort, SD = 13.3), and 230 nights with no removals associated (mean = 8.85 nights per effort, SD = 18.6). Most individuals from sounders were removed during initial trapping efforts, but two separate times a group was trapped during post-removal monitoring because the remainder of the sounder moved out of the trapping area after the initial removal. Trapping effort varied across years (Figure 5). Cumulatively, we spent a total of 131 nights of effort in 2015 (mean = 10.9 nights per effort, SD = 7.06), a total of 103 nights of effort in 2016 (mean = 20.6 nights per effort, SD = 16.81), and a total of 410 nights of effort in 2017 (mean = 45.6 nights per effort, SD = 41.76). Most effort expended in 2017 was on active traps where there were no removals, but the difference between effort when no wild pigs were removed and effort on pre-removal monitoring was negligible.

We collected GPS locations from 22 adult females from 11 sounders. Five adult females from 3 sounders in our northwest section were collared before removals began in July 2015, and 17 adult females from seven sounders that were collared between May 2015 and August 2016 in the southeast section. Collars collected data for an average of 94.9 days (SD = 59.4) with a range from 2 to 217 days. The average number of GPS locations per individual was 4,069 (SD = 1,623). Pairs of individuals within a sounder collared at the same time (n = 9 dyads, n = 2 northwest section, n = 7 southeast section) collected an average of 7,215 locations per sounder (SD = 3,755; mean days of overlap = 54, SD = 38). Home ranges calculated with a 95% kernel density utilization distribution from the northwest section (n = 3) were 6.2 km^2 (+/- 5.31 km^2) and 1.05 km^2 (+/- 1.05 km^2) for 50% kernel core areas. Southeast section home ranges (n = 14) with 95% kernel density utilization distribution were 3.42 km^2 (+/- 0.67 km^2) and 0.67 km^2 (+/- 0.35 km^2) for 50% kernel core areas. Though cumulatively, some GPS points overlapped between sounders (Figure 6), there was no temporal overlap when comparing time stamps between sounders. Additionally, volume of intersection confirmed that collared females from assigned sounders did not spend significant time in the home ranges of collared females of neighboring sounders. Of 48 pairwise comparisons between pigs not in the same sounder, 100% utilization distributions overlapped an average factor of 0.022 (2.2%; SE = 0.005) when GPS data was clipped for the two sets of data to overlap in dates (i.e. only use data when the two collars were active within the same time frame). Using the full dataset yielded a volume of intersection of 0.038 (3.8%; SE = 0.009). When collared adult females within the same sounder (n=6) were analyzed, volume of intersection was an average of 0.824 (82.4%; SE = 0.108) when the data was clipped. Volume of intersection using the full set of data within each sounder was 0.692 (69.2%; SE = 0.105). None of the adult females that were collared during the study made extra-home range movements across the study area (i.e. travel from one end of the section or study area to the other; Jacobsen et al. in press), nor did they target agricultural fields outside of their home ranges.

DISCUSSION

Though ours is not the first study to document the successful removal of wild pigs from an area, we do report our success in the context of a demographically open population and the time frame in which we were successful. Our WSR program removed 96 pigs, took 2.5 years using a single employee on LWMA with some assistance from LWMA personnel, and our removals were done with corral traps. Other removal programs have eradicated demographically closed or isolated populations in a variety of time frames. Channel Islands National Park (215 km^2) eradicated their wild pig population by removing 1,175 pigs over three years using a variety of removal techniques (Lombardo and Faulkner 2000). Other examples include Pinnacles National Monument (57 km^2; McCann and Garcelon 2008), Santiago Island (585 km^2; Cruz et al.

2005), and Annadel State Park in California (20 km^2; Barrett et al. 1988). Each of these examples used a variety of techniques including trapping, aerial shooting, and ground hunting over relatively short time frames (three years) except for Santiago Island. Removal efforts on Santiago Island lasted thirty years.

Trapping effort during our study was highly variable. Our trapping effort varied among trap sites because some sounders exhibited more elusive behavior and required more trap nights. For example, we expended 90 nights of effort in pre-removal monitoring and 17 in post-removal monitoring to remove one sounder, while another sounder only required three days of pre-removal monitoring. Trapping effort between years was markedly greater for 2017 than for 2015 or 2016. The increased effort near the end of the study was a function of the difficulty in trapping the last few individuals in the population. Most of these individuals had previously been exposed to traps, and they had likely experienced loss of pigs from their sounders. For these reasons, complete eradication is much more difficult than population reduction, supporting the assertion of Judge et al. (2017) that complete eradication is often more difficult when there are fewer organisms left on the landscape. Though this assertion was made for island populations, removal of the last few individuals on a landscape where the target species can evade removal by moving off the control area (e.g. move off the management area during control operations) indicates that final removal without consistent monitoring will be unsuccessful. Therefore, continual monitoring is a key feature in a WSR program.

The movements of wild pigs in our study suggested there was high site fidelity within sounders and sounders had relatively small home ranges, a characteristic common in areas where resources are readily available (Schlichting et al. 2016). With our GPS collar and trail camera data, we observed that sounders stayed within a range of certain camera sites. Further, a sounder would often revisit a camera site at approximately the same time every day, and some sounders visited the same camera site on a consistent day of the week. Site fidelity is a known attribute of wild pigs (Graves 1984, Keuling et al. 2008) and contributes to the efficacy of WSR. Additionally, our GPS collar data indicated that sounders had minimal spatial overlap and there were no cases of collared individuals emigrating to areas outside of LWMA or immigrating between the northwest and southeast sections. In cases when spatial overlap between sounders appeared to occur, a more careful examination of the data indicated that the sounders did not have temporal overlap: either the two sounders were not collared at the same time or one sounder was at least 1 km away when another sounder entered its range. Our data suggest that sounders on Lowndes WMA did not overlap in space, which is similar to the findings of Gaston et al. (2008) on this same area. They reported that wild pigs showed high site fidelity, even when exposed to high hunting pressure. Additionally, these findings are similar to Sparklin et al. (2009) who described territoriality between sounders, and Gabor et al. (1999), who suggested that sounders used exclusive space. In contrast, some earlier studies found that home ranges of sounders consistently overlapped (Boitani et al. 1994). Ilse and Hellgren (1995) reported suspicion of home range overlap, but they did not have empirical data to support that suspicion. However, we are confident that sounders on LWMA did not overlap in their space use, nor did we find evidence that individual wild pigs within sounders intermingled with those of other sounders. These observations (high site fidelity and no excursive movements) suggest that areas where wild pig sounders are locally eliminated will likely be recolonized slowly. Our study area qualifies as an open population because it is possible for individuals to immigrate onto LWMA. However, barriers like the Alabama River and major highways can negatively impact animal movement, thus further slowing the immigration of surrounding populations on to LWMA (Kay et al. 2017).

The successful elimination of wild pigs from LWMA was dependent upon continued monitoring efforts throughout the study. Through this monitoring, we gained intimate knowledge of the spatial patterns and composition of the wild pig population on Lowndes WMA (McCann and Garcelon 2008). Initial population surveys served to locate and identify sounders that were present when the study began, and continual monitoring following removal events was essential to detect remnants of partially-eliminated sounders. Finally, by continuing camera surveys after sounders were eliminated, we were able to ensure that if sounders did immigrate on to LWMA, we would detect them at an early stage (Barrett et al. 1988). Previously, wild pigs had been successfully eliminated (with the exception of 2 adult females) in an 89-km^2 area of Fort Benning, Georgia, USA, a U.S. military installation, using WSR between 2007 and 2010 (Ditchkoff and Bodenchuk 2020). However, without further management, the wild pigs that were not removed re-colonized the cleared area (Michael Ramirez, Fort Benning, personal communication). While our implementation of WSR on LWMA was successful for the duration of this study, without the maintenance of an appropriate monitoring and removal program, the area will likely be recolonized by wild pigs at some point, and potentially return to its previous state.

MANAGEMENT IMPLICATIONS

Our WSR program was predicated on surveillance, and we described a simple way of locating and identifying sounders and the individual wild pigs that comprised the population. We believe that if pigs are not detected in an initial survey, but are present in surrounding properties, immigration is possible and surveying at regular intervals (e.g. every three months) will allow for detection of wild pig immigration at an early stage. Our success on Lowndes WMA was heavily dependent on continuous monitoring, identifying sounders, and ensuring the removal of the entire sounder rather than a portion. We believe the implementation of WSR across landscapes is feasible as the principle is applicable to wild pig social behavior. Applying WSR to other conditions and terrains may likely require removal tools different from the heavy, metal corral traps used in our study. However, because the success of our program was dependent on monitoring, not removal technique, we believe that WSR can be successfully implemented anywhere. In addition to providing detailed knowledge of the population prior to removal, our diligence in monitoring, while time consuming, proved effective at documenting the decrease and ultimate elimination of the population.

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Figure 1.1 Map of Lowndes Wildlife Management Area, in Alabama, USA. The bold lines outline the borders of the WMA and delineate our northwest (where wild pigs were removed) and southeast study areas (where no removal operations occurred).

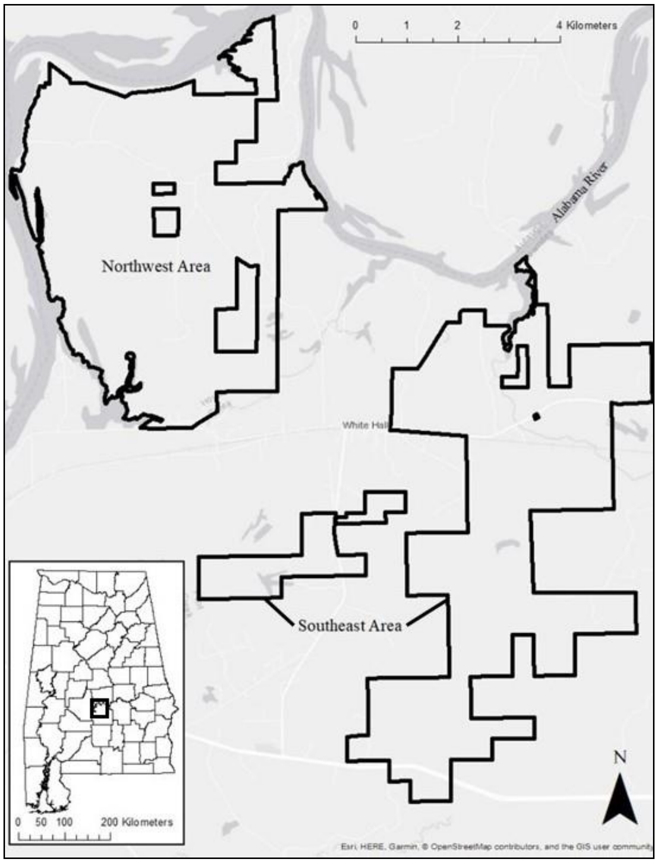


Figure 1.2 The four steps of whole sounder removal for a demographically open wild pig population. Step one involves systematically surveying the area to locate individual wild pigs and sounders. Step two is to identify individuals and sounders based on pelage characteristics, sex, age, and sounder composition. Step three is to condition the wild pigs that are meant to be removed to a trap. Step four is to remove the targeted wild pigs and inventory those that were removed and those that may be left on the landscape. Dotted lines are options dependent on the results of the survey.

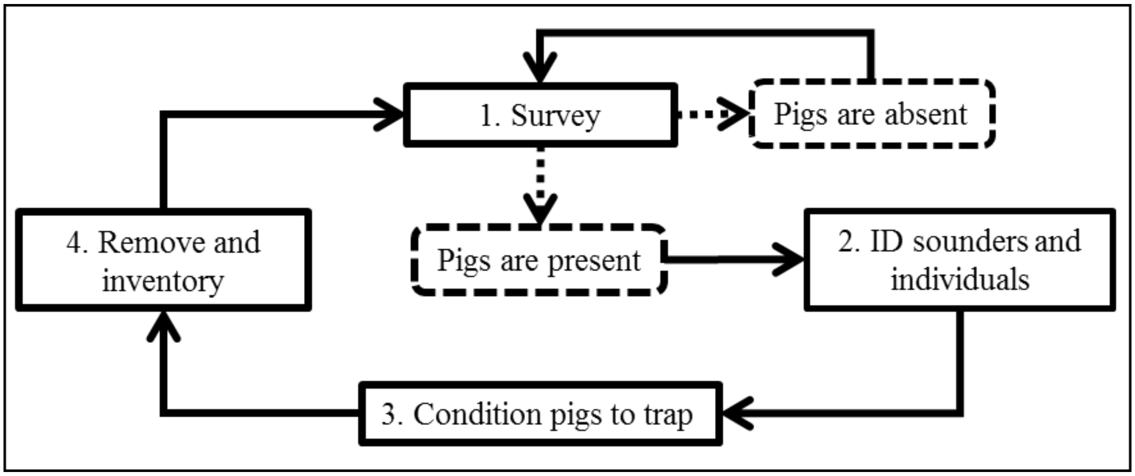


Figure 1.3 Total number of wild pigs counted with minimum counts on Lowndes WMA between November 2014 and June 2018. NW is the northwest section where we removed pigs. SE is the southeast section where we did not remove pigs.

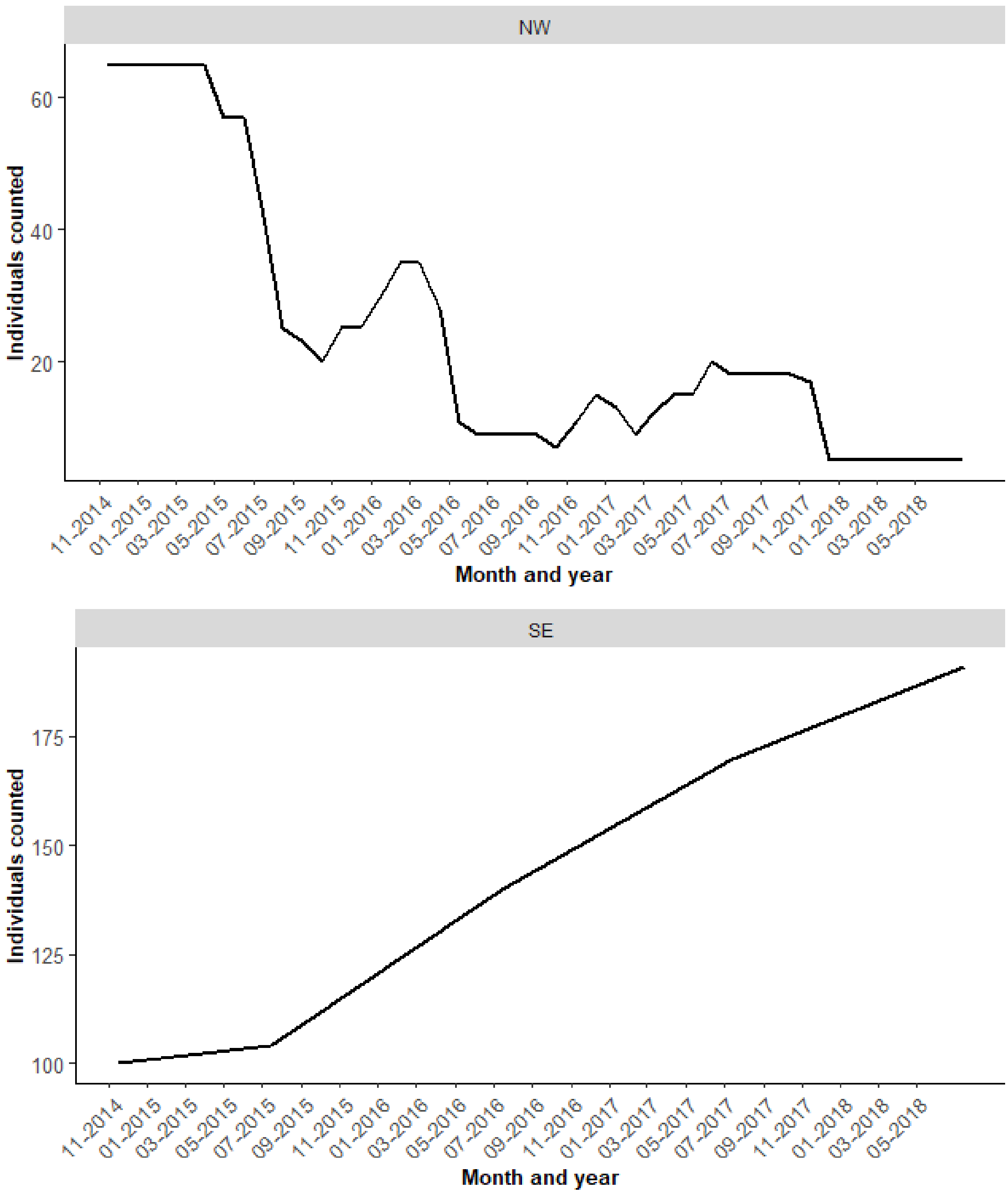


Figure 1.4 Total number of wild pigs removed from Lowndes WMA between July 2015 and December 2017.

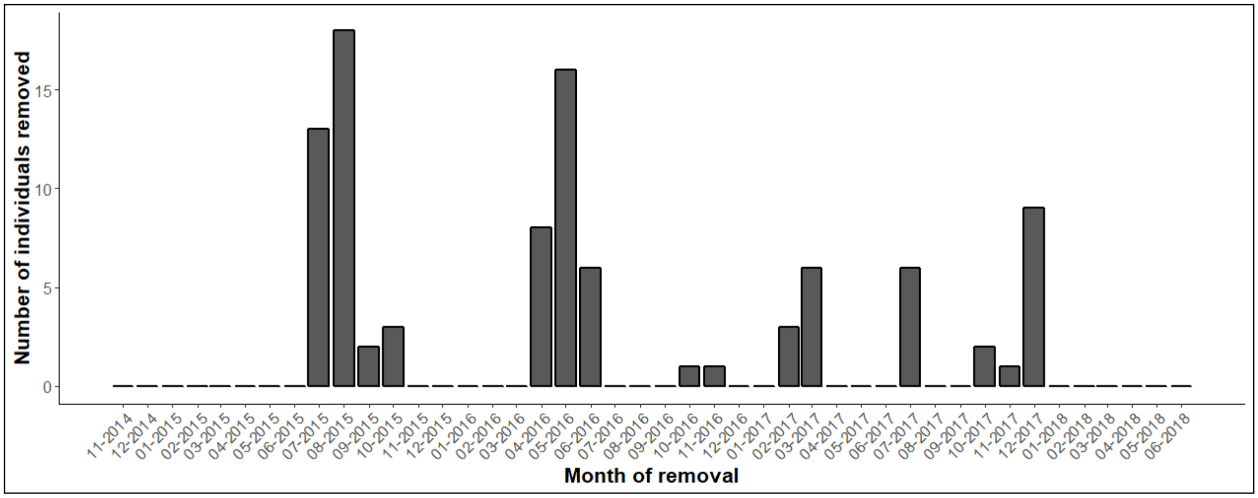


Figure 1.5 Total number of trap nights required for pre-removal, post-removal, and no removal activities during 2015, 2016, and 2017 on Lowndes Wildlife Management Area.

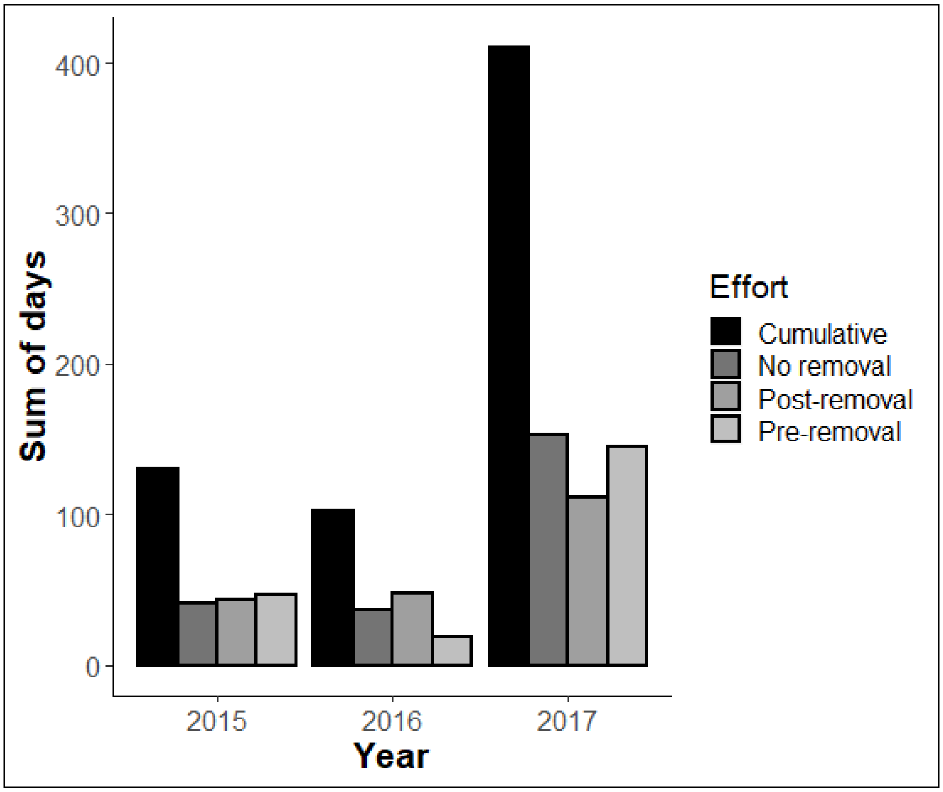
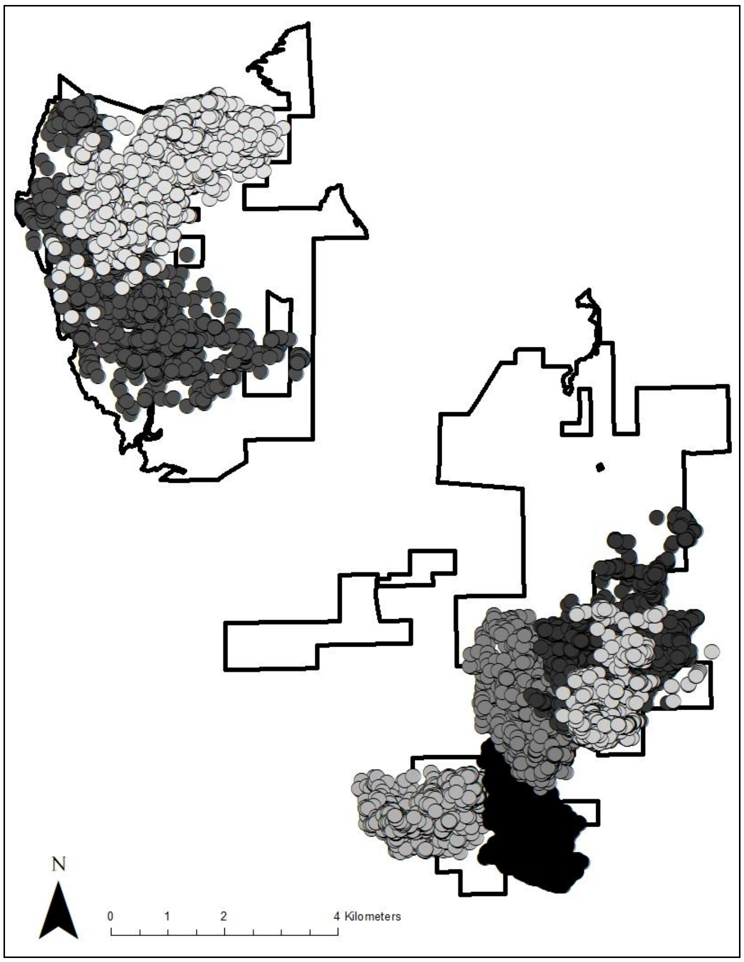


Figure 1.6 GPS locations acquired from seven radio–collared females on Lowndes Wildlife Management Area from April 2015 to August 2016. Data are only reported for individual adult females that accumulated greater than 120 days of data. These individuals represent two sounders in the northwest section and four sounders in the southeast section. No adult females made excursive movements, which indicated high site fidelity in radio-collared sounders.



CHAPTER II: EFFECTS OF WILD PIGS AND THEIR REMOVAL ON TEMPORAL AND SPATIAL ACTIVITIES OF TWO SYMPATRIC NATIVE SPECIES

Abstract

Invasive species have been well documented to negatively impact native wildlife, and these impacts can both directly and indirectly affect native species. In North America, wild pigs (*Sus scrofa*) are an invasive species that is considered one of the most detrimental terrestrial invasive species on the continent. Although wild pigs have been in North America for close to five centuries, our knowledge of their impacts on native wildlife is still in its infancy, and much of our knowledge is based on anecdotal information. Two native wildlife species wild pigs may impact, white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallopavo silvestris*), are of particular concern because of their importance as game species, yet little data exist that empirically describe how white-tailed deer and eastern wild turkey are impacted by wild pigs. The objective of this research was to evaluate interspecific interactions between wild pigs, white-tailed deer, and wild turkey, and how elimination of wild pigs alter the behavior of other sympatric species in the community. We used occupancy and activity analyses to analyze data from annual 7-day camera surveys during 2015 - 2018. We found evidence that wild pigs negatively impact turkeys and deer, but turkey and deer use of baited camera sites did not change following the removal of wild pig sounders. Additionally, turkey activity at baited camera sites seemed to change after wild pigs were eradicated, but we found no such change in deer activity. Our results suggest that wild pigs compete with deer and turkey, and that removal of wild pigs may positively impact turkey activity. We believe that long-term effects of wild pig removal may include positive impacts on deer and turkey populations and that managers should take wild pig presence into account when assessing deer and turkey populations.

Introduction

Invasive species manipulate resources, out-compete native species, and negatively affect ecological communities (Crooks 2002). Additionally, when invasive species have similar ecological requirements as native species interactions often result in negative consequences to the native species (Santulli et al. 2014). Harris and Macdonald (2007) found interference competition between non-native (*Rattus rattus*) and native rats (*Nesoryzomys swarthi*) where non-native rats aggressively excluded native rats at food piles. Santulli et al. (2014) found that non-native American mink (*Neovison vison*) competitively excluded native European mink (*Mustela lutreola*) in Spain, leading to a decrease in the range of the European mink. The influence of invasive species on native species is not limited to those that are closely related. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) in the northwestern United States have been found to alter their spatial patterns when domestic cattle (*Bos taurus*) are present by moving to higher elevations (elk) or avoiding the area altogether (mule deer) (Stewart et al. 2002).

Wild pigs (*Sus scrofa*) are a large invasive species outside of Europe and Asia and they have considerable potential to compete with and negatively impact native species. This species travels in matriarchal social groups called sounders, has few limiting factors like predators, and has a high fecundity (Geisser and Reyer 2005). Wild pigs are dietary and habitat generalists, thus they have the potential to directly and indirectly compete with a wide range of terrestrial wildlife species, and can cause ecological shifts by rooting (Burrascano et al. 2015) in both their native and non-native ranges (Leaper et al. 1999). Wild pigs have also been documented to depredate or disturb native herpetofauna (Jolley et al. 2010). The combination of their generalist characteristics and their widespread distribution across the United States suggests they significant potential to negatively impact native wildlife.

It has often been speculated that wild pigs negatively impact white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallopovo*), two important game species in North America. Keever (2014) and Price Tack (2017) found that presence of wild pigs negatively affected the detectability of white-tailed deer. Wild pigs have also been documented aggressively excluding white-tailed deer from acorns (Taylor and Hellgren 1997) and have been known to drive other species away (Barrett 1982). Additionally, many studies have focused on their potential to destroy nests of ground-nesting animals like northern bobwhite (*Colinus virginianus*), green sea turtles (*Chelonia mydas*), and Galápagos tortoises (*Chelonoidis nigra*) (Coblentz and Baber 1987, Tolleson et al. 1993). There has been speculation that wild pigs significantly impact wild turkey through nest predation or even exclusion (Seward et al. 2004, Jolley et al. 2010). Henry (1969) found when exploring turkey nest depredation in the Southern Appalachians that wild pig depredation was at most compensatory to mesocarnivore nest depredation. In contrast, Sanders et al. (2020) found that 80% of simulated turkey nests were destroyed, indicating that wild pigs have a greater impact on wild turkeys than observed in the past.

While there are few published studies that demonstrate competition between wild pigs, deer, and turkey, stakeholders in the southeastern United States consistently report noticing a negative impact on deer and turkey when wild pigs are present (Mengak 2012, TuckerWilliams 2018). Competition between these species may result in spatial or temporal partitioning, which indicates that wild pigs cause some native species to contract their home ranges or competitively exclude other species (Keever et al. 2017, Price Tack 2017). Most research to date has focused on either direct depredation or dietary overlap (centered around pulse resources like agricultural crops and hard mast) between wild pigs and native species (Mayer 2009). However, there has been no empirical research into the effects of wild pigs and their systematic removal on sympatric large mammals or upland bird species.

Because of on-going efforts to eliminate wild pigs both on the state and federal level, wild pigs are an excellent study species to test an invasive large mammal's effect on sympatric native species. However, the analytical methods used to explore relationships between invasive and native species are widely variable and can indicate different dynamics of a complex system. We used occupancy and activity time analyses to explore the impact wild pig presence and subsequent removal may have on deer and turkey. We expected that wild pigs would have a negative effect on aspects of their spatial and temporal distribution. We also expected that we would document changes in occupancy and activity patterns of turkeys and deer at baited camera sites following removal of wild pigs.

Study Area

We conducted our study between April 2015 and June 2018 on Lowndes Wildlife Management Area (LWMA) in central Alabama (32º21'46"N 86º44'48"W). LWMA was a 67-km^2 property located near White Hall, Alabama, and was managed by the Alabama Department of Conservation and Natural Resource's Division of Wildlife and Freshwater Fisheries for game animals such as white-tailed deer and eastern wild turkey. LWMA lies in the southeastern floodplains and low terraces ecoregion (Griffith et al. 2001). General land cover classes and vegetation of the area was composed of planted pines (*Pinus* spp.), planted hardwoods (*Quercus* spp.), mixed pine and hardwood forest, wildlife openings, and bottomland hardwoods (Gaston et al. 2008). Specifically, much of LWMA had a dominant canopy of water oak (*Quercus nigra*), willow oak (*Quercus phellos*), southern red oak (*Quercus rubra*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*) (Wilson 2018). The understory of LWMA was composed largely of musclewood (*Carpinus caroliniana*), red maple (*Acer rubrum*), and dwarf palmetto (*Sabal minor*) (Wilson 2018). Between 2015 and 2019, average annual temperature was 19°C and average annual rainfall for LWMA was 146 cm. Temperatures in the region reached an average temperature of 8°C in January and 27°C in July (NCEI 2019). Across LWMA, special hunting seasons for wild pigs occurred for two weeks in August and one week in March. Outside of these special seasons, wild pigs could be hunted during any other hunting season using the approved weapons and ammunition for those hunts. The hunting season for white-tailed deer was November - February while the hunting season for eastern wild turkey was March - April.

Methods

We divided LWMA into two sections, the northwest section and the southeast section (Figure 1). The northwest section where we removed pigs was approximately 27 km^2 and was bounded by the Alabama River on its western, northern, and northeastern sides, allowing only a limited area for immigrating pigs. Wild pigs in the treatment section were removed between June 2015 and November 2017. Staff followed whole sounder removal protocols using corral traps (Ditchkoff and Bodenchuk 2020) to target social groups and opportunistically removed adult males (Mayer and Johns 2009). We defined a sounder as a group containing at least one adult female. Our southeast section of the study area was 29 km^2 bordered by Alabama state highways 40 and 80 and some agricultural land. No wild pig removal operations were conducted on this portion of the study area. The two sections were separated by 2.5 km of mixed private and state land composed of agricultural lands, residential area, a gravel mine, and mixed pine and hardwood forests.

We conducted camera trap surveys for 7 days in July and August of 2015, 2016, 2017, and 2018, and deployed Reconyx HC500 (Reconyx, Inc., Holmen, WI, USA) trail cameras 1 m high on trees at least 15 cm diameter at breast height. Each site was baited with 7.5 kg of whole corn 7 days before cameras were deployed. Cameras were set to a 5-minute timelapse between 0500-0900 and 1600-2000 each day, and triggers were set to be motion activated any time throughout the day. Images were collected for six 24-hour periods each year. Sampling occasions for turkey were hour-long periods from 0500-0900 and 1600-2000 using the timelapse detection of turkeys since turkeys are often not detected with passive-infrared sensors (Damm 2010). Sampling occasions for wild pig and deer were hour-long periods throughout the survey using the trigger motion detection of wild pigs and deer. Camera density was one camera per one square kilometer and was chosen to maximize detection of adult female turkeys with poults since poult survival is dependent on spring weather conditions (Healy and Nenno 1985), so poults that have survived to July and August are likely to be recruited into the next year's age class.

We processed and interpreted images from camera surveys in 2015, 2016, and 2017 through Access to identify deer, turkey, and pigs. We processed and interpreted images from the camera survey in 2018 was processed through Timelapse2 (v.2.2.2.5) because we found it was more efficient (Greenberg 2016). We used a single season single species occupancy estimator for site use (Ψ) and detection (p) probabilities of turkey and deer (MacKenzie et al. 2002). Encounter histories were constructed for the occupancy estimator by recording when turkey and deer were present or absent (1 or 0). If camera malfunction or user error caused a survey to be disrupted, all hours that were not surveyed were treated as missing values.

We compared *a priori* models of site use (ψ) and detection (p) using Akaike Information Criterion (AICc), corrected for small sample size in program R package "RMark" (Burnham and Anderson 2002, Laake 2013). We compared models using AICc, difference in AICc from the top model (ΔAIC), and model probability (w). Covariates for these models were pig presence, sounder presence, section (northwest or southeast section of LWMA), and year. After we created initial AIC tables with both pig and sounder covariates, we chose either pig or sounder as the main covariate in future AIC tables (i.e. if sounder was the only covariate that appeared in the best performing models, only sounder was used when producing new, secondary AIC tables to choose best performing models that were < 2 ΔAIC) (Table 2.1, Table 2.2). We used model-averaged estimates from secondary AIC tables for site use and detection (Grueber et al. 2011). Covariates to determine best models in turkey and deer occupancy models included the presence of any pig, the presence of a sounder, section, and year.

We estimated daily activity patterns among the three species using kernel density estimation following Ridout and Linkie's (2009) approach with the "overlap" package in Program R. In addition to exploring differences of any pig activity with deer and turkey, we also separated time stamps that could be assigned to sounders. Our analyses examined pairwise overlaps between species (deer-pig, turkey-pig, deer-sounder, and turkey-sounder) to detect turkey and deer sensitivity to any pig and sounder presence. We converted time stamps of all detections (timelapse and trigger motion) to radial time for all capture events (Meredith and Ridout 2020). We used the coefficient of overlap estimator Δ_4 since sample sizes for each species across years was >75 (Meredith and Ridout 2020). Using a smoothed bootstrap with 10,000 iterations, we produced confidence intervals to determine if the overlap between each section was significantly different across all years (Meredith and Ridout 2020). We defined four time periods for each section. Period 1 was in 2015, period 2 was in 2016, period 3 was in 2017, and period 4 was in 2018. For the northwest section, there was a 35% total decrease in wild pigs for period 1, an 86% total decrease in period 2, a 72% total decrease in period 3, and a 92% total decrease in wild pigs for period 4. For the southeast section, there was a 4% total increase in wild pigs for period 1, a 40% total increase for period 2, a 70% increase for period 3, and a 91% total increase for period 4.

RESULTS

We deployed 66 cameras in 2015 between 22 July and 19 August, 69 cameras in 2016 between 11 July and 10 August, 64 cameras in 2017 between 10 July and 13 August, and 71 cameras in 2018 between 9 July and 9 August. We collected a total of 580,779 images (42.9% from the NW section; 57.1% from the SE section). Of these images, 5,697 (1.0%) were of turkey, 83,135 (14.3%) were of deer, and 69,373 (11.9%) were of pigs. The remaining images were of either non-target species (e.g. opossum [*Didelphis virginiana*] and raccoon [*Procyon lotor*]) or were images that were falsely triggered or were timelapse with no animal present. For analysis of turkey occupancy, we consolidated timelapse capture histories by hour, which meant that only 434 (7.6%) of these turkey images were used. For analysis of deer occupancy, we consolidated capture histories by hour and used the picture from the series of 3 pictures per trigger with the greatest number of deer. Therefore, only 20,070 (24.1%) of these deer images were used.

The best models for estimating site use and detection of turkeys indicated the presence of a sounder was the most important factor (Table 2.1). Site use estimates between sites where sounders were present and sites where sounders were absent varied between sections and across years. Probability of site use in the northwest section ranged from 1.4% to 10.9% greater where wild pig sounders were not present than where sounders were present (Table 2.2). The probability of site use in the southeast section ranged from 1.1% to 10.6% greater at sites where wild pig sounders were absent than where wild pig sounders were present. Detection probabilities were not significantly different between sites with wild pig sounders and sites without wild pig sounders in 2015 and 2018, but detection probabilities were significantly different in 2016 and 2017. Detection probabilities in the northwest section ranged from 4.2% to 8.9% greater at sites where wild pig sounders were absent than where wild pig sounders were present. In the southeast section, detection probabilities ranged from 3.5% to 7.5% greater at sites where wild pig sounders were not present than where wild pig sounders were present (Table 2.3).

The best models for estimating occupancy and detection indicated the presence of a wild pig, regardless of sex or age class, was the most important factor for predicting occupancy and detection of deer (Table 2.4). Sites in the northwest section where wild pigs were absent had a 15.1% to 18.6% greater probability of use by deer than sites where wild pigs were present. Sites in the southeast section had a 16.5% to 19.8% greater probability of use by deer where wild pigs were absent than sites where wild pigs were present (Table 2.5). However, there was a difference in detection probability of deer between sites where wild pigs were present and sites where wild pigs were not present (Table 2.6). In the northwest section at sites where wild pigs were absent, probability of detecting deer was 3.8% to 4.9% greater. In the southeast section at sites where wild pigs were absent, probability of detecting deer was 2.8% to 3.8% greater.

Activity estimates for turkeys and deer in the northwest section had few variations between periods. Turkeys were more active following sunrise and prior to sunset (crepuscular), and deer were more active during crepuscular and nocturnal periods (Figure 2.5). In contrast, activity patterns of wild pigs varied among years, with greater activity during the day in periods 3 and 4 than periods 1 and 2. In the southeast section, activity estimates for turkeys, deer, and pigs remained relatively consistent throughout the study (Figure 2.6). However, peak activity times for turkeys in this section differed from those in the northwest section. While turkeys in the northwest section were mostly active at bait sites just after sunrise and prior to sunset, they were active at these sites throughout the day in the southeast section. Activity patterns of deer and pigs were similar between sections. Overlap estimates of activity between pigs and turkey in the northwest and southeast sections were 0.19 (confidence interval [CI]: 0.18-0.24) and 0.28 (CI: 0.27-0.29), respectively, and overlap estimates of activity between pigs and deer in the northwest and southeast sections were 0.68 (CI: 0.67-0.70) and 0.84 (CI:0.83-0.85), respectively. Overlap estimates of activity between sounders and turkey in the northwest and southeast sections were 0.11 (CI: 0.08-0.14) and 0.22 (CI: 0.20-0.24), respectively, and overlap estimates of activity between sounders and deer in the northwest section and southeast sections were 0.58 (CI: 0.54-0.62) and 0.79 (CI: 0.77-0.81), respectively.

DISCUSSION

Our results suggest that wild pigs influence presence of wild turkey at baited camera sites. There was a consistent trend in greater use of baited sites when wild pigs were absent. More specifically, because the covariate “sounders” was present in our best performing models to explain turkey use and detection probabilities, our data suggest that sounders have a greater impact on turkey presence than individual wild pigs. No previous published data have reported such a relationship. It is possible that wild pigs are competing with wild turkeys through interference or exploitative competition (Barrett 1978, McShea and Schwede 1993, Tolleson et al. 1995), or directly through agonistic behavior. Korschgen (1967) estimated that a medium-sized wild pig will consume ten times as much food as a medium-sized turkey, and sounders will consume greater amounts of food than a single wild pig or smaller group (e.g. bachelor group). It is possible that the difference we found in site use and detection probabilities is due to exploitative competition where sounders were able to locate and consume the corn at baited sites before wild turkeys located the sites. Wild pigs are known to consume large amounts of food resources (e.g. corn or acorns; Elston and Hewitt 2010) that may have been otherwise available to wild turkeys. Additionally, wild pigs are also known to display agonistic behavior toward other species, specifically, aggressively protecting food resources from species such as white-tailed deer (Taylor and Hellgren 1997). It is possible that wild pig sounders may have been displaying this agonistic behavior, although we were not able to observe it in our images. Finally, wild pigs are known to predate nests of ground-nesting species including upland game birds like northern bobwhite (*Colinus virginianus*) and turkeys (Rollins and Carroll 2001, Dreibelbis et al. 2008, Perot 2011).

Deer site use and detection probabilities were influenced by the presence of wild pigs. Though not statistically significant, differences in site use estimates between where wild pigs were present and where wild pigs were absent indicate there may be interference or exploitative competition between white-tailed deer and wild pigs. Additionally, the difference in detection probabilities between sites where wild pigs were present and wild pigs were absent was statistically significant and further supports the belief that there is competition between these two species. Contrary to our findings with turkeys, which were more sensitive to the presence of a sounder, the presence of any wild pig, regardless of age class, sex, or group size, negatively impacted white-tailed deer. Keever (2014) and Price Tack (2017) indicated that when estimating white-tailed deer abundance in their studies, wild pigs negatively influenced their results, and both speculated that interference competition was the cause. Taylor and Hellgren (1997) reported that wild pigs aggressively exclude deer from food resources, and Barrett (1982) reported that deer are passive during confrontations with wild pigs. It is possible that aggressive exclusion occurred in our study and caused the stark difference in detection probabilities between sites with and without wild pigs. Additionally, wild pigs may have negatively influenced the use of bait sites by deer due to their efficiency at locating and consuming bait. Further, our results may have been partially influenced by the timing of fawn births in Alabama: the peak of conception for white-tailed deer on LWMA is 13 August (C.W. Cook, Alabama Division of Wildlife and Freshwater Fisheries, unpublished data). The majority of adult female deer would have been pregnant, fawning, or with a newborn fawn during our camera surveys, and may have avoided baited sites where wild pigs were present to a greater degree because of competitive exclusion or risk to fawns (Ditchkoff and Mayer 2009, Conner et al. 2016).

Although numerous studies (Seward et al. 2004, Elston and Hewitt 2010, Jolley et al. 2010,) have speculated that wild pigs negatively impact wild turkeys and deer, removal of entire sounders in the northwest section did not affect use of, or detection at, baited sites by turkeys or deer. Though we did not detect a change in turkey or deer behavior following our removal efforts, other studies have found a positive effect on populations of native species after wild pig removal. Donlan et al. (2007) found that Galápagos rail (*Laterallus spilonotus*) populations increased from 18 to 279 in the years following eradication of wild pigs on Santiago Island. Similarly, the Lord Howe Island woodhen (*Hypotaenidia sylvestris*) recovered after some intervention when wild pigs were eradicated and woodhen were reintroduced (Miller and Mullette 1985). It is possible that our removals had a positive influence on turkey and deer populations, but our study did not extend long enough to capture the effects. Our study only extended one nesting season following eradication of pigs in the northwest section. Similarly, we may not have seen an effect of our removals on deer because our data did not capture any fawning periods when there were zero sounders present in the northwest section. Many of the studies that have documented recovery of native populations following eradication of an invasive species have required more than one season of data after complete eradication to detect an effect (Cruz et al. 2005, Donlan et al. 2007, Aguirre-Muñoz et al. 2011).

Despite not detecting a change in turkey site use following wild pig removals, we did find that timing of turkey activity changed in response to our whole sounder removal program. There was a distinct shift to morning activity of turkeys in the northwest section following pig removal, but this shift was not apparent in the southeast section. This shift of activity suggests that wild turkeys may have avoided baited camera sites during morning hours due to the potential of encountering pigs. Gonnerman (2017) and Stewart (2019) both reported elevated activity of female turkeys at baited sites in the morning, further suggesting that avoidance of bait sites in the morning may have been due to wild pigs. Wild turkey activity relative to wild pigs has not been studied before now, but wild pigs are known to affect other species. Wild pigs have been shown to affect the temporal activity of white-lipped peccaries (*Tayassu peccari*) around fruit trees (Galetti et al. 2015). The authors suggested that this shift was due to wild pigs actively defending this food resource. While we cannot confirm that the temporal shift in wild turkeys was because of any agonistic behaviors by wild pigs, the data suggest that wild turkeys were excluded from the baited sites. If this is common, then wild turkeys may also be excluded from other nutritionally important pulse resources such as hard mast, etc.

While deer may have avoided sites where wild pigs were present, we did not find evidence that timing of deer use of baited sites changed in response to wild pig removal. Thus, deer and wild pigs may have displayed greater spatial than temporal partitioning at our baited sites. However, it is possible that wild pigs have little effect on white-tailed deer when resources are abundant because the two species may display niche partitioning similar to how Ilse and Hellgren (1995) found that wild pigs and collared peccaries partition space use between wet and dry areas. Additionally, we may not have detected temporal partitioning between deer and wild pigs because deer were able to utilize baited sites where wild pigs were absent or waited until wild pigs left bait to approach. The latter theory aligns with Barret's (1982) finding that white-tailed deer defer to wild pigs at common food sources. Higdon et al. (2019) similarly found no temporal partitioning of adult deer and coyotes, but they did find greater differences in activity between nursery groups and coyotes. That study may indicate that it is important to examine sex and age class differences in activity between deer and wild pigs.

MANAGEMENT IMPLICATIONS

Our study covered general deer and turkey interactions with wild pigs and wild pig sounders through two general facets of analysis. The extent of impacts of wild pigs on deer and turkey may be greater at a more refined scale (e.g. impacts of wild pigs on different age classes of turkey). Therefore, more detailed studies are needed to navigate the relationship between wild pigs, deer, and turkey. We do, however, believe that removal of wild pigs would positively impact deer and turkey populations. Declines in turkey populations throughout the Southeast have been recently documented (Bryne et al. 2012, ADCNR 2015, Eriksen et al. 2016), and it is possible that these declines are at least partially due to increasing wild pig populations (Snow et al. 2017). If wild pig removal were to positively impact deer and turkey, these impacts could extend to economic benefits for state wildlife agencies and wildlife conservation. Examples of benefits include increased initiative to remove wild pigs, increased hunting opportunity for deer and turkey, and increased wildlife viewing opportunities. This impact may also extend to inherent cultural value of deer, turkey, and other native wildlife.

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Table 2.1 Comparison of detection (*p*) and use (psi; Ψ) models for wild turkey using camera trap surveys on Lowndes Wildlife Management Area in Alabama, summer 2015-2018. For each model, values for AICc, difference in AICc (ΔAICc), model probability (*w*), number of parameters (K), and deviance are shown.

Model	AICc	ΔAICc	*w*	K
p(Section + Sounder)Psi(Section + Sounder + Year)	1536.13	0.00	0.14	11
p(Section + Sounder)Psi(Section)	1536.43	0.29958	0.12	6
p(Sounder)Psi(Section + Sounder + Year)	1536.71	0.58095	0.1	10
p(Section + Sounder)Psi(.)	1537.14	1.00851	0.08	5
p(Section + Sounder)Psi(Section + Year)	1537.4	1.27635	0.07	9
p(Section + Sounder)Psi(Sounder + Year)	1537.59	1.46625	0.07	10
p(Sounder)Psi(Section)	1537.73	1.60141	0.06	5
p(Section + Sounder)Psi(Section + Sounder)	1538.55	2.42121	0.04	8
p(Sounder)Psi(Section + Year)	1538.55	2.42651	0.04	8
p(Section + Sounder)Psi(Year)	1538.57	2.44181	0.04	8
p(Sounder)Psi(Sounder + Year)	1538.79	2.65915	0.04	9
p(Section + Sounder)Psi(Sounder)	1539.04	2.90775	0.03	7
p(Sounder)Psi(Section + Sounder)	1539.15	3.02645	0.03	7
p(Sounder)Psi(.)	1539.44	3.31457	0.03	4
p(Sounder)Psi(Sounder)	1540.14	4.00908	0.02	6
p(Sounder)Psi(Year)	1540.72	4.59445	0.01	7
p(Section + Sounder + Year)Psi(Section)	1541.35	5.22245	0.01	9
p(Section + Sounder + Year)Psi(Section + Sounder + Year)	1541.55	5.42152	0.01	14
p(Section + Sounder + Year)Psi(.)	1541.9	5.76781	0.01	8
p(Sounder + Year)Psi(Section + Sounder + Year)	1542.01	5.88494	0.01	13
p(Section + Sounder + Year)Psi(Section + Year)	1542.58	6.4481	0.01	12
p(Sounder + Year)Psi(Section)	1542.84	6.71451	0	8
p(Section + Sounder + Year)Psi(Sounder + Year)	1542.94	6.81144	0	13
p(Section + Sounder + Year)Psi(Year)	1543.71	7.5867	0	11
p(Sounder + Year)Psi(Section + Year)	1543.83	7.7014	0	11
p(Sounder + Year)Psi(Sounder + Year)	1544.02	7.8878	0	12
p(Section + Sounder + Year)Psi(Section + Sounder)	1544.15	8.0208	0	11
p(Sounder + Year)Psi(.)	1544.37	8.24375	0	7
p(Section + Sounder + Year)Psi(Sounder)	1544.57	8.43785	0	10
p(Sounder + Year)Psi(Section + Sounder)	1544.78	8.65575	0	10
p(Sounder + Year)Psi(Sounder)	1545.71	9.58215	0	9
p(Sounder + Year)Psi(Year)	1545.99	9.86525	0	10

p(Year)Psi(Section + Sounder + Year)	1550.94	14.8098	0	11
p(Section + Year)Psi(Section + Sounder + Year)	1552.68	16.5501	0	12
p(Year)Psi(Sounder + Year)	1553.1	16.9732	0	10
p(Year)Psi(Section + Sounder)	1553.2	17.071	0	8
p(Year)Psi(Section)	1554.03	17.9037	0	6
p(Year)Psi(Sounder)	1554.24	18.1164	0	7
p(Section + Year)Psi(Sounder + Year)	1554.67	18.538	0	11
p(.)Psi(Section + Sounder + Year)	1554.83	18.7045	0	8
p(Section + Year)Psi(Section + Sounder)	1554.89	18.7616	0	9
p(Year)Psi(Section + Year)	1555.07	18.9425	0	9
p(Section + Year)Psi(Section)	1555.69	19.5576	0	7
p(Section + Year)Psi(Sounder)	1555.78	19.6507	0	8
p(Year)Psi(.)	1556.53	20.4045	0	5
p(Section + Year)Psi(Section + Year)	1556.79	20.6569	0	10
p(Section)Psi(Section + Sounder + Year)	1556.86	20.7337	0	9
p(.)Psi(Sounder + Year)	1557.06	20.9295	0	7
p(.)Psi(Section + Sounder)	1557.31	21.1827	0	5
p(Year)Psi(Year)	1557.88	21.7511	0	8
p(Section + Year)Psi(.)	1558	21.8669	0	6
p(.)Psi(Section)	1558.25	22.1265	0	3
p(.)Psi(Sounder)	1558.41	22.2842	0	4
p(Section)Psi(Sounder + Year)	1559.01	22.8819	0	8
p(.)Psi(Section + Year)	1559.04	22.9098	0	6
p(Section)Psi(Section + Sounder)	1559.29	23.1644	0	6
p(Section + Year)Psi(Year)	1559.41	23.2803	0	9
p(Section)Psi(Section)	1560.2	24.073	0	4
p(Section)Psi(Sounder)	1560.33	24.2	0	5
p(.)Psi(.)	1560.82	24.6882	0	2
p(Section)Psi(Section + Year)	1561.03	24.9047	0	7
p(.)Psi(Year)	1561.9	25.7761	0	5
p(Section)Psi(.)	1562.68	26.5561	0	3
p(Section)Psi(Year)	1563.82	27.6891	0	6

Table 2.2 Site use probabilities (Ψ) of wild turkeys on Lowndes Wildlife Management Area in Alabama using single season single species occupancy modeling in RMark. Model averages use covariates of section (northwest or southeast section of the study area) and year.

Estimate (Ψ)	Standard error	Lower confidence limit (95%)	Upper confidence limit (95%)	Section	Year	Sounder
0.28205	0.08986699	0.14134943	0.4838816	NW	2015	No
0.27586	0.07763337	0.15099722	0.4493265	NW	2016	No
0.19806	0.06015193	0.10520093	0.3415942	NW	2017	No
0.20314	0.06360968	0.10555748	0.3551236	NW	2018	No
0.17278	0.09495485	0.05374645	0.4343961	NW	2015	Yes
0.26197	0.10926815	0.10494517	0.5179742	NW	2016	Yes
0.18461	0.07248311	0.08097618	0.3678044	NW	2017	Yes
0.13378	0.08862703	0.03334522	0.4087911	NW	2018	Yes
0.20633	0.06877108	0.10245377	0.3718986	SE	2015	No
0.20154	0.06287967	0.10502964	0.351866	SE	2016	No
0.14238	0.05348624	0.06573277	0.2814768	SE	2017	No
0.20314	0.06360968	0.10555748	0.3551236	SE	2018	No
0.12422	0.07317099	0.03656875	0.3464224	SE	2015	Yes
0.18991	0.08266349	0.07560074	0.401923	SE	2016	Yes
0.13119	0.05665947	0.05392401	0.2857396	SE	2017	Yes
0.0967	0.06889165	0.02230792	0.3343377	SE	2018	Yes

Table 2.3 Detection probabilities (*p*) of eastern wild turkey on Lowndes Wildlife Management Area in Alabama using single season single species occupancy modeling in RMark. Model averages use covariates of section (northwest or southeast section of the study area), year, and the presence or absence of sounders at the site.

Estimate (*p*)	Standard error	Lower confidence limit (95%)	Upper confidence limit (95%)	Section	Year	Sounder
0.07513	0.01099191	0.05622279	0.09971116	NW	2015	No
0.12221	0.01496836	0.09577288	0.15470612	NW	2016	No
0.12115	0.01567116	0.09363736	0.15537201	NW	2017	No
0.07586	0.01125475	0.05653785	0.10107562	NW	2018	No
0.03307	0.01229727	0.01583838	0.0677506	NW	2015	Yes
0.03365	0.01146102	0.01715495	0.06496824	NW	2016	Yes
0.0333	0.01113778	0.01718569	0.06355536	NW	2017	Yes
0.03345	0.01334022	0.01518283	0.07209384	NW	2018	Yes
0.0627	0.01105034	0.04422522	0.08817425	SE	2015	No
0.1027	0.01382624	0.07859591	0.13314038	SE	2016	No
0.10181	0.01453253	0.07665112	0.13402995	SE	2017	No
0.06333	0.01135602	0.04439402	0.08957894	SE	2018	No
0.02774	0.01204653	0.01174783	0.06408424	SE	2015	Yes
0.0282	0.01137039	0.01270199	0.06141888	SE	2016	Yes
0.02791	0.01112475	0.01268849	0.0602661	SE	2017	Yes
0.02807	0.01294528	0.01126738	0.06820595	SE	2018	Yes

Table 2.4 Comparison of detection (*p*) and use (psi; Ψ) models for white-tailed deer using camera trap surveys on Lowndes Wildlife Management Area in Alabama, summer 2015-2018. For each model, values for AICc, difference in AICc (ΔAICc), model probability (*w*), and number of parameters (K).

Model	AICc	ΔAICc	*w*	K
p(Section + Pigs + Year)Psi(Pigs)	15960.95	0.00	0.31	8
p(Section + Pigs + Year)Psi(Section + Pigs)	15961.4	0.4491345	0.25	9
p(Section + Pigs + Year)Psi(Pigs + Year)	15961.53	0.5823912	0.24	11
p(Section + Pigs + Year)Psi(Section + Pigs + Year)	15961.99	1.0379038	0.19	12
p(Section + Pigs + Year)Psi□Section)	15969.29	8.342	0.00	8
p(Section + Pigs + Year)Psi(.)	15970.17	9.2202726	0.00	7
p(Section + Pigs + Year)Psi(Section + Year)	15970.59	9.6443912	0.00	11
p(Section + Pigs + Year)Psi(Year)	15971.56	10.611867	0.00	10
p(Section + Pigs)Psi(Pigs)	16006.86	45.9112907	0.00	5
p(Section + Pigs)Psi(Section + Pigs)	16007.26	46.3117645	0.00	6
p(Section + Pigs)Psi(Pigs + Year)	16007.29	46.346	0.00	8
p(Section + Pigs)Psi(Section + Pigs + Year)	16007.7	46.7511345	0.00	9
p(Pigs + Year)Psi(Pigs)	16012.71	51.7642726	0.00	7
p(Pigs + Year)Psi(Section + Pigs)	16013.12	52.177	0.00	8
p(Pigs + Year)Psi(Pigs + Year)	16013.25	52.303867	0.00	10
p(Pigs + Year)Psi(Section + Pigs + Year)	16013.67	52.7233912	0.00	11
p(Section + Pigs)Psi(Section)	16015.22	54.2722907	0.00	5
p(Section + Pigs)Psi(.)	16016.15	55.197669	0.00	4
p(Section + Pigs)Psi(Section + Year)	16016.38	55.428	0.00	8
p(Pigs + Year)Psi(Section)	16021.01	60.0642726	0.00	7
p(Pigs + Year)Psi(.)	16021.94	60.9947645	0.00	6
p(Pigs + Year)Psi(Section + Year)	16022.27	61.323867	0.00	10
p(Pigs + Year)Psi(Year)	16023.29	62.3461345	0.00	9
p(Pigs)Psi(Pigs)	16068.95	108.004669	0.00	4
p(Pigs)Psi(Section + Pigs)	16069.33	108.3782907	0.00	5
p(Pigs)Psi(Section + Pigs + Year)	16069.72	108.773	0.00	8
p(Section + Year)Psi(Pigs)	16074.28	113.3352726	0.00	7
p(Section + Year)Psi(Section + Pigs)	16074.71	113.767	0.00	8
p(Section + Year)Psi(Pigs + Year)	16074.82	113.867867	0.00	10
p(Section + Year)Psi(Section + Pigs + Year)	16075.25	114.3053912	0.00	11
p(Pigs)Psi(Section)	16077.3	116.349669	0.00	4
p(Pigs)Psi(.)	16078.26	117.3107199	0.00	3

p(Pigs)Psi(Section + Year)	16078.41	117.4602726	0.00	7
p(Pigs)Psi(Year)	16079.46	118.5147645	0.00	6
p(Section + Year)Psi(Section)	16082.66	121.7152726	0.00	7
p(Section + Year)Psi(.)	16083.56	122.6147645	0.00	6
p(Section + Year)Psi(Section + Year)	16083.92	122.970867	0.00	10
p(Section + Year)Psi(Year)	16084.91	123.9611345	0.00	9
p(Section)Psi(Pigs)	16110.13	149.185669	0.00	4
p(Section)Psi(Section + Pigs)	16110.52	149.5682907	0.00	5
p(Section)Psi(Pigs + Year)	16110.52	149.5732726	0.00	7
p(Section)Psi(Section + Pigs + Year)	16110.91	149.96	0.00	8
p(Section)Psi(Section)	16118.51	157.566669	0.00	4
p(Section)Psi(.)	16119.46	158.5137199	0.00	3
p(Section)Psi(Section + Year)	16119.62	158.6762726	0.00	7
p(Section)Psi(Year)	16120.66	159.7157645	0.00	6
p(Year)Psi(Pigs)	16161.74	200.7897645	0.00	6
p(Year)Psi(Section + Pigs)	16162.15	201.2002726	0.00	7
p(Year)Psi(Pigs + Year)	16162.22	201.2751345	0.00	9
p(Year)Psi(Section + Pigs + Year)	16162.64	201.690867	0.00	10
p(Year)Psi(Section)	16170.11	209.1587645	0.00	6
p(Year)Psi(.)	16171.03	210.0812907	0.00	5
p(Year)Psi(Section + Year)	16171.31	210.3661345	0.00	9
p(Year)Psi(Year)	16172.33	211.381	0.00	8
p(Section + Pigs)Psi(Year)	16179.27	218.3172726	0.00	7
p(.)Psi(Pigs)	16205.92	244.9687199	0.00	3
p(.)Psi(Section + Pigs)	16206.28	245.332669	0.00	4
p(.)Psi(Section + Pigs + Year)	16206.63	245.6772726	0.00	7
p(.)Psi(Section)	16214.29	253.3437199	0.00	3
p(.)Psi(.)	16215.26	254.3102666	0.00	2
p(Pigs)Psi(Pigs + Year)	16255.55	294.5992726	0.00	7
p(.)Psi(Pigs + Year)	16453.33	492.3777645	0.00	6
p(.)Psi(Section + Year)	16459.41	498.4577645	0.00	6
p(.)Psi(Year)	16664.4	703.4502907	0.00	5

Table 2.5 Site use probabilities (Ψ) of white-tailed deer on Lowndes Wildlife Management Area in Alabama using single season single species occupancy modeling in RMark. Model averages use covariates of section (northwest or southeast section of the study area), year, and the presence or absence of pigs at the site.

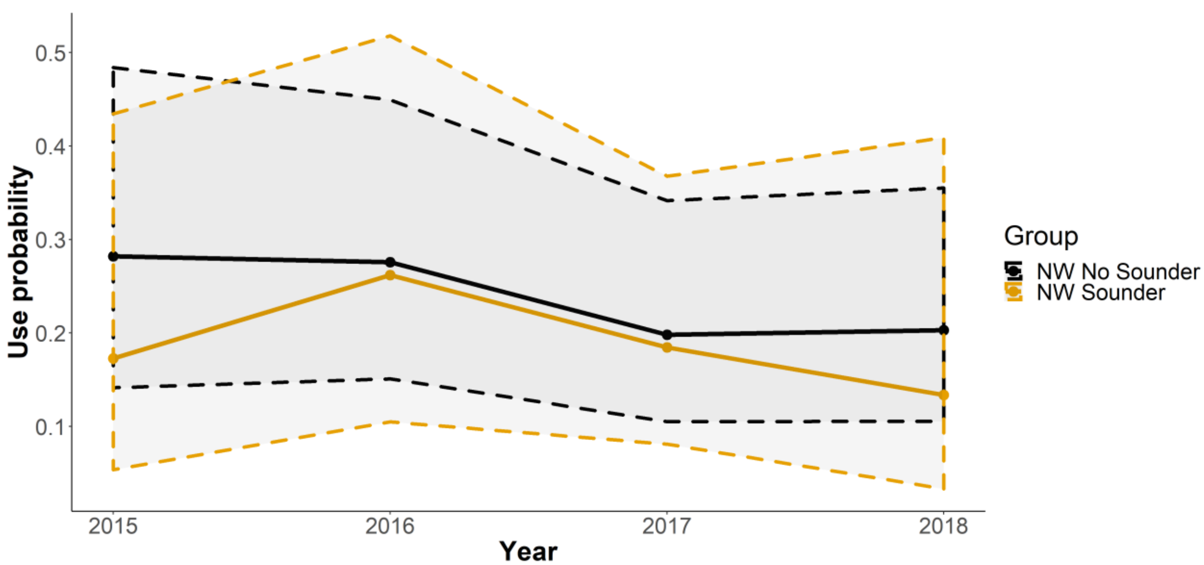
Estimate (Ψ)	Standard error	Lower confidence limit (95%)	Upper confidence limit (95%)	Section	Year	Pig
0.82751	0.04511368	0.720836	0.8991257	NW	2015	No
0.85907	0.05011441	0.7303275	0.9320652	NW	2016	No
0.80347	0.05913315	0.6624299	0.8949258	NW	2017	No
0.83499	0.04357467	0.7313666	0.9038967	NW	2018	No
0.65285	0.06800505	0.5108711	0.7720137	NW	2015	Yes
0.70792	0.07918112	0.5336372	0.8369724	NW	2016	Yes
0.61738	0.08712642	0.4391896	0.7687647	NW	2017	Yes
0.66497	0.06441291	0.5296763	0.77768	NW	2018	Yes
0.80211	0.05051301	0.6847735	0.8832149	SE	2015	No
0.83765	0.0565067	0.6956069	0.9209462	SE	2016	No
0.77565	0.06563884	0.6227393	0.8786564	SE	2017	No
0.81044	0.04904915	0.6957413	0.888808	SE	2018	No
0.61421	0.06318784	0.4856006	0.7286319	SE	2015	Yes
0.67296	0.07893655	0.5046554	0.8060511	SE	2016	Yes
0.57771	0.08371637	0.4111545	0.7282863	SE	2017	Yes
0.6269	0.05966545	0.5047455	0.7347652	SE	2018	Yes

Table 2.6 Detection probabilities (*p*) of white-tailed deer on Lowndes Wildlife Management Area in Alabama using single season single species occupancy modeling in RMark. Model averages use covariates of section (northwest or southeast section of the study area), year, and the presence or absence of pigs at the site.

Estimate (*p*)	Standard error	Lower confidence limit (95%)	Upper confidence limit (95%)	Section	Year	Pig
0.10009	0.00484177	0.090988965	0.109984444	NW	2015	No
0.10459	0.00451488	0.096068422	0.11377793	NW	2016	No
0.10504	0.00502459	0.0955961	0.1153079	NW	2017	No
0.13985	0.00544135	0.1295201	0.1508575	NW	2018	No
0.06365	0.00381916	0.056560627	0.071556711	NW	2015	Yes
0.06664	0.00351746	0.06006333	0.073869235	NW	2016	Yes
0.06694	0.00392762	0.05963615	0.07505646	NW	2017	Yes
0.09039	0.0043229	0.08226507	0.09922576	NW	2018	Yes
0.07403	0.00374898	0.067005412	0.081717718	SE	2015	No
0.07746	0.00388027	0.070188134	0.085414897	SE	2016	No
0.0778	0.00422761	0.06991199	0.0865049	SE	2017	No
0.10464	0.00495939	0.09530893	0.1147647	SE	2018	No
0.04658	0.00262161	0.041707224	0.052000581	SE	2015	Yes
0.04881	0.00258462	0.04398845	0.05413448	SE	2016	Yes
0.04904	0.00289182	0.04366907	0.05502484	SE	2017	Yes
0.06667	0.00329025	0.06049895	0.07341095	SE	2018	Yes

Figure 2.1 Model averaged probability of use (ψ) of eastern wild turkey on Lowndes Wildlife Management Area in Alabama with wild pig sounder presence, year, and section as covariates. (a) The northwest section (NW) was the wild pig removal area where pigs were removed between April 2015 and December 2017. (b) In the southeast section (SE), no pigs were removed. Solid lines are estimates and dotted lines incorporate a 95% confidence interval.

(a)



(b)

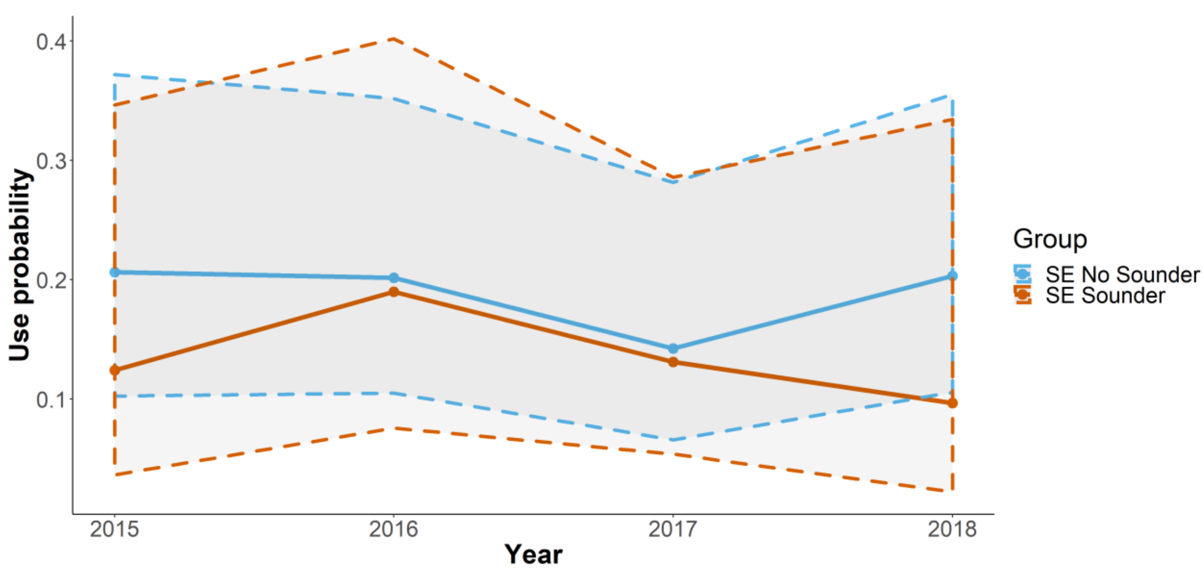
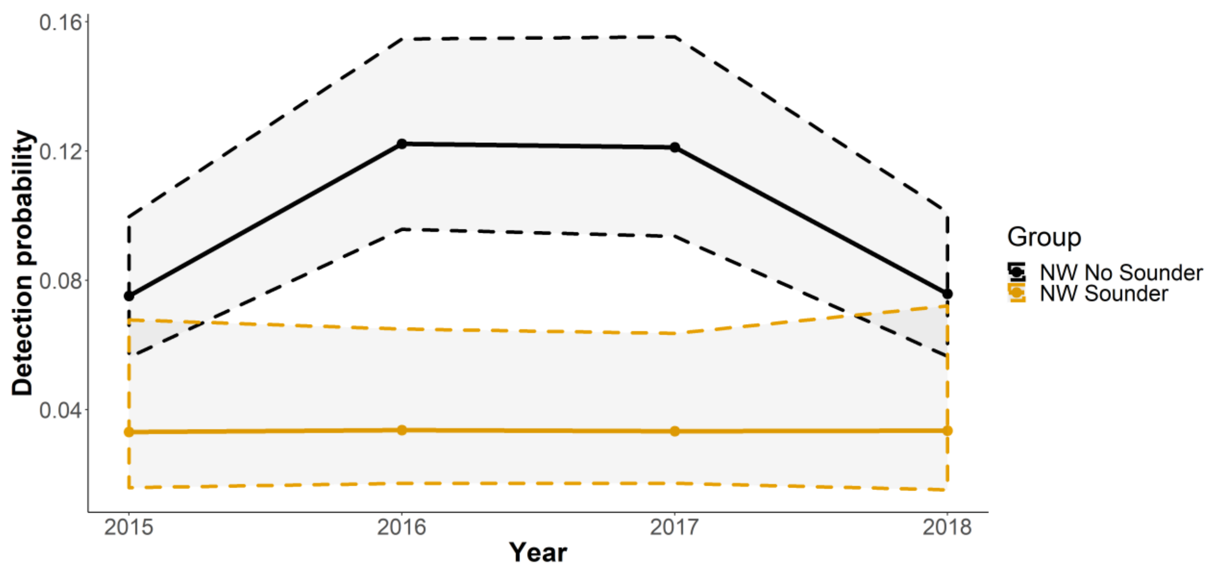


Figure 2.2 Model averaged probability of detection (*p*) of eastern wild turkey on Lowndes Wildlife Management Area in Alabama with wild pig sounder presence, year, and section as covariates. (a) The northwest section (NW) was the wild pig removal area where pigs were removed between April 2015 and December 2017. (b) In the southeast section (SE), no pigs were removed. Solid lines are estimates and dotted lines incorporate a 95% confidence interval.

(a)



(b)

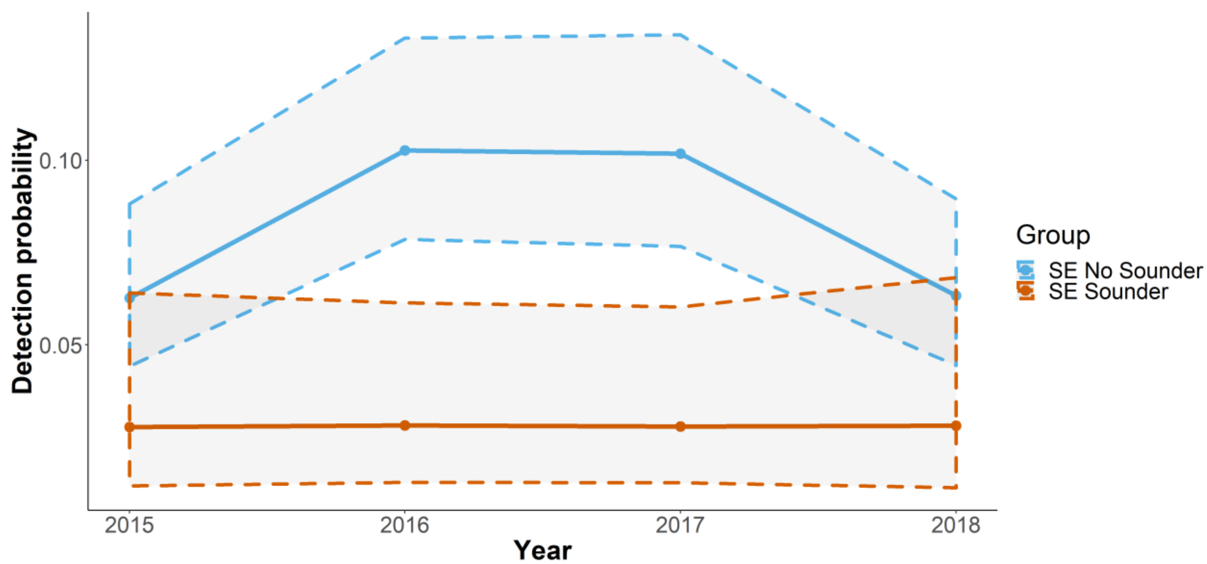
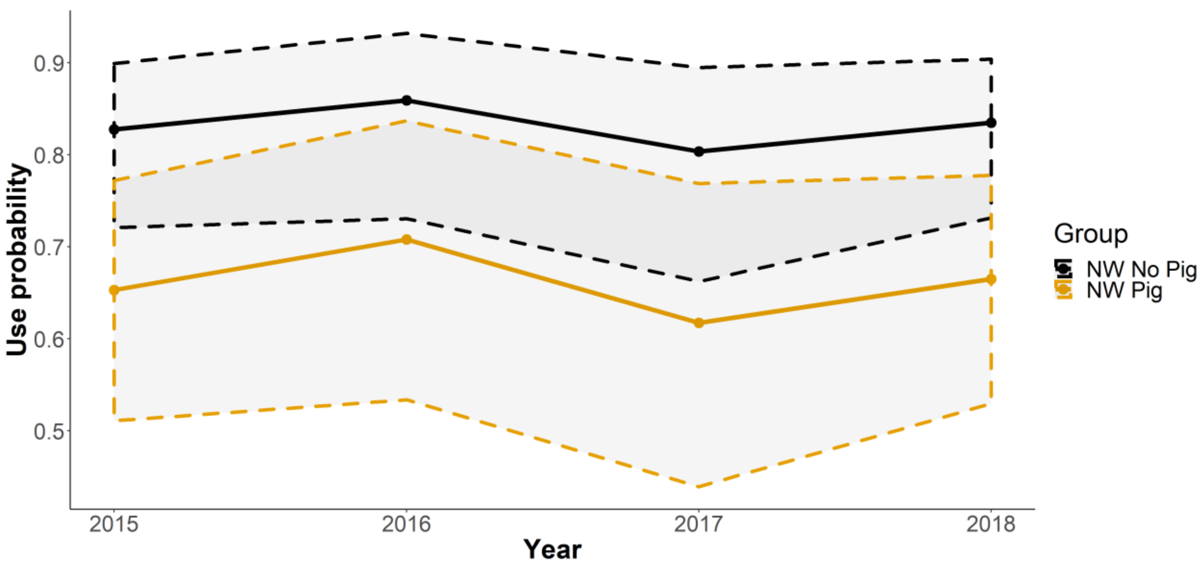


Figure 2.3 Model averaged probability of use (ψ) of white-tailed deer on Lowndes Wildlife Management Area in Alabama with wild pig sounder presence, year, and section as covariates. (a) The northwest section (NW) was the wild pig removal area where pigs were removed between April 2015 and December 2017. (b) In the southeast section (SE), no pigs were removed. Solid lines are estimates and dotted lines incorporate a 95% confidence interval.

(a)



(b)

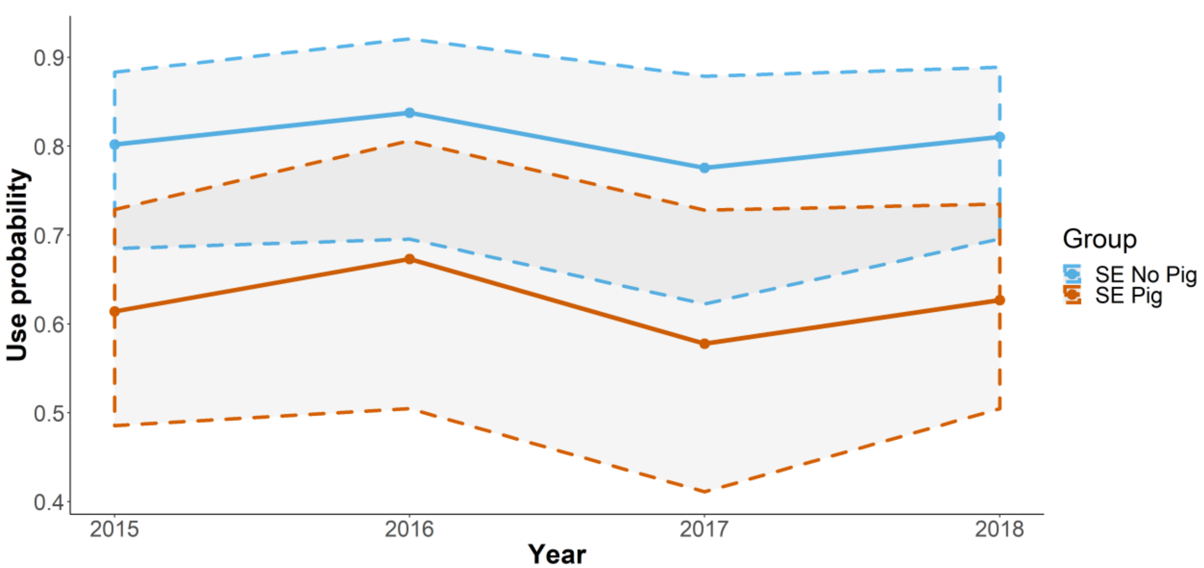
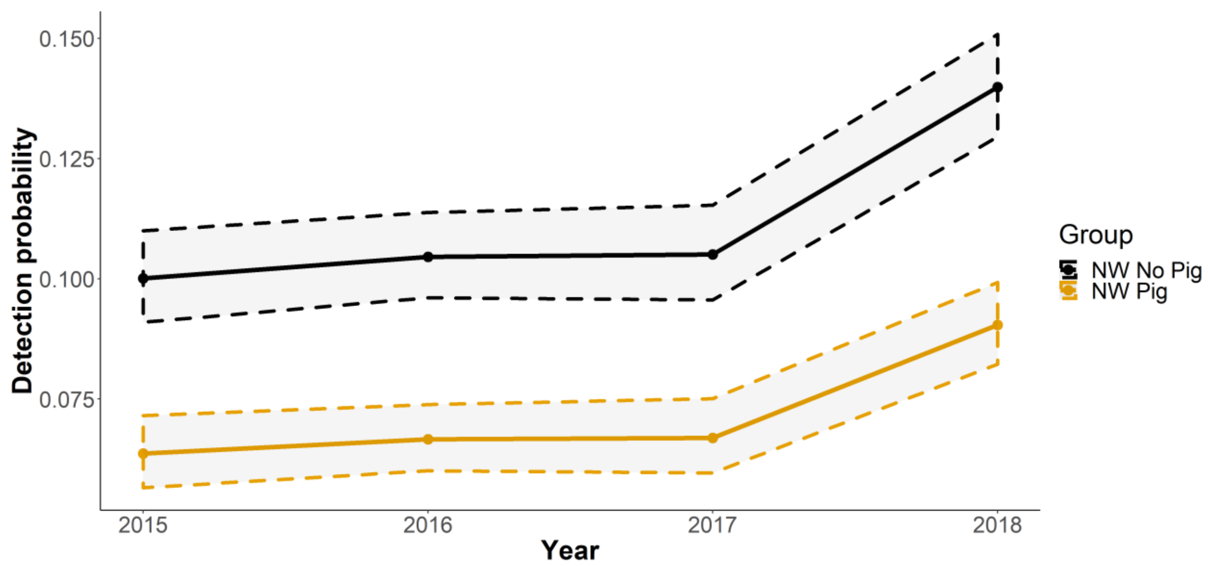


Figure 2.4 Model averaged probability of detection (*p*) of white-tailed deer on Lowndes Wildlife Management Area in Alabama with wild pig sounder presence, year, and section as covariates. (a) The northwest section (NW) was the wild pig removal area where pigs were removed between April 2015 and December 2017. (b) In the southeast section (SE), no pigs were removed. Solid lines are estimates and dotted lines incorporate a 95% confidence interval.

(a)



(b)

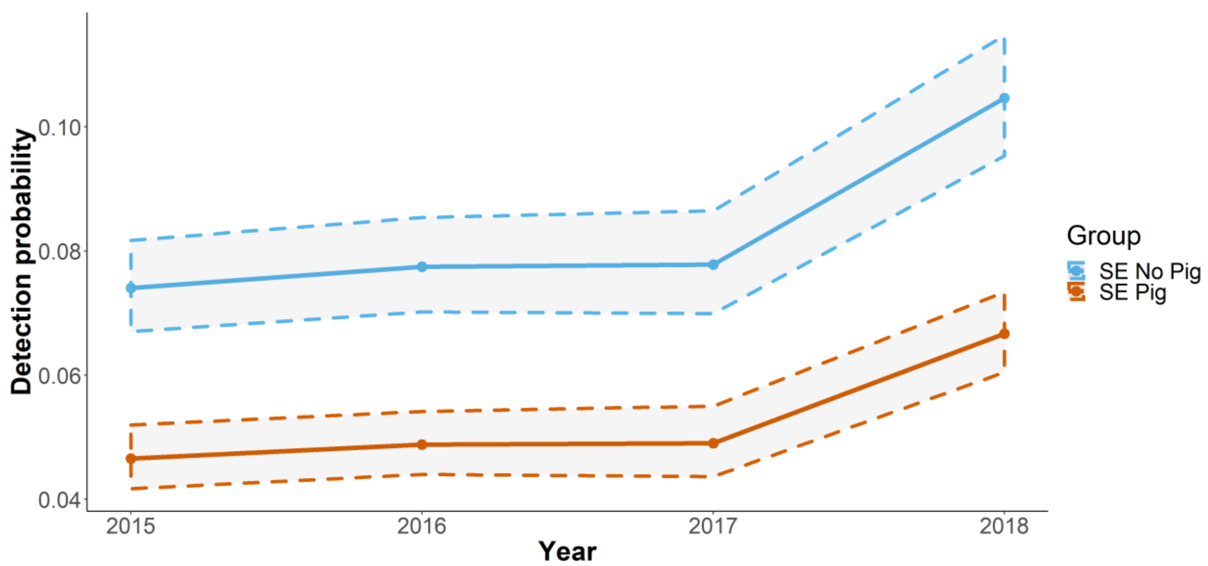


Figure 2.5 Activity patterns of wild pigs, white-tailed deer, and wild turkey in the northwest section (NW) of Lowndes Wildlife Management Area in Alabama during week-long trail camera surveys in July-August of 2015, 2016, 2017, and 2018. Wild pig sounders were removed between April 2015 and December 2017. (a) Period 1, 2015, there was a 35% total decrease in wild pigs (b) Period 2, 2016, there was a 86% total decrease in wild pigs (c) Period 3, 2017, there was a 72% total decrease in wild pigs (d) Period 4, 2018, there was a 92% total decrease in wild pigs.

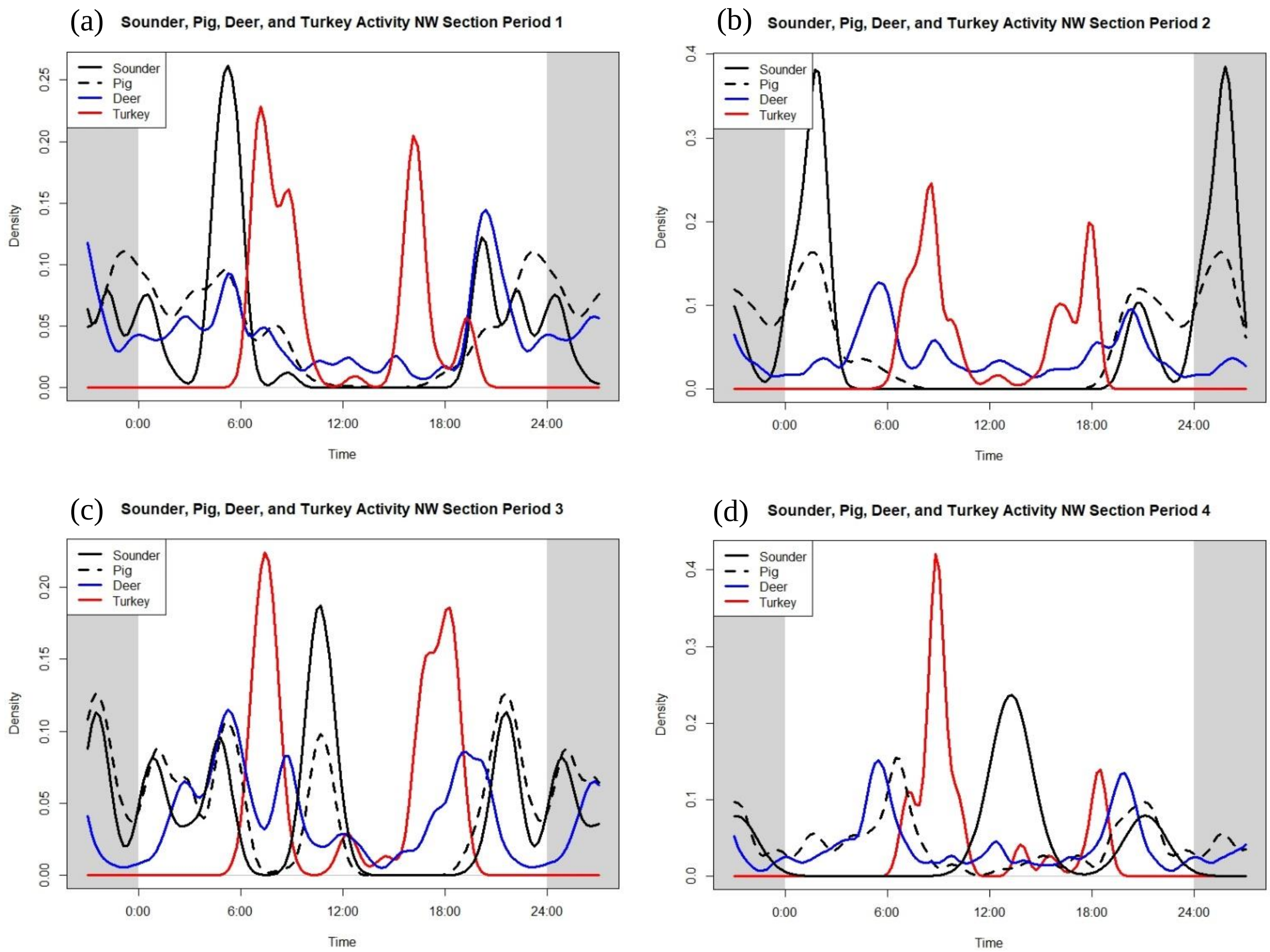
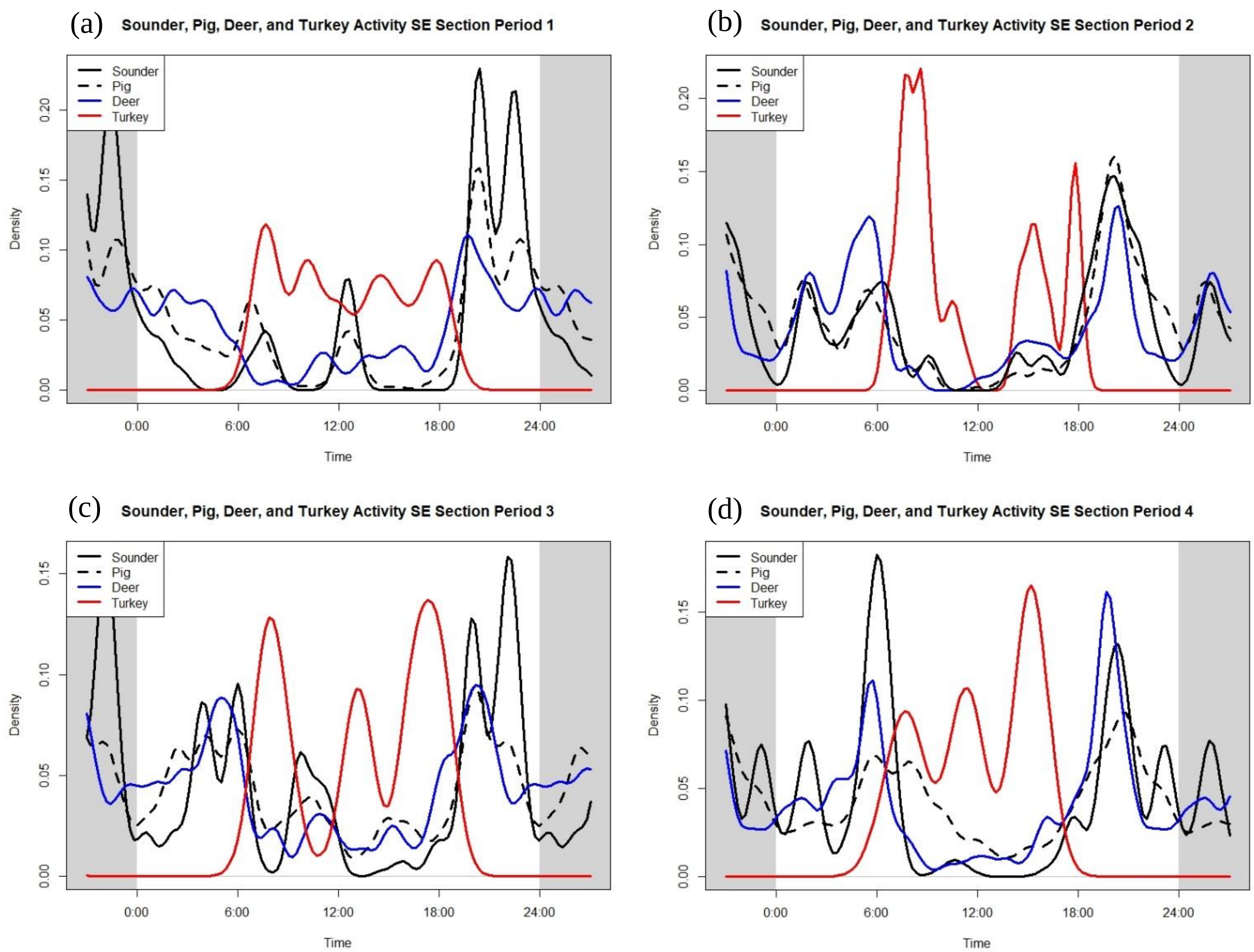


Figure 2.6 Activity patterns of wild pigs, white-tailed deer, and wild turkey in the southeast section (SE) of Lowndes Wildlife Management Area in Alabama during week-long trail camera surveys in July-August of 2015, 2016, 2017, and 2018. Wild pigs were not removed in the southeast section. (a) Period 1, 2015, there was a 4% total increase in wild pigs (b) Period 2, 2016, there was a 40% total increase in wild pigs (c) Period 3, 2017, there was a 70% total increase in wild pigs (d) Period 4, 2018, there was a 91% total increase in wild pigs.



Appendix

Table A.1. Wild pig removals on Lowndes WMA from May 2015 to December 2017.

			Age and sex				
Sounder	Date	No. removed	AF[1]	AM[2]	JF[3]	JM[4]	Unknown
LT01	5/19/15	9	2	-	-	-	7
LT02	7/15/15	5	1	-	-	4	-
LT03	7/22/15	8	-	-	4	4	-
	5/7/16	6	-	-	4	2	-
	5/16/16	3	2	1	-	-	-
	7/31/17	6	1	-	1	4	-
LT04	8/12/15	7	-	-	5	2	-
	12/14/17	9	2	2	3	2	-
LT05	8/14/15	4	1	-	2	1	-
LT06	8/31/15	7	1	-	4	2	-
LT07	10/19/15	3	-	-	1	2	-
	11/29/16	1	1	-	-	-	-
LT08	4/21/16	8	1	-	5	2	-
LT09	5/27/16	7	4	-	-	3	-
	6/2/16	6	-	-	3	3	-
	3/17/17	6	-	-	4	2	-
NA[5]	9/17/15	1	1	-	-	-	-
NA	9/25/15	1	-	1	-	-	-
NA	10/18/16	1	-	1	-	-	-

NA	2/4/17	3	-	-	-	3	-
NA	10/5/17	1	-	1	-	-	-
NA	10/5/17	1	-	1	-	-	-
NA	11/8/17	1	-	1	-	-	-
NA	12/8/17	1	-	1	-	-	-

[1]Adult females

[2]Adult males

[3]Juvenile females

[4]Juvenile males

[5]Not associated with a previously identified sounder