

Impacts of wild pigs on acorn availability as a food source for native wildlife

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ABSTRACT

Context. Wild pigs (*Sus scrofa*) are a non-native invasive species that causes millions of dollars in damage each year to agriculture in the United States of America, destroys native plant communities, and competes with native wildlife for seasonally available pulse resources such as acorns. Despite many anecdotal observations and diet studies suggesting wild pigs reduce acorn availability for other wildlife species, no studies have comparatively examined acorn consumption among species in a natural environment (i.e. competition). **Aims.** Our objective was to estimate the consumption of acorns by wild pigs relative to that of other native wildlife species. **Methods.** We established 40 monitoring stations beneath acorn-producing trees in a 3406-ha study area in eastern Alabama with an approximate density of 9 pigs/km². At each monitoring station, we placed five acorns on a 1-m × 1-m sand pad and positioned a game camera to record acorn fate during 2-week intervals once a month from September to February 2018–2019 and 2019–2020. Cameras were set to capture images once every minute continuously during the survey period. Additionally, we constructed acorn traps from 18.9-L plastic buckets to estimate the timing and relative amounts of acorns that were potentially available for consumption at each monitoring station. **Key results.** From approximately 7.3 million camera images, we observed 15 wildlife species consuming 707 acorns over the 2 years. Aside from animal consumption, acorn fate was categorised as lost due to flooding ($n = 153$), remaining on the sand pad at time of camera failure ($n = 720$), or not consumed during the sampling period ($n = 536$). **Key conclusions.** Top acorn consumers were squirrel (*Sciurus* spp.), white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), and wild pig. In the 2018–2019 sampling period, wild pigs consumption accounted for 23.4% ($n = 87$) of the total consumed acorns. After wild pig removal efforts were initiated in the summer and autumn of 2019, wild pigs consumed only 7.2% ($n = 24$) of consumed acorns. **Implications.** Wild pigs consume a significant number of acorns and likely reduce the availability of this pulse resource for other native wildlife species and may potentially influence oak regeneration.

Keywords: acorns, Alabama, camera survey, competition, invasive species, native wildlife, *Sus scrofa*, wild pig.

Introduction

Invasive wild pigs (*Sus scrofa*) cause significant damage to agriculture (Anderson *et al.* 2016; McKee *et al.* 2020; Strickland *et al.* 2020), forestry (Mengak 2016; Poudyal *et al.* 2017), and native flora and fauna (Campbell and Long 2009; Anderson *et al.* 2016; Strickland *et al.* 2020) throughout their range in North America. Moreover, wild pigs negatively impact water (Bolds *et al.* 2021; Bradley and Lockaby 2021) and soil quality and they compete with native wildlife for resources (Bevins *et al.* 2014). As wild pig populations continue to expand throughout North America, greater focus has been placed upon understanding their interactions with other animals (Beasley *et al.* 2018), and especially their interactions with economically, socially, and ecologically important game species such as white-tailed deer (*Odocoileus virginianus*) and eastern wild turkeys

(*Meleagris gallopavo*) for pulse resources such as soft (fleshy fruits such as berries) and hard (shelled fruits such as acorns and seeds) mast.

Many wildlife species utilise acorns as part of their seasonal diet. For example, white-tailed deer rely on acorns as a nutritional base of their diet during autumn, making up 50% of their overall diet or as high as 76–90% when readily available (Harlow *et al.* 1975; McShea and Schwede 1993). Likewise, Johnson *et al.* (1995) reported that acorns were the most important item for white-tailed deer throughout the autumn months in southern Appalachian forests. Similarly, squirrels (*Sciurus* spp.) rely heavily on acorns for immediate consumption and also for caching for later use (Havera and Smith 1979; Fox 1982). Other animals, such as American black bears (*Ursus americanus*) prefer acorns because they supply high amounts of carbohydrates to build up fat stores for winter that may subsequently impact their survival and reproduction. For example, Rogers (1976) found that in years of hard mast failure, only 33% of females reproduced compared with 59% in years of hard mast presence; moreover, female weights decreased substantially during hard mast failures. Eiler *et al.* (1989) found a negative correlation of black bear cub mortality, and a positive correlation of cub production, with acorn production because acorns provide high levels of fat for both the cub and mother during gestation and lactation when energy expenditure is high. Likewise, ruffed grouse (*Bonasa umbellus*) consume acorns due to their many nutritional benefits. In poor mast years, grouse metabolic energy (ME) gained from their diet was 20% lower than years with high mast availability (Servello and Kirkpatrick 1988). This decrease in ME can have significant implications because ME is positively associated with clutch size, egg weight, and hatchability (Beckerton and Middleton 1982). Similarly, acorns provide an autumn staple in the diets of eastern wild turkeys. Barnett and Barnett (2008) stated acorns were one of the greatest preferred food items for autumn and winter diets of turkeys. Goodrum *et al.* (1971) reported turkeys requiring 31 kg of acorns per individual in 180 days for survival due to the high nutrition acquired from this hard mast. Given the relative importance of acorns in the diet of these and many other animals, the recent introduction of an additional competitor for acorns will have some impact.

Acorns are also an important component of the diet of wild pigs (Henry and Conley 1972; Ditchkoff and Mayer 2009), overlapping considerably with many other native wildlife species. Wild pigs, like many wildlife species, prefer this energy-rich food source when available and will consume acorns in great amounts (Massey *et al.* 1996; Geisser 1998). In South Carolina, 88% of wild pig stomachs contained acorn matter, making up to 79% of total stomach contents during the winter months (Wood and Roark 1980). Barrett (1978) suggested that female wild pigs in poor condition may double their weight when acorns become available. In a diet study in the Mediterranean, Fournier-Chambrillon *et al.* (1995)

reported that 90% of the 82 wild boar stomachs and 138 faeces they sampled contained acorns during periods of mast production, and Cutini *et al.* (2013) reported that mast seeding positively correlated with piglet densities during a 20-year period in the northern Apennines of Italy.

Most of the current understanding of the impact of acorn consumption and resource competition by wild pigs on other native wildlife has been inferred from studies of dietary overlap. Because acorns are seasonally available, animals have only a finite window of time to access this food resource. McShea and Schwede (1993) demonstrated that resource competition may propagate one species, which may be more aggressive and dominant in competition, while preventing other mast-dependent species from accessing the resource. For example, Berger (1985) explained the potential for larger animals, such as wild pigs, to have a physical advantage and displace smaller animals from areas of resource (i.e. acorn) access. Barrett (1982) found that wild pigs dominated confrontations with black-tailed deer (*Odocoileus hemionus columbianus*), causing the deer to abandon habitat types shared with wild pigs in the Sierra Foothills of California. In Alabama, Keever (2014) used time-lapse camera surveys and N-mixture models and suggested wild pigs caused deer to spatially and temporally partition resources, attempting to avoid interference competition with wild pigs within the same habitat. The intake rate of acorns by deer is 30–40% greater than for browse, which is often of lower quality (Elston and Hewitt 2010). Deer are forced to shift to other food resources that take longer to consume and are lower preference, avoiding a greater quality food to avoid interference competition with wild pigs.

Besides acorns, wild pigs and deer have other dietary overlaps, potentially creating a larger issue for coexistence on the landscape. For example, using the MacArthur and Levins (1967) index, Taylor and Hellgren (1997) found dietary overlap of wild pigs and deer in southern Texas to be as high as 0.40 (0 = no overlap, 1.0 = total overlap), noting this to likely be an underestimate due to the categorisation methods of the data used. When acorn consumption by deer is limited, biological processes can be impacted. For example, in the southern Appalachians, deer weights, development of antlers, and population dynamics (e.g. fawn recruitment) were negatively impacted by lack of acorn consumption (Wentworth *et al.* 1992). Elston and Hewitt (2010) found the rate of food intake for wild pigs (17.4 g/min) was lower than other species in their study including white-tailed deer (18.0 g/min) and wild turkey (21.8 g/min). However, they also found wild pigs deshelled acorns to consume only the greatest nutritional internal components, discarding the shell. Although deshelling requires a longer processing time, it also results in greater quality of food intake. White-tailed deer and wild turkey eat acorns whole. For these reasons, Elston and Hewitt (2010) suggested that wild pigs are effective competitors at foraging, consuming, and processing acorns,

potentially making them dominant in interference competition with other wildlife.

A high level of competition in dietary overlap among wild pigs and other native wildlife can be inferred from the results from many food habit studies (e.g. Taylor *et al.* 1998; Ditchkoff and Mayer 2009). However, most of these studies relied solely on *post hoc* comparisons of stomach contents without understanding the interactions of these competitors for a limited resource. Although several diet studies have documented the consumption of acorns by wild pigs, no studies have estimated the relative consumption of acorns by wild pigs in the presence of other competing consumers. Moreover, no studies have examined how native animal consumption of acorns may change once wild pig densities are reduced. Therefore, our objective was to estimate acorn consumption of wild pigs relative to that of other competing native wildlife species and to measure changes in acorn consumption by native wildlife after wild pigs were removed. Although non-replicated both spatially and temporally, we contend our study provides some initial insight into the role wild pigs may play in competing for this valuable resource.

Materials and methods

Study area

Our study was conducted in Macon County, Alabama on 3406 ha of privately owned land managed primarily for recreational hunting of northern bobwhite (*Colinus virginianus*) and white-tailed deer (*O. virginianus*). Most (>90%) of the property was forested, consisting of mixed pine and hardwood, both upland and bottomland hardwood stands of various oaks (*Quercus* spp.), and loblolly pine (*Pinus taeda*) plantations of multiple ages. Forested wetlands mainly of bald cypress (*Taxodium distichum*) and low-density loblolly and longleaf (*Pinus palustris*) pine savannahs were intermixed across the property. Most of the pine forests were managed with prescribed fire on a 2–3-year return interval to maintain early succession plant communities. Several annual and perennial wildlife food plots were maintained throughout the property for hunting purposes. Additionally, 13 ponds totalling 12.5 ha and 73.6 km of permanent or intermittent streams transected the property, with many of these streams flowing into Cubahatchee Creek. Mean annual precipitation was 134.6 cm. Upland soils were primarily Oktibbeha clay loam or Conecuh fine sandy loam, whereas bottomlands were predominantly frequently flooded Urbo–Una–Mooreville and Kinston–Mooreville complex soils with elevations ranging from approximately 82.3–115.8 m above mean sea level. As part of a larger study, camera surveys conducted during April 2019 estimated wild pig density to be 9 pigs/km². The landowner was instructed to maintain typical wild pig removal efforts while researchers conducted systematic

removal operations of wild pigs beginning in March 2019 and continuing throughout the study.

We measured the relative consumption of acorns by wildlife during five 14-day observation periods from October to February 2018–2019 (pre-removal of wild pigs) and again during the same period in 2019–2020 (post-removal of wild pigs) to determine changes in acorn consumption among wildlife species when wild pig numbers were reduced. As part of a larger comprehensive study, beginning March 2019 and continuing through the second acorn sampling period, wild pig removal operations were conducted systematically throughout the property using corral-style traps at an approximate density of one trap per 4 km² ($n = \sim 40$ trap sites). Once a wild pig sounder had been identified via camera surveys, pre-baiting using corn occurred for ~ 1 week. Corral traps were installed in these same locations, allowing habituation to the trap for increased efficiency of trapping effort. All animal capture, handling, and euthanasia was approved by the Auburn University Institutional Animal Care and Use Committee (permit #2017-3143).

Site selection

In early autumn in 2018, we identified 40 acorn-producing trees of various *Quercus* species (13 white oak, 27 red oak) throughout the study area from previous work on the property, known locations provided by the area manager, and by walking through forest stands and visually inspecting trees for acorn production. We intentionally selected acorn-producing trees that were distributed throughout the property to ensure likely interaction with different wild pig sounders based on results from earlier camera surveys conducted on the property. When acorn-producing trees occurred in clusters, we selected only acorn-producing trees that were >50 m apart in an attempt to maintain some level of independence among camera stations. We acknowledge that some species (i.e. wild pig, white-tailed deer, etc.) can travel this distance or greater within a short time frame. However, under our study parameters, 50 m was close to the greatest distance we could have each site separated from each other based on travel logistics (i.e. drivable roads, avoiding areas requested by land manager, etc.) and oak/acorn presence. We placed camera traps only beneath trees that were producing acorns because many species would naturally be foraging under these trees; therefore, avoiding biases associated with bait attraction. These same trees were inspected for acorn development during early autumn in 2019 and were used again during the 2019–2020 sampling period if they were producing acorns. In cases where the oak was not producing in the second year, new acorn-producing trees nearby were used.

Camera traps

At each acorn-producing tree, we established a camera trap beneath the tree canopy to monitor acorn consumption by

wildlife. We attached a game camera (PC800 HyperFire Professional IR, Reconyx, Holmen, WI, USA) to either the selected acorn-producing tree or another smaller tree beneath the canopy of the acorn-producing tree. To observe acorns on the ground via game cameras, we cleared away ground debris and placed a 1-m × 1-m × 1-cm pad of play sand as a contrasting background. The centre of each sand pad was 2.5 m from the base of the acorn-producing tree; the game camera was attached 1-m high and angled downward toward the sand pad. We verified the angle of the camera using a laser pointer and level, and by confirming the correct image field of view by either viewing images on the camera or downloading them to a laptop. We then searched beneath the acorn-producing tree and collected five acorns, which we placed in a quincunx pattern, with the outermost acorns approximately 15 cm from the outside edge of the sand pad. Cameras were set to run 24 h/day for 14 consecutive days with a 1-min delay between each image. Occasionally we visited and cleared leaves and other ground debris that obstructed view of the acorns on the sand pad. We did not replenish acorns that were taken during the 14 days of observation except for the December 2018 sampling period, when miscommunication among field staff resulted in missing acorns being replaced midway through the sampling period. At the end of each 14-day observation period, we retrieved the camera cards and uploaded images to a laptop for later viewing. At the beginning of each sampling period, we replaced the batteries and installed a new memory card, verified the angle of the camera relative to the sand pad, and replenished the acorns on the pad.

Acorn availability

To index relative acorn fall during each sampling period, we placed two 18.9-L plastic buckets to serve as acorn traps beneath the canopy of each acorn-producing tree where camera stations were established. Acorn traps were placed about 0.6–4.5 m from the base of the acorn-producing tree, depending upon canopy width. These acorn traps were used to estimate acorn fall and thus the timing and relative amount of acorns available for consumption over each period. To prevent animals from removing acorns within the buckets, we drilled four small holes in the side of the bucket near the top and equidistant around the rim and used zip ties to secure a circular piece of plastic snow fence (approximately 0.4 m diameter) shaped into a cone and placed within the bucket. The plastic snow fence was placed approximately halfway up the side of the bucket. An additional hole was drilled in the bottom of the bucket to allow water drainage and to allow the insertion of a 1-m length of 12.7-mm diameter steel rod (e.g. rebar) to stake the bucket to the ground to prevent the bucket from tipping. We welded a washer approximately 0.3 m from one end of the rod to provide a larger surface area between the plastic bucket and rebar to anchor the bucket to the

ground. We then placed one of the two acorn traps within the field of view of the game camera so that images of any animals that attempted to remove acorns from the traps could be recorded. We checked acorn buckets at the end of each 14-day collection period, counted and recorded the number of acorns collected during the period, and reset the acorn trap.

Image analysis

At the end of each 14-day sampling period, we reviewed each image sequentially to determine acorn fate as either consumed or not consumed by wildlife and by which species. We classified an acorn as consumed if we captured images of an acorn in the animal's mouth or being held in any manner by the animal and then absent in subsequent images. We assumed that acorns carried away by animals were consumed. Because we used a 1-min delay between images, an animal could remove an acorn between image captures. As such, we considered an acorn as consumed if an animal appeared in any one of a sequence of five images before or after an acorn disappeared from the sand pad. We recorded observations of acorn consumers to species-level for most animals where possible, except for birds other than turkeys and small mammals. Blue jays, crows, etc. were grouped as 'birds' and small mammals such as voles and mice were grouped as 'small mammals'. When we could not readily identify a consumer (e.g. blurred image or animal entered and left the camera field between the 1-min delay), we classified the observation as unknown consumer. We observed one instance of a human removing two acorns from the sand pad. Acorns remaining on the sand pad after each sampling period were recorded as not consumed whereas those acorns that were missing from the sand pad were classified as per their likely fate on the basis of supporting evidence from camera images (e.g. flooding) or by inspection of the site at the end of each sampling period (e.g. wild pig rooting covering acorns). We categorised acorns that were presumably not consumed as either lost due to flooding, wind, or covered with ground debris due to wild pig rooting activity. During this study, we experienced several instances of camera failure. When a failure occurred, we only considered acorn exposure until the time at which the camera ceased capturing images.

We knew the approximate pre-removal density of pigs at the study area from concurrent research (9 pigs/km²), with 443 pigs removed between May and September 2019. However, we did not know the density of other species such as deer, raccoon (*Procyon lotor*), nine-banded armadillo (*Dasypus novemcinctus*), and all other species we observed in images. Therefore, we had to assume that each species had an equal probability of detecting the acorns, despite the number of each species on the landscape. Additionally, we assumed that the sand pad did not influence an animal's ability to detect an acorn. Despite the sand pad's atypical presence at

the base of a tree, we needed to implement this technique to effectively view and account for acorn fate. We used Chi-square Goodness of Fit tests to determine if acorn assumption varied among species and throughout the five sampling periods each year. We did not test differences between years due to inherent variability in acorn availability and wild pig densities. Results were considered significant at $\alpha > 0.05$.

Results

We collected approximately 3.5 million and 3.8 million images during 2018–2019 and 2019–2020, respectively, culminating in a total of 118 944 camera hours. A total of 2200 acorns were under surveillance, of which 707 were consumed by 15 wildlife species. We experienced several camera failures ($n = 183$ camera failure instances) over both years that prevented the assignment of fate to acorns under observation at a time of camera failure (2018 $n = 298$ acorns; 2019 $n = 422$ acorns). We collected 193 and 220 acorns in acorn traps during the 2018–2019 and 2019–2020 masting seasons, respectively. Peak acorn fall occurred in October–November during 2018–2019 but later (November–December) in 2019–2020. We did not observe any animals attempting to remove acorns from the acorn bucket traps.

During 2018–2019 (pre-removal of wild pigs), 372 acorns were consumed by 13 species, 323 were left on the sand pad at the end of the 14 day period, 177 were lost to a disturbance

(flooding, blown away, covered, rooting, etc.), and 298 were left on the sand pad at a time of camera failure. Acorn consumption (as a percentage of all acorns consumed) varied among species ($\chi^2 = 445.8$, $P < 0.01$; Fig. 1) with wild pigs (23.4%), white-tailed deer (21.2%), and squirrels (18.8%) accounting for most of the acorns consumed followed by unknown animals (9.1%), raccoons (6.5%), birds (6.5%), small mammals (5.4%), armadillos (4.0%), rabbits (1.6%), and opossums (1.6%; *Didelphis virginiana*). Coyotes (*Canis latrans*), eastern wild turkeys, and a turtle consumed <1.0% of acorns (Fig. 1). Two acorns were removed by a human (<1.0%). Acorn consumption by white-tailed deer increased as acorn masting peaked during November (61 acorns consumed) but declined thereafter (a total of 10 were consumed from December to February). However, consumption of acorns by wild pigs peaked in December (32 acorns consumed) and was greater than that of white-tailed deer throughout the remainder of the sampling period (57 were consumed from December to February; Fig. 2).

During 2019–2020 (post-removal of wild pigs), we observed 335 acorns consumed by 13 wildlife species (Fig. 1), 213 left on the sand pad after the 14-day period, 30 lost to a disturbance (flooding, blown away, covered, rooting, etc.), and 422 left on the sand pad at the time of a camera failure. Acorn consumption among species varied ($\chi^2 = 625.1$, $P < 0.01$). The top three consumers post-removal were squirrel (39.7%), white-tailed deer (17.6%) and raccoon (9.9%) and wild pig consumption of acorns accounted for 7.2%. Other species consuming acorns included birds (4.2%),

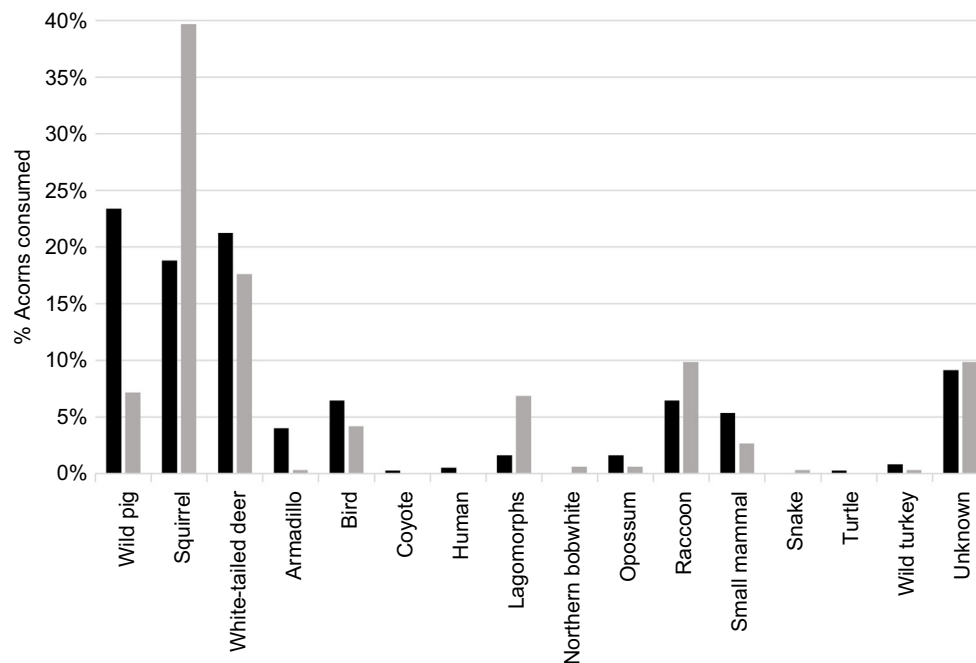


Fig. 1. Species-specific consumption of acorns (as a percentage of all acorns consumed during a season) during pre-removal (2018–2019; black bars) and post-removal (2019–2020; grey bars) of wild pigs in Macon County, Alabama.

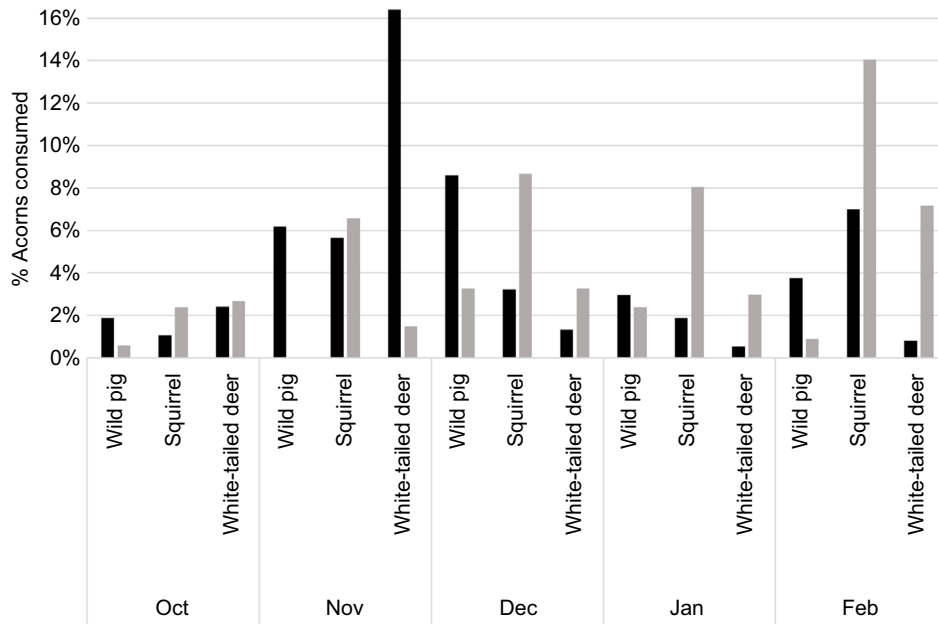


Fig. 2. Monthly consumption of acorns (as a percentage of all acorns consumed by year) by the three greatest acorn-consuming species during pre-removal (2018–2019; black bars) and post-removal (2019–2020; grey bars) of wild pigs in Macon County, Alabama.

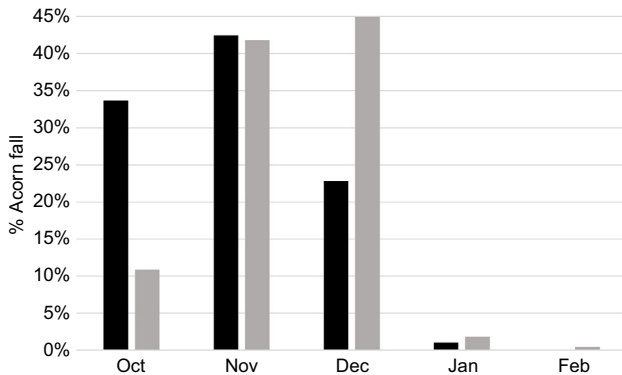


Fig. 3. Monthly acorn fall (as a percentage of total acorn fall within individual years) during pre-removal (2018–2019; black bars) and post-removal (2019–2020; grey bars) in Macon County, Alabama. Data collected via acorn traps under acorn-producing oaks.

rabbits (6.9%), small mammals (2.7%) and unknown animals (9.9%). Armadillos, northern bobwhite, eastern wild turkeys, opossums, and snakes consumed <1.0% each (Fig. 1). Squirrel and white-tailed deer acorn consumption increased steadily from October to February, peaking in February. Wild pig consumption of acorns peaked in December coinciding with peak mastings but declined in subsequent months (Figs 2, 3).

Discussion

We observed that wild pigs consumed a substantial number of acorns throughout the periods during which we conducted

our study. Our data suggest acorn fall was at or above average in the southeastern USA for both years in our study (Greenberg and Parresol 2002; Rose et al. 2012). Before removal, wild pigs consumed 23.4% of the total acorns consumed by all species. High consumption rates were not unexpected because wild pigs have been shown to seek this resource when available. For example, Wood and Roark (1980) found acorns comprised 79.8% of the total dry weight of wild pig stomach contents during winter months. Likewise, using DNA metabarcoding, Anderson et al. (2018) found that 94% of sampled wild pig stomachs contained acorns. This high rate of acorn consumption by wild pigs reduces availability for other wildlife species. After removal, we detected an approximate 70% decrease in consumption of acorns by wild pigs, potentially allowing native species to increase their acorn consumption.

We found the most significant impact of wild pig presence was on the use of acorns by grey squirrels. Following wild pig removal, consumption of acorns by squirrels nearly doubled. Grey squirrels are hard mast specialists and rely heavily on acorns for their dietary needs during winter (Wilson et al. 2020). Population density of grey squirrels are linked to acorn availability and populations have been known to crash when acorns are unavailable (McShea 2000). Survival of summer-born young and adults, emigration, and female fecundity depend on hard mast availability (Nixon et al. 1975), suggesting that acorn consumption by wild pigs may negatively impact local populations of grey squirrels. Moreover, we observed squirrel use of acorns during all months of the study, showing potential competition between wild pigs and

squirrels during the entire period acorns are available. Because both species can detect and access cached acorns below the soil surface, there is also considerable potential for direct competition during winter and spring, when acorns are often unavailable above the soil surface. In this way, wild pigs may be directly and negatively impacting squirrel populations.

Despite our initial thoughts, the consumption of acorns by white-tailed deer did not seem to be impacted by removal of wild pigs. Consumption of acorns by white-tailed deer was greatest during November, coinciding with the period of greatest natural acorn fall and availability of acorns on the forest floor. It seems that white-tailed deer focus their search, and thus consumption, of acorns when availability is greatest and shift focus to other food sources when the cost of searching outweighs the benefit. Keever (2014) and McDonough *et al.* (2022) suggested wild pigs may displace or exclude white-tailed deer from pulse resources such as acorns, forcing white-tailed deer to adjust their foraging behaviours either spatially or temporally to avoid competition. Our results tend to support Keever's (2014) assertion that high densities of wild pigs were associated with lesser densities of white-tailed deer, owing to interference competition.

Although we do not know the ultimate fate of acorns that were lost from game camera view due to disturbance (i.e. flooding, covered by leaf litter, camera failure, etc.) or left at the end of the observational period, we assume that these acorns were consumed in proportion to those we observed on camera. However, the proportion of acorns observed to be consumed by wild pigs could have a negative impact on oak regeneration. Because these acorns were never cached by squirrels or had the time to settle into the detritus on the forest floor, they could never begin development into seedlings. For an acorn to successfully germinate, develop into a seedling, and ultimately be recruited into the forest canopy, it must avoid consumption by wildlife as an acorn, over-browsing by herbivores as a seedling, diseases, and a host of other fates. The addition of wild pigs to the ecosystem can negatively alter the recruitment rate of oaks in hardwood forests that are already experiencing decreased regeneration (McDonald *et al.* 2003).

Management implications

Our findings suggest that wild pigs have the potential to consume a biologically relevant portion of the acorns that are produced each year. As invasive wild pigs shift their diet to focus on seasonally available resources, the accessibility of these pulse resources diminishes, and inherent competition increases between these species. McDonough *et al.* (2022) explained that white-tailed deer and wild pigs directly compete for acorns and other ephemeral resources. Our study found that the intensive removal of wild pigs increases the consumption of acorns by other species, mainly grey squirrels. Wild pigs are unmanaged in some parts of the country, and may have increased influence on white-tailed deer and other wildlife

species. We found when wild pigs are actively managed, they have little effect on deer, and when removed, their impact on squirrels diminishes. Because of this, managers should work to reduce or remove wild pigs from their land to decrease wild pigs' negative impacts.

References

- Anderson A, Sloomaker C, Harper E, Holderiath J, Shwiff SA (2016) Economic estimates of feral swine damage and control in 11 US states. *Crop Protection* **89**, 89–94. doi:10.1016/j.cropro.2016.06.023
- Anderson WM, Boughton RK, Wisely SM, Merrill MM, Boughton EH, Robeson MS, Piaggio AJ (2018) Using DNA metabarcoding to examine wild pig (*Sus scrofa*) diets in a subtropical agro-ecosystem. *Proceedings of the Vertebrate Pest Conference* **28**, 90–95. doi:10.5070/v42811017
- Barrett RH (1978) The feral hog at Dye Creek Ranch, California. *Hilgardia* **46**, 283–355. doi:10.3733/hilg.v46n09p283
- Barrett RH (1982) Habitat preferences of feral hogs, deer, and cattle on a Sierra Foothill Range. *Journal of Range Management* **35**, 342–346. doi:10.2307/3898314
- Barnett SW, Barnett VS (2008) The wild turkey in Alabama. Alabama Department of Conservation and Natural Resources, Montgomery, AL, USA.
- Beasley JC, Ditchkoff SS, Mayer JJ, Smith MD, Vercauteren KC (2018) Research priorities for managing invasive wild pigs in North America. *The Journal of Wildlife Management* **82**, 674–681. doi:10.1002/jwmg.21436
- Beckerton PR, Middleton ALA (1982) Effects of dietary protein levels on ruffed grouse reproduction. *The Journal of Wildlife Management* **46**, 569–579. doi:10.2307/3808547
- Berger J (1985) Interspecific interactions and dominance among wild Great Basin ungulates. *Journal of Mammalogy* **66**, 571–573. doi:10.2307/1380939
- Bevins SN, Pedersen K, Lutman MW, Gidlewski T, Deliberto TJ (2014) Consequences associated with the recent range expansion of nonnative feral swine. *BioScience* **64**, 291–299. doi:10.1093/biosci/biu015
- Bolds SA, Lockaby BG, Ditchkoff SS, Smith MD, Vercauteren KC (2021) Impacts of a large invasive mammal on water quality in riparian ecosystems. *Journal of Environmental Quality* **50**, 441–453. doi:10.1002/jeq2.20194
- Bradley EA, Lockaby G (2021) Invasive wild pigs: a significant disturbance in coastal forests. *Forests* **12**, 1042. doi:10.3390/f12081042
- Campbell TA, Long DB (2009) Strawberry-flavored baits for pharmaceutical delivery to feral swine. *Journal of Wildlife Management* **73**, 615–619. doi:10.2193/2008-326
- Cutini A, Chianucci F, Chirichella R, Donaggio E, Mattioli L, Apollonio M (2013) Mast seeding in deciduous forests of the northern Apennines (Italy) and its influence on wild boar population dynamics. *Annals of Forest Science* **70**, 493–502. doi:10.1007/s13595-013-0282-z
- Ditchkoff SS, Mayer JJ (2009) Wild pigs food habits. In 'Wild Pigs: Biology, Damage, Control Techniques and Management'. (Eds JJ Mayer and IL Brisbin Jr.) pp. 105–143. (Savannah River National Laboratory: Aiken, SC, USA)
- Eiler JH, Wathen WG, Pelton MR (1989) Reproduction in black bears in the southern Appalachian Mountains. *The Journal of Wildlife Management* **53**, 353–360. doi:10.2307/3801137
- Elston JJ, Hewitt DG (2010) Intake of mast by wildlife in Texas and the potential for competition with wild boars. *The Southwestern Naturalist* **55**, 57–66. doi:10.1894/TAL-03.1
- Fournier-Chambillon C, Maillard D, Fournier P (1995) Diet of the wild boar (*Sus scrofa* L.) inhabiting the Montpellier garrigue. *Journal of Mountain Ecology* **3**, 174–179.
- Fox JF (1982) Adaptation of gray squirrel behavior to autumn germination by white oak acorns. *Evolution* **36**, 800–809. doi:10.2307/2407893
- Geisser H (1998) The wild boar (*Sus scrofa*) in the Thurgau (Northeastern Switzerland): population status, damages and the influence of

- supplementary feeding on damage frequency. *Gibier Faune Sauvage* **15**, 547–554.
- Goodrum PD, Reid VH, Boyd CE (1971) Acorn yields, characteristics, and management criteria of oaks for wildlife. *The Journal of Wildlife Management* **35**, 520–532. doi:10.2307/3799707
- Greenberg CH, Parresol BR (2002) Dynamics of acorn production by five species of Southern Appalachian oaks. In ‘Oak forest ecosystems: ecology and management for wildlife’. (Eds WJ McShea, WM Healy) pp. 149–172. (Johns Hopkins University Press: Baltimore, MD, USA)
- Harlow RF, Whelan JB, Crawford HS, Skeen JE (1975) Deer foods during years of oak mast abundance and scarcity. *The Journal of Wildlife Management* **39**, 330–336. doi:10.2307/3799910
- Havera SP, Smith KE (1979) A nutritional comparison of selected fox squirrel foods. *The Journal of Wildlife Management* **43**, 691–704. doi:10.2307/3808748
- Henry VG, Conley RH (1972) Fall foods of European wild hogs in the Southern Appalachians. *The Journal of Wildlife Management* **36**, 854–860. doi:10.2307/3799440
- Johnson AS, Hale PE, Ford WM, Wentworth JM, French JR, Anderson OF, Pullen GB (1995) White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian Forests. *The American Midland Naturalist* **133**, 18–35. doi:10.2307/2426344
- Keever AC (2014) Use of N-mixture models for estimating white-tailed deer populations and impacts of predator removal and interspecific competition. Thesis, Auburn University, Auburn, AL, USA.
- MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* **101**, 377–385. doi:10.1086/282505
- Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriologica* **41**, 307–320. doi:10.4098/AT.arch.96-29
- McDonald RI, Peet RK, Urban DL (2003) Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a Piedmont forest. *Journal of Vegetation Science* **14**, 441–450. doi:10.1111/j.1654-1103.2003.tb02170.x
- McDonough MT, Ditchkoff SS, Smith MD, Vercauteren KC (2022) A review of the impacts of invasive wild pigs on native vertebrates. *Mammalian Biology* **102**, 279–290. doi:10.1007/s42991-022-00234-6
- McKee S, Anderson A, Carlisle K, Shwiff SA (2020) Economic estimates of invasive wild pig damage to crops in 12 US states. *Crop Protection* **132**, 105105. doi:10.1016/j.cropro.2020.105105
- McShea WJ (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* **81**, 228–238. doi:10.1890/0012-9658(2000)081[0228:TIOACO]2.0.CO;2
- McShea WJ, Schwede G (1993) Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy* **74**, 999–1006. doi:10.2307/1382439
- Mengak MT (2016) 2015 Georgia wild pig survey final report. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA.
- Nixon CM, McClain MW, Donohoe RW (1975) Effects of hunting and mast crops on a squirrel population. *The Journal of Wildlife Management* **39**, 1–25. doi:10.2307/3800460
- Poudyal NC, Caplenor C, Joshi O, Maldonado C, Muller LI, Yoest C (2017) Characterizing the economic value and impacts of wild pig damage on a rural economy. *Human Dimensions of Wildlife* **22**, 538–549. doi:10.1080/10871209.2017.1368103
- Rogers L (1976) Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. In ‘Transactions of the 41st North American wildlife and natural resources conference, 21–25 March 1976, Washington, DC, USA’. pp. 431–438. (Wildlife Management Institute: Washington, DC, USA)
- Rose AK, Greenberg CH, Fearer TM (2012) Acorn production prediction models for five common oak species of the eastern United States. *The Journal of Wildlife Management* **76**, 750–758. doi:10.1002/jwmg.291
- Servello FA, Kirkpatrick RL (1988) Nutrition and condition of ruffed grouse during the breeding season in southwestern Virginia. *The Condor* **90**, 836–842. doi:10.2307/1368840
- Strickland BK, Smith MD, Smith AL (2020) Wild pig damage to resources. In ‘Invasive wild pigs in North America’. (Eds KC Vercauteren, JC Beasley, SS Ditchkoff, JJ Mayer, GJ Roloff, BK Strickland) pp. 143–168. (Taylor & Francis Group: Boca Raton, FL, USA) doi:10.1201/b22014-7
- Taylor RB, Hellgren EC (1997) Diet of feral hogs in the Western South Texas plains. *The Southwest Naturalist* **42**, 33–39.
- Taylor RB, Hellgren EC, Gabor TM, Ilse LM (1998) Reproduction of feral pigs in Southern Texas. *Journal of Mammalogy* **79**, 1325–1331. doi:10.2307/1383024
- Wentworth JM, Johnson AS, Hale PE, Kammermeyer KE (1992) Relationships of acorn abundance and deer herd characteristics in the Southern Appalachians. *Southern Journal of Applied Forestry* **16**, 5–8. doi:10.1093/sjaf/16.1.5
- Wilson SB, Steury TD, Gitzen RA, Ditchkoff SS (2020) Fall and winter diets of eastern gray squirrels in a seasonally flooded ecosystem in Alabama. *Southeastern Naturalist* **19**, 771–780. doi:10.1656/058.019.0414
- Wood GW, Roark DN (1980) Food habits of feral hogs in Coastal South Carolina. *The Journal of Wildlife Management* **44**, 506–511. doi:10.2307/3807990

Data availability. The data that support this study cannot be shared publicly for privacy of the landowner but may be shared upon reasonable request to the corresponding author.

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