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ABSTRACT: In the United States, costs of wild pig damage to natural resources and control exceed $1.5 billion annually. Aerial gunning from helicopters can rapidly reduce wild pig populations, and understanding wild pig behavioral response to aerial gunning may offer insight into control measures to enhance efficacy of removal campaigns. We used camera trapping to quantify wild pig detection rates and activity patterns during four periods (Before, During, After, and Long After i.e., approximately one month after cessation) associated with a helicopter aerial gunning campaign that took place only during daylight hours. Relative to Before aerial gunning, daytime wild pig detection rates among study periods were similar but nighttime detection rates declined During, After, and Long After gunning. However, wild pig detection rates within closed canopy forests increased During and After the campaign relative to Before, suggesting that aerial gunning increased wild pig preference for overhead cover. There were nuanced differences in wild pig activity patterns among study periods, likely because pigs were largely nocturnal before the study began. Despite these differences, ground-based hunting efforts just before dawn and after dusk within closed canopy forests may increase pig removals during aerial gunning campaigns by reducing 'safe times' and 'safe places.'

KEY WORDS: aerial gunning, animal behavior, anti-predator behavior, invasive species, predation risk, *Sus scrofa*, wild pig

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INTRODUCTION

Wild pigs (*Sus scrofa*) are listed as one of the top 100 most invasive species globally and are found on all continents except Antarctica (Barrios-Garcia and Ballari 2012, Global Invasive Species Database 2022). Spanish explorers introduced wild pigs to North America in the 1500s. Subsequent releases, regular escapes from enclosures, and free-range grazing practiced until the 1900s, led to widespread wild pig populations (Graves 1984). In the southeastern United States, Eurasian boar were sometimes used to stock hunting preserves, while domestic or feral swine have been translocated illegally for hunting purposes (Hansen and Karstad 1959, Hernández et al. 2018, McCann et al. 2018). In 2021, wild pigs were reported in 31 states (APHIS National Feral Swine Damage Management Program 2022). In the United States, wild pig numbers increased from 2.4 million in 1982 to approximately 6.9 million in 2016 (Lewis et al. 2019). Economic losses were approximately $1.5 billion annually in 2007 (Pimentel 2007); more recent but localized estimates (Anderson et al. 2016, McKee et al. 2020, Mengak 2016) suggest severe local impact.

Costs associated with removing wild pigs from private land are high (Anderson et al. 2016). Common methods of control often include corral trapping, drop netting, snares (in some states), poisoning (outside of the United States), using Judas pigs, and/or aerial gunning (Massei et al. 2011, Anderson et al. 2016). The cost of wild pig removal varies among removal techniques. For example, Bodenchuk (2014) reported a cost of $62.51/pig removed using snares as opposed to $18.27/pig removed using aerial gunning. Although efficacy of aerial gunning for wild pig removal and effects of aerial gunning on wild pig movements have been studied (Saunders and Bryant 1988, Lombardo and Faulkner 1999, Campbell et al. 2010, Parkes et al. 2010, Davis et al. 2018), pig diel activity and landcover use in response to aerial gunning has received little research effort, especially in a landscape consisting of an approximately equal mix of row crop and forests where high pig densities create much conflict with humans (Lewis et al. 2017, Boyce et al. 2020). Understanding wild pig behavioral responses to aerial gunning may prove useful for devising more holistic pig control protocols that enhance efficacy of aerial gunning.

To quantify effects of aerial gunning on wild pig behavior, we used camera trapping to monitor wild pigs' diel activity patterns and use of closed and open canopy forest in southwestern Georgia, U.S.A. in association with

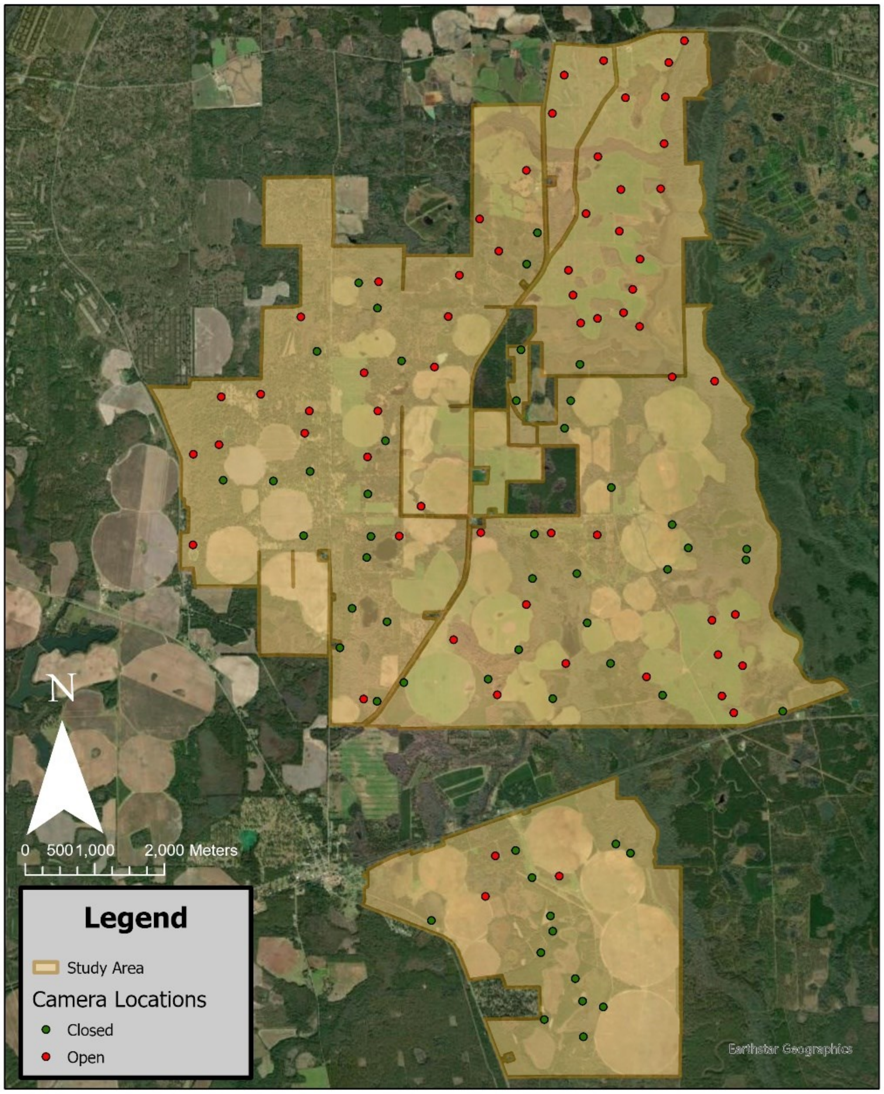

Figure 1. Map of camera locations (n = 114) across our study area in Calhoun, County, Georgia. Camera locations are separated into closed canopy (green circles) and open canopy (red circles) cover types.

an aerial gunning campaign. Because aerial gunning only occurred during daylight, we expected pigs to be more active at night during and after aerial gunning. We predicted that pig use of closed canopy forests would be greater during and after gunning than before gunning as we assumed closed canopy forests provided cover from aerial gunning.

METHODS

Study Area

The 70.6 km^2 study area included three private properties in Calhoun County, Georgia (Figure 1) with abundant wild pig populations. Dominant landcover types included row crops (36%), forested wetlands (32%), pecan (*Carya illinoinensis*) orchard (13%), pine forests consisting of longleaf (*Pinus palustris*) and loblolly pine (*P. taeda*; 13%), and mixed hardwood-pine (3%), with the remainder of the area consisting of scattered wildlife openings and riparian areas. Row crops were predominately corn (*Zea mays*), cotton (*Gossypium sp.*), and peanuts (*Arachis hypogaea*). Summer daily temperature averaged 34°C and winter daily temperature averaged 17°C. Monthly precipitation in summer averaged 150.6 mm and 100.8 mm in winter (U.S. Climate Data 2022). Elevation across the landscape ranged from 53.5 m to 79.8 m above sea level.

Helicopter Operations

Authorized United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Wildlife Services personnel conducted aerial gunning from a Hughes OH-6 helicopter on 11 days between 18 January and 4 February 2021, with efforts focused on the study area and neighboring properties. Flights followed detailed protocols outlined in the Wildlife Services Aviation Safety and Operation Manual (2021) for flight duration, weather conditions, helicopter maintenance, etc. The gunner used a 12-ga shotgun and non-toxic shot. The removal team recorded helicopter flights paths using onboard

GPS via the Map Plus app (App Store Preview Map Plus 2022). The app documented duration of flight as well as longitude and latitude; these data were used to quantify actual flight time over the study area. When possible, the aircraft herded wild pigs to open areas for ease of removal. Wildlife Services personnel carried out removal efforts in accordance with the Wildlife Services Aviation Safety and Operations Manual (2021). As Wildlife Services personnel conducted wild pig removal efforts, this portion of the study was exempt from Institutional Animal Care and Use Committee (IACUC) approval.

Data Collection

We conducted passive camera trapping surveys using Browning Strike Force HD Pro X (Morgan, UT) motion triggered IR cameras. To determine camera locations, we overlaid 40-ha cells onto the study area. Within each cell, we located a well-defined wildlife trail and deployed a single camera approximately 1.5 m from the trail and 1.0 m above the ground. Active agricultural practices precluded placement of camera within row crops. We checked cameras monthly to remove SD memory cards, replace batteries, clear vegetation, and maintain cameras. Cameras captured one image when triggered with a programmed 30 s delay between successive images. In addition to on-site visual assessment, we used 3-m resolution satellite imagery collected on 28 Jan 2021 (accessed from www .planet.com on 30 Apr 2023) to classify forest canopy as open or closed based on whether overhead cover was detectable or not at the camera location.

We used four sampling periods associated with the 2021 helicopter gunning effort. We classified images obtained during the last five consecutive days prior to the gunning campaign (13-17 Jan 2021) as "Before" removal, 21-25 Jan 2021 as "During" removal, 05-09 Feb 2021 as "After" removal, and 28 Feb-04 Mar 2021 as "Long After" removal. We filtered detections using a 15-minute time-to-independence and assumed any additional photos within the interval were of the same individual at a given camera. We conducted this camera trapping study under the approval of the University of Georgia's IACUC protocol A2020 04-028-Y1-A0, approved on 13 May 2020.

Statistical Analysis

We estimated the effects of aerial pig removal on the number of independent detections of wild pigs at each camera during diurnal and nocturnal hours using Poisson regression executed with the 'lmer4' package (Bates et al. 2015). To account for the difference in day and night length we included log(hours) as an offset term in our Poisson regression models. We included period relative to gunning (i.e., Before, During, After, and Long After), canopy cover classification (open or closed), time of day (day or night), and all two-way interactions as predictor variables. Specifically, we predicted wild pig detection rate as a function of individual predictors (single variable models), all combinations of two predictor variables and their interactions (two variable models), a global model that contained all three predictor variables and all two-way interactions, and a null model with no predictor variables. We calculated the Akaike Information Criteria (AIC), delta AIC (Δ AIC), and Akaike weights (AICw) using the 'qpcR' package (Ahmed and Kim 2018). We used an information theoretic approach to identify the most parsimonious model (Burnham and Anderson 2002) and considered models within 4 Δ AIC as competing models. Predictors were considered informative when their 95% confidence intervals did not overlap zero. All analyses were performed in Program R 4.1.2 (R Core Team 2021).

RESULTS

Aerial gunning removed 241 wild pigs in 21.1 hours of flight time over our study area for an average of 11.4 pigs removed/hour. We monitored 114 camera traps during each period (570 camera days each period; Table 1). Aerial gunning removal resulted in an approximate 46% decline in wild pig detections between Before and After gunning.

Our global model predicting pig detection rate performed best; there were no competing models as the second-best model had a Δ AIC = 18.644 (Table 2). Therefore, we made inferences using the global model. All two-way interactions were informative, so we graphed predicted values as a function of sampling period for each canopy cover type (Figure 2). Period had no effect on daytime detection rates. All nighttime detection rates were greater than daytime detection rates regardless of period. Nighttime detection rates were lower During, After, and Long After aerial gunning than Before aerial gunning (Figure 2a). Wild pig detection rates in open canopy forests were similar among all periods. Wild pig detection rates in closed canopy forest were greater During, After, and Long After gunning than within open canopy forest. Within closed canopy forests, detection rates During and After gunning were greater than Before and Long After gunning (Figure 2b). When averaging across periods, nighttime wild pig detection rates were greater in open canopy than in closed canopy forests (Figure 2c).

Table 1. Wild pig detection rate across the Before, During, After, and Long After periods, where each period duration was 5 days, from 114 camera traps deployed in Calhoun County, Georgia during Jan-Mar 2021.

Period	# Pigs Detected	# Cameras that Detected Pigs	# Camera Days in Period	Pigs/camera /day
Before	370	50	570	0.65
During	250	44	570	0.44
After	201	42	570	0.35
Long After	178	38	570	0.31

Table 2. Comparison of global model, next competing model, and null model assembled for the Poisson regression to predict wild pig detections camera^{-1} day^{-1}. All coefficients are relative to a model using the Before period, Day (i.e., time-of-day), and Open canopy cover as the referent condition and estimated using data collected from 114 camera surveys deployed in Calhoun County, Georgia during Jan-Mar 2021.

Model	AIC	Δ AIC	AICw
(Period * Time of Day) + (Period * Canopy Cover) + (Time of Day * Canopy Cover) + log(hours)	6336.2	0	1
(Period * Time of Day) + (Period * Canopy Cover) + log(hours)	6354.9	18.64	0
Null	6920.5	584.30	0

DISCUSSION

Aerial gunning is a proven, effective method of rapid depopulation of wild pigs (Saunders and Bryant 1988, Dexter 1996, Lombardo and Faulkner 1999, Parkes et al. 2010, Massei et al. 2011, Bodenchuk 2014, Davis et al. 2018). We hypothesized that aerial gunning would result in increased wild pig detections within closed canopy forests and that aerial gunning would affect wild pig activity patterns. We found evidence to support both predictions.

Wild pig detections largely occurred at night; thus, we observed little to no effect of gunning period on daytime detections. However, detections at night were greater Before gunning than During, After, or Long After gunning (Figure 2a). Importantly, we suggest that lower detection rates during latter periods (i.e., After and Long After) of our study are primarily due to reduced pig abundance associated with control efforts rather than changes in pig behavior. However, wild pig detection rates in closed canopy increased over time despite pig removals, suggesting a behavioral response to helicopter gunning.

Game animals alter movement activity patterns and habitat selection in response to hunters (Sweeney et al. 1971, Tolon et al. 2009, Little et al. 2016) and wild predators (Cherry et al. 2015, Conner et al. 2016, Gulsby et al. 2018, Crawford et al. 2021). Because aerial gunning provides risk from above, we expected wild pig detection rates to increase in areas with canopy cover as pigs were essentially responding to a large and efficient aerial predator.

Potash et al. (2019) distinguished between “ceiling” and “wall” cover and noted that prey use of each type of cover is based on their predator community; ceiling cover is more important in avoidance of aerial predators and wall cover is more important in avoidance of ground-based predators. Wall cover, i.e., dense vertical vegetation, is important to wild pigs when hunted from the ground (Keuling and Massei 2021). In France, however, Saïd et al. (2012) observed that wild pigs avoided areas with dense vegetation after years of recreational hunting, presumably a learned response to hunters repeatedly focusing their efforts in densely vegetated areas. Similarly in Alabama, Gaston et al. (2008) showed that during hunting seasons wild pigs shifted preference from wetlands to pine/mixed forests in response to hunter use of wetlands.

In our study, wild pig detections were greater within closed canopy forests (i.e., areas with greater ceiling cover) during the helicopter gunning effort even though overall wild pig detections declined due to wild pig depopulation. Others (Saunders and Bryant 1988, Davis et al. 2018) similarly suggest the importance of ceiling cover to wild pigs during aerial gunning campaigns. Collectively, study results of wild pig response to ground-based hunting (Gaston et al. 2008, Saïd 2012, Keuling and Massei 2021) and aerial gunning (Saunders and Bryant 1988, Lombardo and Faulkner 1999, Parkes et al. 2010, Davis et al. 2018) suggest that combining aerial and ground-based removal efforts may increase efficacy of wild pig control efforts.

Animals become more nocturnal in response to human activities (Gaynor et al. 2018, Li et al. 2021), and this seems more pronounced in omnivores than in carnivores (Li et al. 2021). For these reasons, we expected wild pigs to become more nocturnal in response to diurnal aerial gunning, yet this was not well supported by our data. On our study area sport hunting was common, and the white-tailed deer (*Odocoileus virginianus*) hunting season ended only a few days prior to the aerial gunning campaign. Further, much of the study area was used for production agriculture and daytime use of the area by people is great. Thus, we suggest our prediction was incorrect because pigs were largely nocturnal before our study began, likely in response to long-term diurnal human activity.

Risk induced trait responses (Peacor et al. 2020) such as avoidance of risky times and places (Laundré et al. 2001, Creel et al. 2008) are common in scientific literature, and numerous studies report risk-induced trait responses in carnivore-ungulate systems. Studies of mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*; Brown et al. 1999), coyotes (*Canis latrans*) and white-tailed deer (Crawford et al. 2021), and wolves (*Canis lupus*) and elk (*Cervus elaphus*; Creel and Winnie Jr. 2005) all provide examples of ungulates demonstrating heightened vigilance, avoidance of high-risk areas, and, in some cases, increased herd size to reduce the risk of predation. In our study, we suggest the helicopter – functionally a diurnal predator – imposed spatiotemporally variable risk. However, the behavioral responses exhibited by wild pigs only partially mirror those reported in other carnivore-ungulate systems; while wild pigs were primarily nocturnal throughout the study, there was compelling evidence for increased use of cover while the helicopter was active when compared to the period before aerial gunning commenced. Nonetheless, we suggest ground-based wild pig removal efforts in association with aerial gunning may increase efficacy of overall control.

Ground-based hunting and trapping during periods when aerial gunning is occurring but focused on inactive times, i.e., crepuscular and nocturnal efforts, may reduce wild pigs’ perception of a ‘safe time’ and may provide an additive effect on control efforts. Similarly, focusing non-aerial control efforts within closed canopy forests may

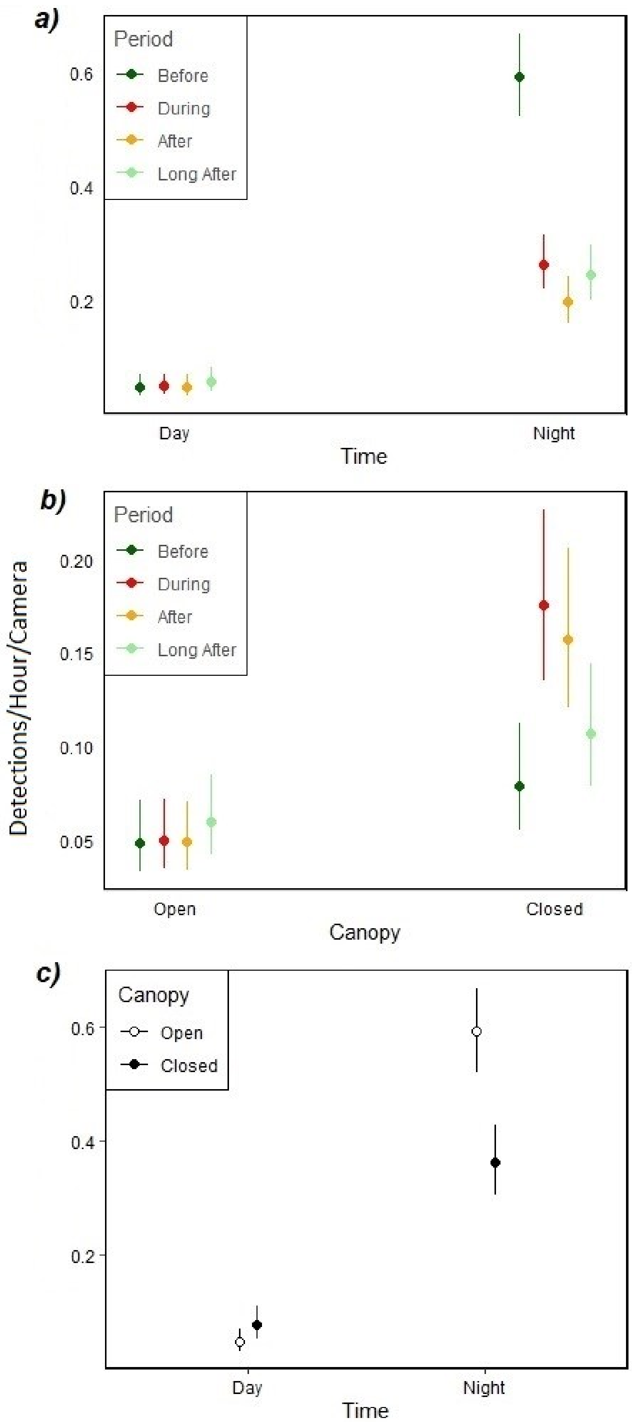

Figure 2. Wild pig detection rates (detections camera^{-1} day^{-1}) predicted using our top Poisson regression estimating the effects of period (Before, During, After, Long After), time-of-day (Day or Night), and canopy closure (Open or Closed) on period-time-canopy specific counts of independent detections at 114 camera traps deployed in Calhoun County, Georgia during Jan-Mar 2021. We detected significant interactive effects of a) time-of-day and period, b) canopy closure and period, and c) time-of-day and canopy closure on detection rates. Error bars indicate 95% confidence intervals.

reduce perception of 'safe places' further increasing control efficacy. Placing bait and traps within closed canopy forests prior to aerial removal efforts may precondition animals and make them more susceptible to trapping during the gunning campaign.

Many studies report adverse long-term effects of antipredator behavior on ungulate populations. For example, selection of safer but low-quality habitat can reduce individual growth rates and fecundity, and consequently, reduce population growth rates (Lima 1998, Creel and Christianson 2008, Creel et al. 2011). Research including long-term effects of removal efforts on wild pig habitat use, social behavior and structure, and reproduction may be particularly valuable. In addition, few studies have measured the impact of techniques used to remove invasive animals on non-target species. While control of invasive and destructive wild pigs is the first step to restoring their invaded ecosystems, non-target species may also perceive control efforts as predation risk. Thus, quantifying responses of non-target species to invasive species removal methods may inform future control efforts. Outcomes of these exposures may extend beyond the primary target to affect predator-prey interactions (Schmitz et al. 1997). Future research is recommended to measure impact of perceived predation risk (Peacor et al. 2022) on non-target species when exposed to invasive species control efforts.

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