No panacea attractant for wild pigs (Sus scrofa), but season and location matter

Nathan P. Snow
USDA, Animal and Plant Health Inspection Service, nathan.p.snow@aphis.usda.gov

Caitlin A. Kupferman
University of Georgia

Michael J. Lavelle
National Wildlife Research Center, michael.j.lavelle@aphis.usda.gov

Kim M. Pepin
USA National Wildlife Research Center, USDA-APHIS, kim.m.pepin@aphis.usda.gov

Madeline H. Melton
University of Georgia

Authors

Nathan P. Snow, Caitlin A. Kupferman, Michael J. Lavelle, Kim M. Pepin, Madeline H. Melton, Whitney J. Gann, Kurt C. Vercauteren, and James C. Beasley

Applied Animal Behaviour Science 254 (2022) 105705

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

No panacea attractant for wild pigs (*Sus scrofa*), but season and location matter

Nathan P. Snow[a,*], Caitlin A. Kupferman[b,c], Michael J. Lavelle[a], Kim M. Pepin[a], Madeline H. Melton[b,c], Whitney J. Gann[d], Kurt C. VerCauteren[a], James C. Beasley[b,c]

[a] *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, CO, USA*
[b] *Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA*
[c] *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA*
[d] *Texas Parks and Wildlife, Chaparral Wildlife Management Area, Cotulla, TX, USA*

ARTICLE INFO

Keywords:
Olfactory
Feral swine
Wild boar
Trapping
Wildlife damage management
Bait

ABSTRACT

Wild pigs (*Sus scrofa*) are a prolific invasive species throughout many regions of the world that cause extensive economic and environmental damage. Trapping is a common strategy for reducing their populations with baits (i.e., food) and attractants (e.g., scents) used to lure wild pigs into traps. However, there is little information on which scent attractants may attract wild pigs more readily and rapidly across regions and seasons. We examined 60 scent attractants for wild pigs that could be used to increase trapping success across three seasons (winter, spring, and fall) and in two geographic regions, including a warm and semi-arid rangeland (South Texas, USA) and a warm and moist mixture of upland and bottomland forests (South Carolina, USA). We found little evidence that most scents attracted wild pigs. Only strawberry extract and creosote bush oil increased the probabilities of visitation, and only in Texas during the fall season. No other scents attractants performed better than the control (i.e., no scent) in both study locations. More wild pigs visited sites during the fall season regardless of scent attractant used. The location of a site mattered more than which attractant was used, and a post hoc analysis revealed that distances to roads and water flowlines (i.e., permanent or ephemeral drainages, streams, and rivers) increased the probabilities of visitation during some seasons. We conclude there was no panacea scent that was more effective than controls in attracting wild pigs across regions and seasons. Placement of sites and seasonality were more important for attracting wild pigs, suggesting the location of traps or bait sites may be more important than the specific attractants used for management activities. Future research should include monitoring movements of wild pigs relative to scent attractants and evaluation of baits (e.g., food-rewards) for drawing wild pigs to sites.

1. Introduction

Native and introduced wild pigs (*Sus scrofa*) occur in much of the World and are increasing in range and populations in many regions (Barrios-Garcia and Ballari, 2012; McClure et al., 2015; Lewis et al., 2017; Snow et al., 2017). Where introduced in places such as North America and Australia, wild pigs often outcompete native species, damage agriculture, threaten domestic livestock production, and adversely impact natural resources (Hone, 1990; Lavelle et al., 2017; Beasley et al., 2018; Lewis et al., 2019). Management of these populations typically involves lethal control using traps, toxicants (i.e., currently used in some countries such as Australia and New Zealand; and being tested for use in other countries such as United States and Canada), and ground or aerial shooting (Massei et al., 2011; Sullivan, 2015; Beasley et al., 2018). For trapping and toxicants, managers must successfully attract wild pigs from surrounding areas and entice them to enter a trap or consume a toxic agent, respectively (Campbell and Long, 2008; Lavelle et al., 2017; Beasley et al., 2018). This need has led to the development of numerous commercial and homemade formulations of bait and attractants, however comprehensive evaluation of these products has not ensued (Lavelle et al., 2017). Even evaluations of attractants for domestic pigs have yielded few highly desired options (e.g., Sundman et al., 2022). Determining which products are preferred by wild pigs throughout seasons and geographic regions could help increase the

* Corresponding author.
E-mail address: nathan.p.snow@usda.gov (N.P. Snow).

https://doi.org/10.1016/j.applanim.2022.105705
Received 12 May 2022; Received in revised form 8 July 2022; Accepted 11 July 2022
Available online 13 July 2022
0168-1591/Published by Elsevier B.V.

efficacy of control methods.

For this study, we define scent attractants as odor-based, non-foodstuffs that are employed to entice wild pigs to an area. Following this definition, scent attractants are different from baits in that the latter are foodstuffs that may or may not be odorous and are used to motivate wild pigs to visit a specific location (e.g., inside a trap), consume hidden pharmaceuticals (e.g., toxic bait), or spend time in a particular location (e.g., near a hunting stand). Although baits are important for the endpoint of control practices for wild pigs, we only evaluated scent attractants in this study to inform the initial attraction of wild pigs from surrounding areas to the focal location through their odor. Scent attractants have been recommended to increase the efficacy of traps, toxic baits, and hunting by drawing wild pigs from farther distances (McIlroy et al., 1993; Engeman et al., 2013; Karlin and Khan, 2020) than bait alone, or encouraging wild pigs to overcome neophobic behavior at sites (e.g., to enter a trap or eat from a bait station; Hannes and Heinz-Ulrich, 2004; Massei et al., 2011; Ballari et al., 2015).

Scent attractants are worthy of investigation for wild pigs because *suidae* animals have advanced olfactory systems and rely heavily on scents for social interaction and foraging (Mayer and Brisbin, 1986, 2009; Brunjes et al., 2016.). Wild pigs are opportunistic omnivores and use scents to find a variety of foodstuffs (Schley and Roper, 2003; Broom and Fraser, 2007), such as locating hidden or seasonal foods (e.g., truffles; Gieling et al., 2011; Brunjes et al., 2016). Wild pigs also deploy and seek social- and reproduction-related scents, with nine scent-glands adapted for these activities (Mayer and Brisbin, 1986, 2009; Brunjes et al., 2016). For this study, we considered all kinds of attractants, including food-, social-, and curiosity-related scents, because it is unknown which type might influence the behaviors of wild pigs most (Lavelle et al., 2017).

Despite efforts to exploit the olfactory systems of wild pigs, it remains challenging to remove enough wild pigs to reduce their population growth and spread (Snow et al., 2020). One reason may be that wild pigs are difficult to attract from far distances. Research has shown that sites using just whole-kernel corn (i.e., no scent attractants) should be spaced 1–1.5 km apart to attract most wild pigs in an area (McRae et al., 2019; Snow and VerCauteren, 2019), however this dense spacing makes it difficult to control wild pigs over large regions. Additionally, wild pigs may become neophobic of commonly used baits (e.g., whole kernel corn) if they associate them with danger (Campbell et al., 2013; Snow et al., 2016). Therefore, scent attractants that can help attract wild pigs from far distances and overcome neophobia are needed (Lavelle et al., 2017).

Other challenges in attracting wild pigs may be that some scents are preferred during different times and in different regions. Preferred food resources for wild pigs (e.g., ripe acorns or maturing corn) are available seasonally (Schley and Roper, 2003; Ferretti et al., 2018), therefore food-based attractants may be more preferred based on season. Specifically, preferred food-based attractants may be more effective at drawing in wild pigs when naturally occurring foods are less abundant (McIlroy et al., 1993; Massei et al., 2011; Ferretti et al., 2018). Similarly, fluctuations in pheromones and olfactory cues from wild pigs occur during seasonal peaks in reproduction (Choquenot et al., 1993; Bieber and Ruf, 2005; McIlroy and Gifford, 2005; Comer and Mayer, 2009; Lavelle et al., 2017; Snow et al., 2020), which could make social-based attractants more preferred. Finally, we expect that preferences of wild pigs could vary by geographic region where food resources or timing in reproductive seasons may differ.

Considering variation among seasons and regions, previous studies of attractants for wild pigs have been few, limited in scope (i.e., geographically, or few attractants tested), and produced varying results. A study in southern Texas, USA demonstrated that strawberry was a preferred attractant for wild pigs (Campbell and Long, 2008), but a follow-up study demonstrated that strawberry-flavored baits performed poorly (Campbell and Long, 2009). A pilot study in the UK revealed wild boars rubbed on stakes coated with birch wood tar, however the animals were actually observed visiting the control stakes treated with water more frequently (Massei et al., 2021). Similarly, a study in a national park in Tennessee, USA found that control sites with recently turned soil outperformed all attractants in drawing wild pigs (Wathen et al., 1988). Finally, a summer study in central Alabama, USA indicated that wild pigs found sites with urine-based attractants quicker than sites without urine, but those animals also quickly moved away from the sites (Sandoval et al., 2019).

Our objective was to compare a wide variety of potential attractants (i.e., mostly commercially available and a few naturally available scents) that we anticipated would attract wild pigs from reviewing literature and expert opinion, and identify which were most preferred across seasons and geographic regions. Specifically, we compared visitations during spring, winter, and fall seasons when there would be differences in food availability and reproductive activities. We also compared across two geographic regions with distinct climatic regimes, which were representative of much of the invaded range of wild pigs in the USA. Ultimately, we hoped to identify panacea attractants that were preferred during all seasons and in both regions. Our secondary objective was to identify which season wild pigs were most likely to visit focal sites. Finally, post hoc we examined which landscape variables influenced the visitation rates of wild pigs to focal sites.

2. Materials and methods

2.1. Study areas

We conducted attractant trials across two study areas in the USA representing distinct physiographic regions: South Carolina and southern Texas. In South Carolina, we carried out trials on the Savannah River Site (SRS), a ~800 km^2 site managed by the U.S. Department of Energy (DOE). Annually, the SRS averages 14–25 °C, 46–90 % relative humidity, and 114 cm of precipitation (https://www.ncei.noaa.gov). The SRS is located in the Sandhills and Upper Atlantic Coastal Plains of South Carolina, USA. The SRS is comprised of a mix of riparian areas, upland pine habitat, and bottomland hardwood forest (White and Gaines, 2000). Pine forests are dominated by slash pine (*Pinus elliottii*), loblolly pine (*Pinus taeda*), and longleaf pine (*Pinus palustris*), and hardwood forests are dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), American beech (*Fagus grandifolia*), and American sweetgum (*Liquidambar styraciflua*). Despite being managed since the 1950 s, the SRS has an abundant wild pig population that is widely distributed across the landscape (Keiter et al., 2017), although wild pig activity is more concentrated within riparian areas (Clontz et al., 2021). The potential density of wild pigs in the SRS is estimated at 6–8 animals/km^2 (Lewis et al., 2019). Wild pigs breed throughout the year in this region and are found in groups of 2–22 animals (Mayer et al., 2019). The SRS is ~90 % natural and managed forests and restricted from public access. Thus, numerous other mammal species such as white-tailed deer (*Odocoileus virginianus*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) are abundant throughout the site (Webster and Beasley, 2019).

In southern Texas, we conducted trials on the Chaparral Wildlife Management Area (CWMA) near Cotulla, Texas. The CWMA is ~61.5 km^2 and located in the south Texas Plains, southwest of San Antonio in Dimmit and La Salle Counties. The CWMA averages 16–30 °C, 52–87 % relative humidity, and 55 cm of precipitation annually (https://www.ncei.noaa.gov). The area is dominated by mesquite (*Prosopsis* spp.), thorn-scrub habitat with sandy soil, although mixed brush habitat such as guajillo (*Senegalia berlandieri*), honey mesquite (*Prosopis glandulosa*), blackbrush acacia (*Vachellia rigidula*), twisted acacia, (*Vachellia schaffneri*), whitebrush (*Aloysia gratissima*), and tasajillo (*Cylindropuntia leptocaulis*) is also present (Seigler et al., 2007). Until 2002, domestic livestock grazed on the CWMA, altering the landscape and contributing to the current prevalence of thorn-scrub woodland (Seigler et al., 2007). The CWMA supports a robust population of wild pigs as well as javelina

(*Dicotyles tajacu*) and non-native warthogs (*Phacochoerus africanus*) (Gabor et al., 2001; VerCauteren et al., 2019). The potential density of wild pigs in the CWMA is estimated at 3–5 animals/km^2 (Lewis et al., 2019). Wild pigs breed throughout the year but with a peak during January–May, and are found in groups of 5–20 animals (Gaskamp et al., 2019). Like SRS, there is limited public access on the CWMA, but public deer hunts are conducted during fall hunting season as well as occasional hunts for wild pigs, javelinas, bobwhite quail (*Colinus virginianus*), and coyotes.

2.2. Study design

2.2.1. Pilot trials

To our knowledge there is little information on how wild pigs respond to scent attractants in natural settings, thus we conducted pilot trials on the SRS to ensure our study design adequately measured responses of wild pigs. We also used pilot trials to narrow the number of attractants that would be evaluated in subsequent seasons. We initially identified 60 potential attractants to include in pilot trials by using a recent review on attractants (Lavelle et al., 2017) as a guide (Supplemental Table 1). We also included a control (no scent) attractant, which we used as a reference treatment for comparing all other attractants.

We used existing GIS vegetation layers to delineate areas on the SRS where wild pig activity was likely to be greatest using ArcMap 10.7.1 (Environmental Systems Research Institute, Redlands, CA, USA). Wild pigs were widely dispersed throughout the SRS, but concentrated their movements within riparian areas, bottomland habitat, and mixed forests with high canopy cover (Clontz et al., 2021). We generated random points within these land covers that were a minimum of 350 m apart and within 150 m from roads to facilitate accessibility. Then, we randomly selected 90 sites from the random points as our focal sites.

We conducted pilot trials across two periods: three weeks in early-April 2020 and four weeks in late-May–late-June 2020. The break between the two cycles was to evaluate our treatment procedure, make any necessary adjustments, and allow time for any lingering scents from the previous cycle to dissipate. Sixty-four sites were used in the first period and all 90 sites were used in the second period.

We created plaster-based scent-tabs (DAP®, Baltimore, MD, USA) for each attractant treatment following the methods outlined by (Webster and Beasley, 2019). Each tab was evenly coated and soaked in an attractant for one hour before deployment. During the April period we soaked the control treatment tabs in ultrapure water but found this caused the tabs to partially dissolve following deployment. Therefore, during the May–June period, and all subsequent trials, the control treatment tabs were not soaked.

During pilot trials we deployed the scent-tabs on a t-post, mounted ~1.5 m above the ground with a 101.6 cm white PVC pipe slid over the t-post to protect from non-target animals accessing the scent tabs. We attached the scent tabs using a wire ~122 cm off the ground. We attached the scent tab with wire so that it was suspended ~7.5–15 cm away from the t-post to prevent scent contamination on the post. We placed a remote camera (HyperFire 2 Professional White Flash; Reconyx®, Holmen, WI) 3.7 m away and 0.6 m off the ground facing the scent tab. Cameras were set to take three pictures per motion-activated trigger with one second between pictures and zero seconds between triggers. Camera settings, memory cards, and batteries were checked each time sites were visited to set or replenish attractants.

At each site, we randomly assigned an attractant that was presented for three days, with day of deployment representing day 1 of each attractant trial. After which we removed the first attractant and replaced it with a new, randomly assigned attractant. After another three days, we removed the second attractant and replaced with a third attractant for another three days. After the third attractant, we moved the site to a new location within 50–100 m from the original location. We moved the sites to minimize potential scent build-up, human-disturbance, and habituation by wild pigs. This cycle was repeated 18 times (i.e., 54-day pilot trial with three days per replicate). We ensured that no scent was placed at the same site twice during the same cycle. We always placed six control scents (i.e., no scent) during each three-day cycle to ensure we adequately measured variation at control sites throughout the pilot study. All research methods were approved by the United States Department of Agriculture, National Wildlife Research Center, Institutional Animal Care and Use Committee (protocol: QA-2620).

Table 1
List of 28 scent attractants (and 1 control) evaluated under the full study design for wild pigs in South Carolina and Texas, USA during 2020–2021.

Scent attractant	Manufacturer (City, State, Country)	Type
Control: unscented plaster tabs	DAP® (Baltimore, MD, USA)	NA
The Hog Bomb Sow N Heat	Hunters Specialties (Cedar Rapids, IA, USA)	Pheromone
Black Gold Wild Boar Attractant™	Wild Boar USA (Hallettsville, TX, USA)	Pheromone
Boarmasters Texas T Sticky Sweet	Boarmasters Wildlife Attractants (Chubbuck, ID, USA)	Food
Boarmasters Super Hot Hog Urine Scent-Dominant Boar	Boarmasters Wildlife Attractants (Chubbuck, ID, USA)	Pheromone
Creosote Bush Oil	Creosote Bush Salve Company (Alpine, TX, USA), borderlandsJewelry (Ciudad Benito Juarez, Mexico)	Curiosity or insecticide
Demeter Earthworm	Demeter Fragrance Library, Inc (Great Neck, NY, USA)	Food
Dry Pig-Krave	Nutriad, Inc, Adisseo (Hampshire, IL, USA)	Food
Dunlap Lure: DP Sauce Black Anise	Dunlap Lures (Alpena, MI, USA)	Curiosity or food
Pig Oil™	Elusive Wildlife (Conroe, TX, USA)	Pheromone
F&T Fur Harvester's Acorn Oil	F&T Fur Harvester's Trading Post (Alpena, MI, USA)	Food
F&T Fur Harvester's Blackberry Oil	F&T Fur Harvester's Trading Post (Alpena, MI, USA)	Food
F&T Fur Harvester's Caramel Essence Oil	F&T Fur Harvester's Trading Post (Alpena, MI, USA)	Food
F&T Fur Harvester's Fish Oil	F&T Fur Harvester's Trading Post (Alpena, MI, USA)	Food
Fatty Acid Scent	Pocatello Supply Depot (Pocatello, ID, USA)	Curiosity or food
Garlic oil (multiple brands, all 100 % garlic oil)	Bulk Apothecary (Aurora, OH, USA), Plant Guru (Plainfield, NJ, USA), Artizen (Denver, CO, USA)	Food
LorAnn Oils Watermelon Flavor	LorAnn Oils (Lansing, MI, USA)	Food
Methyl Anthranilate (Avian Migrate™)	Avian Enterprises® LLC (Sylvan Lake, MI, USA)	Food
Olive Nation Strawberry Extract	Olive Nation LLC (Avon, MA, USA)	Food
Pig Out® Wild Beast Bait	Evolved Habitats®, GSM Outdoors (Irving, YX, USA)	Food
Tuff Tusk™ Wild Hog Attractant	Razorback Outfitters LLC (McDade, TX, USA)	Food
Tink's® Specialty Power Pig Sow-in-Heat Estrous	Arcus Hunting, LLC (Covington, GA, USA)	Pheromone
WCS™ Apple Essence (wild)	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Cheese Oil	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Cinnamon Oil	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Orange Oil	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Peanut Butter Oil	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Sweet Corn Essential Oil	Wildlife Control Supplies (Suffield, CN, USA)	Food
WCS™ Synthetic Fermented Egg	Wildlife Control Supplies (Suffield, CN, USA)	Curiosity or food

2.2.2. Full seasonal trials

We desired to retain all the attractants for the full seasonal trials but based on results from the pilot trials, we opted to exclude the lowest performing attractants to increase replicates and maximize statistical power for comparison of the top-performing attractants. We identified that 23 of the initially identified attractants had ≤ 3 total visitations by wild pigs during the pilot trials (out of the 9–27 replicates each attractant was tested), which we deemed as having little support for continued testing. We also narrowed the pool of attractants by selecting the top-performing attractant from sets of redundant scents (e.g., no two corn-based scents), which eliminated another 9 attractants. Finally, we added one additional attractant (garlic oil) to the full seasonal trials which was unlike other scents and deemed worthy of evaluation. Overall, we proceeded with 29 attractants (including a control) in the full seasonal study (Table 1) which encompassed an array of scent attractant-types (e.g., food, pheromone, and curiosity). We defined the seasons as fall (October–December 2021), winter (January–March 2021) and spring (April–June 2021). However, we used the pilot trials (April–June 2020) as the spring season data at SRS because we had adequate sample sizes from the pilot trials.(Fig. 1).

We made some minor adjustments to improve our presentation of attractants based on observations during pilot trials. Specifically, we placed a second scent tab ~1–2 cm above the ground and ~7.5–15 cm from the post suspended from a wire to increase scent dispersion at each station. We also increased the amount of time scent tabs were soaked in each treatment to 24 h. We placed the scent tabs in light-weight cages made from plastic chicken fencing that we secured to the t-post with wire to protect scent tabs from wildlife tampering (Fig. 2). We excluded

Fig. 2. Example of a wild pigs visiting a scent-station deployed in South Carolina and Texas, USA during 2020–2021. Scent-infused tabs were protected by wire mesh and deployed at the base and ~1.5 m high on a t-post. Scent-stations were standardized with remote cameras mounted 3.7 m away and 0.6 m off the ground to maintain consistent fields of view.

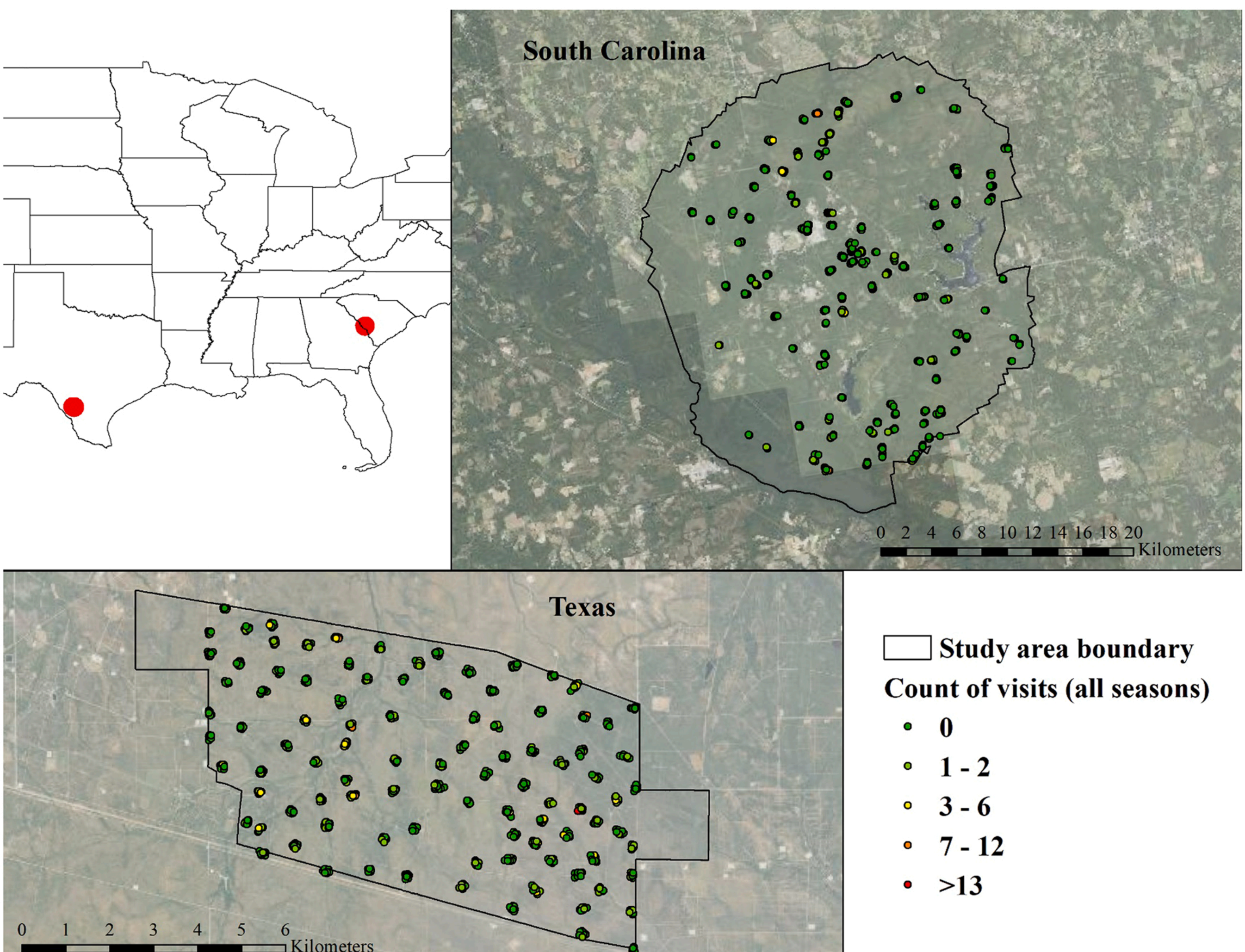

Fig. 1. Study areas and visitation by wild pigs in South Carolina and Texas, USA during 2020–2021.

the white PVC pipe from covering the t-post in case wild pigs were responding to the visual stimuli. Lastly, we increased the time each attractant was deployed at each station to seven days in attempt to garner greater visitation rates and increase our ability to discern differences among attractants. We refreshed the scent tabs with newly soaked scent tabs approximately halfway through the seven-day-cycle for each attractant at each site. We did not know how long each scent might be attractive to wild pigs, but previous research has shown that wild pigs are likely to visit a bait site within 5–6 days, or else not likely to visit at all (Lavelle et al., 2018; Snow and VerCauteren, 2019).

We deployed attractants at CWMA and SRS for 8-week seasons from October–December 2021 (fall) and January–March 2021 (winter). We also deployed at CWMA during April–June 2021 (spring), so ultimately each study area included three full seasons. We allowed for a four-week resting period between all seasons. We established 90–98 stations at each study area for each season, respectively. We selected bait station locations on CWMA like described above in the pilot trial (i.e., ≥350 m apart and ≤150 m from roads). We considered the entire CWMA as suitable for wild pigs (W. Gann, CWMA, personal communication) in which random locations were generated. We deployed scents at the randomly generated locations for each season, respectively, unless we encountered site restriction(s) (e.g., flooding, etc.) that required us to generate new random location(s).

We randomly assigned a scent treatment to each random site for a seven-day-cycle, so that each site had eight attractants placed during each season. We were able to deploy ~50 % of the treatments in one day, thus we deployed the first half of the treatments on day 1 and the second half on day 2. All treatments were deployed for an entire seven-day-cycle regardless of the day deployed. After the completion of a seven-day-cycle, we relocated the sites to new locations 50–100 m from the previous location, and 50–100 m from the original site location. We deployed a new randomly selected treatment at the new site to initiate another seven-day-cycle. We repeated this procedure for eight, seven-day-cycles during each season. We ensured that no treatment was placed at the same site twice during the same season.

In CWMA we used a slightly different camera model (HyperFire 2 Professional Infrared; Reconyx®) than SRS, but we expect this did not impact our observations because both were covert, and we used the same camera settings in each study area (i.e., settings described in the pilot trial). Overall, each treatment was deployed at 24 sites each season except for the control treatment, which we randomly placed at 69 sites per season. We increased the replicates of the control treatment because we considered this as the baseline (i.e., reference treatment), in which we compared all other treatments, and we attempted to account for any variation in the baseline by increasing the number of replicates.

2.3. Image processing

All images were imported into the Colorado Parks and Wildlife Photo Database for image processing (Ivan and Newkirk, 2016) for the pilot study, and Microsoft Excel for the main study. We used a single-observer technique to identify and count the number of wild pigs in each image. Any wild pig viewed in an image was considered as visiting the site, which we used to create indices of visitation among all scent treatments (i.e., we used indices because our scent stations and camera placements were standardized). We considered unique visitation events as any sequence of images with visitation that were separated by ≥ 15 mins from the previous visitation. For each visitation event, we recorded date, time, and the maximum number of wild pig present (i.e., the greatest number of wild pigs observed in a single image during the visitation event). For each visitation, we recorded the number of each sex observed (i.e., male, female, or unknown).

2.4. Analysis of attractants

We plotted the mean number of visits by scent treatment and 95 % confidence intervals (CIs) of those means for each study area by season and sex. We standardized means for treatment scents relative to the control treatments by subtracting the mean number of visits observed at control sites. We plotted the standardized means and CIs to examine for any scent treatments that had greater or fewer visits than the control sites by examining if the 95 % CIs overlapped zero.

Then, we evaluated how well each scent treatment attracted wild pigs using two response variables; one to compare the likelihood of wild pig visitation, the other to compare how rapidly wild pigs found and visited each scent treatment. For the likelihood-of-visitation variable, we generated a binomial variable (yes/no) for whether any wild pigs were detected at a site during each replicate for each scent treatment. We used the binomial variable to evaluate which scent treatment increased the probability that wild pig visited a site. For the time-to-visitation variable, we recorded the day-of-first-visit by a wild pig since deployment of each scent treatment during each replicate.

We modeled the response variables using Integrated Nested Laplace Approximation (INLA) (Martino and Rue, 2009) using the INLA package (Lindgren and Rue, 2015) in Program R (version 4.1.1, The R Foundation for Statistical Computing, Vienna, Austria). We used a binomial distribution to model the likelihood-of-visitation, and a Poisson distribution for time-to-visitation. We evaluated the SRS and CWMA data separately and evaluated the results to identify any similarities. For each study area, we evaluated all combinations of model structures from the global model of: Response ~ Intercept + Scent + Season + Scent × Season (i.e., total of 5 model structures) and included Site ID as a random effect in each model to account for random variation and repeated measures from sites. We evaluated the importance of the random effect by comparing these models to those without the random effect of site ID.

We compared models using deviance information criterion (DIC) (Spiegelhalter et al., 2014), and made inferences using the top-ranked models (i.e., lowest DIC by ≥2.0 points) for each response variable. We also evaluated absolute goodness-of-fit using the area under the receiver operating characteristic curve (AUC) using the ROCR package (Sing et al., 2005) for the binomial models and R^2 values (i.e., squared correlation of observed and predicted) for the Poisson models.

For making inferences about the attractiveness of the scent treatments, we removed the intercept from the top-ranked models and designated the control treatments (i.e., no scent) as the reference for comparing all other treatments, and we designated the winter season as the reference for comparing all other seasons. This allowed us to interpret the responses in terms of how much more likely or rapidly visitation occurred to attractants relative to control sites in the winter. We evaluated the median parameter estimates and 95 % credible intervals (CIs) of those estimates for non-overlap of zeros to indicate statistical and biological differences between attractants and seasons, respectively. We also calculated the average predicted values for each attractant and season, respectively, and their 95 % prediction intervals (PIs) for making inferences.

2.5. Post hoc analysis of landscape

Because the random effect of site improved the model fit significantly by DIC, we concluded that the locations of the sites seemed to be highly influential to visitation by wild pigs. Thus, we conducted a post hoc analysis to evaluate what characteristics of the sites influenced the probability of visitation by wild pigs. Specifically, we calculated metrics of three landscape features for each site. First, we calculated the distances to the nearest water flowline (https://www.usgs.gov/national-hydrography/national-hydrography-dataset; accessed 03 Jan 2021), with the hypothesis that sites nearer to flowlines would have higher probability of visitation. Flowlines were considered as permanent or ephemeral drainages, streams, and rivers. Second, we calculated distance to the nearest road (i.e., paved road, gravel road, or dirt path), with the hypothesis that sites closer to roads would have higher probability of visitation. Third, we calculated the proportion of shelter landcover (see below) within 100 m buffer of the sites, with the hypothesis that sites with more shelter would have higher probability of visitation.

To define landcovers for our analysis, we used the 2019 National Land Cover Database (NLCD; https://www.mrlc.gov/data; accessed 03 Jan 2021) and reclassified from 15 to 4 land cover types for the South Carolina study site, and from 13 to 4 land cover types for the Texas study site. For both study sites we defined the 4 collapsed land covers as: shelter, open, developed, and other. The shelter land cover was comprised of deciduous, evergreen, and mixed (South Carolina only) forests; shrub/scrub; and woody wetland land covers. The open land cover was comprised of grassland/herbaceous, pasture/hay, cultivated crops (South Carolina only), and emergent herbaceous wetland land covers. The developed land covers were comprised of all intensities of developed land cover types (i.e., developed-open-space, low-, medium-, and high- intensity development). The other land covers were comprised of open water and barren land covers. Overall, the South Carolina study site was comprised of 85 % shelter, 8 % open, 4 % developed, and 2 % other land covers. The Texas study site was comprised of 69 % shelter, 30 % open, < 1 % developed, and < 1 % other land covers. We used the landscapemetrics package (Hesselbarth et al., 2019) in Program R to calculate the proportion of land cover types within 100 m buffers around each of the sites. We used 100 m buffers to keep our inferences localized to each site based on findings from previous research (Snow et al., 2021).

We conducted an intercorrelation analysis of the post hoc covariates to identify any correlated pairs of covariates (i.e., $|r| = 0.60$), and subsequently excluded one of the correlated covariates we anticipated would have the least influence on wild pig visitation. We evaluated the following binomial mixed-model using INLA: Visits (yes/no) ~ Season + Distance to road + Distance to flowline + Proportion of shelter + (Season × Distance to road) + (Season × Distance to flowline) + (Season × Proportion of shelter). We included Site ID as a random effect. We evaluated the interactions to determine if effects of landscape covariates varied by season. We did not evaluate main effects if interaction terms in the models were significant.

3. Results

3.1. Analysis of attractants

Overall, we deployed scent attractants at 105 sites in South Carolina and 98 sites in Texas across the 3 seasons. We collected and analyzed > 300,000 trail camera images during those deployments. The average likelihood-of-visitation by a wild pig to a bait site across all seasons in South Carolina was 0.05 and in Texas was 0.18. The average time-to-visitation for wild pigs to site in South Carolina was 4.45 days and in Texas was 4.60 days. We found evidence that only two scent attractants had greater visitation than the control treatments (i.e., strawberry extract and creosote bush oil), however this was only in the Texas study area during the fall season (Supplementary Figure 1). Otherwise, there was a high amount of variability amongst visitation to the scent attractants and no others performed better than the control treatments. We found no evidence that any scent attractants performed better for female or male wild pigs (Supplementary Figure 2).

The top-ranked model for predicting the likelihood-of-visitation in South Carolina and Texas both included season and the random effect of site (Table 2). In South Carolina, fall had a higher probability of visitation than winter ($\beta = 0.63$; 95 % CI = 0.33–0.93), and the spring had a similar probability as winter ($\beta = 0.21$; 95 % CI = −0.11 to 0.54). The South Carolina model predicted that the probability of visitation in fall was 0.18 (95 % PI = 0.14–0.22), spring was 0.13 (95 % PI = 0.09–0.16), and winter was 0.10 (95 % PI = 0.07–0.14). In Texas, fall had a higher probability of visitation than winter ($\beta = 1.14$; 95 % CI = 0.85–1.44), and spring had a lower probability than winter ($\beta = -0.72$; 95 % CI = −1.07 to −0.38). The Texas model predicted that the probability of visitation in fall was 0.26 (95 % PI = 0.20–0.32), spring was 0.05 (95 % PI = 0.03–0.07), and winter was 0.10 (95 % PI = 0.07–0.13).

The top-ranked model for predicting the time-to-visitation in South Carolina and Texas also included season and the random effect of site (Table 3). However, there was a competing top-ranked model for South Carolina that just included season (i.e., no random effect). Inferences were similar between the competing top-models thus we used the top-

Table 2
Model selection table from binomial models evaluating the likelihood of visitation by wild pigs in South Carolina and Texas, USA during 2020–2021.

Model	DIC	AUC
SOUTH CAROLINA		
visits ~ intercept + season + (site random effect)	1659.31	0.80
visits ~ intercept + (site random effect)	1674.15	0.79
visits ~ intercept + scent + season + (site random effect)	1683.40	0.80
visits ~ intercept + scent + (site random effect)	1699.37	0.79
visits ~ intercept + scent + season + scent×season + (site random effect)	1746.55	0.82
visits ~ intercept + season	1816.53	0.73
visits ~ intercept	1827.74	0.50
visits ~ intercept + scent + season	1849.23	0.61
visits ~ intercept + scent	1860.92	0.60
visits ~ intercept + scent + season + scent×season	1943.41	0.65
Post hoc		
visits ~ intercept + season + road + flowline + shelter + season×road + season×flowline + season×shelter + (site random effect)	1656.15	0.80
TEXAS		
visits ~ intercept + season + (site random effect)	1565.90	0.85
visits ~ intercept + scent + season + (site random effect)	1587.53	0.85
visits ~ intercept + (site random effect)	1705.16	0.82
visits ~ intercept + scent + (site random effect)	1728.51	0.82
visits ~ intercept + scent + season + scent×season + (site random effect)	1826.42	0.87
visits ~ intercept + season	1846.76	0.81
visits ~ intercept + scent + season	1879.47	0.69
visits ~ intercept	1948.99	0.50
visits ~ intercept + scent	1982.43	0.61
visits ~ intercept + scent + season + scent×season	2163.17	0.72
Post hoc		
visits ~ intercept + season + road + flowline + shelter + season×road + season×flowline + season×shelter + (site random effect)	1564.77	0.85

Table 3
Model selection table from Poisson models evaluating the time-to-first-visitation by wild pigs to site in South Carolina and Texas, USA during 2020–2021.

Model	DIC	MSE	R^2
SOUTH CAROLINA			
day ~ intercept + season + (site random effect)	1303.29	3.07	0.17
day ~ intercept + season	1304.07	3.08	0.17
day ~ intercept + scent + season + (site random effect)	1335.81	2.82	0.22
day ~ intercept + scent + season	1336.67	2.85	0.21
day ~ intercept + (site random effect)	1358.54	2.97	0.25
day ~ intercept + scent + season + scent×season + (site random effect)	1378.57	2.36	0.22
day ~ intercept + scent + season + scent×season	1379.55	2.37	0.21
day ~ intercept + scent + (site random effect)	1381.89	2.71	0.22
day ~ intercept	1391.01	3.70	0.00
day ~ intercept + scent	1418.43	3.49	0.05
TEXAS			
day ~ intercept + season + (site random effect)	1527.95	3.28	0.20
day ~ intercept + scent + season + (site random effect)	1534.90	2.94	0.17
day ~ intercept + (site random effect)	1537.16	3.39	0.22
day ~ intercept + scent + (site random effect)	1546.77	3.07	0.21
day ~ intercept + scent + season + scent×season + (site random effect)	1571.34	2.47	0.20
day ~ intercept + season	1572.32	4.01	0.01
day ~ intercept	1576.07	4.06	0.00
day ~ intercept + scent + season	1579.26	3.69	0.06
day ~ intercept + scent	1584.13	3.74	0.06
day ~ intercept + scent + season + scent×season	1614.70	3.20	0.10

ranked model for reporting. In South Carolina, fall had similar time-to-visitation as winter (β = 0.01; 95 % CI = −0.14 to 0.16), and spring had a quicker time-to-visitation than winter (β = −0.78; 95 % CI = −0.97 to −0.58). However, spring season in South Carolina was the pilot trial which had quicker replicates (i.e., three days), thus the relationship may be an artifact of the design. The South Carolina model predicted that time-to-visitation in fall was 3.11 days (95 % PI = 2.82–3.45), spring was 1.42 days (95 % PI = 1.21–1.66), and winter was 3.09 days (95 % PI = 2.75–3.45). In Texas, time-to-visitation during both fall (β = −0.15; 95 % CI = −0.32 to 0.03) and spring (β = 0.13; 95 % CI = −0.06 to 0.32) were similar to winter, respectively. The Texas model predicted that time-to-visitation in fall was 2.33 days (95 % PI = 2.07–2.62), spring was 3.09 days (95 % PI = 2.63–3.63), and winter was 2.73 days (95 % PI = 2.37–3.13).

3.2. Post hoc analysis of landscape

Landscape covariates were all uncorrelated in both study areas. For South Carolina and Texas, respectively, the post hoc analyses revealed the lowest DIC rankings compared with the above binomial models (Table 2). In South Carolina during winter, we found that sites closer to roads had increased probabilities of visitation by wild pigs which was not observed during fall and spring seasons (Table 4; Fig. 3). Also in South Carolina, sites with greater proportions of shelter land cover had increased probabilities of visitation during the spring season. In Texas during winter, we found that sites closer to flowlines had increased probabilities of visitation by wild pigs which was not observed during the fall and spring seasons.

4. Discussion

To our knowledge, this study represents the most comprehensive analysis of potential scent attractants for wild pigs throughout the world; including an extensive evaluation of a broad suite of attractants (60 total) across three seasons and two distinct geographical regions. Despite this, we surprisingly found little evidence that any scent attractants performed better than control sites with no scents. Only a strawberry extract scent and a creosote bush oil scent in Texas during the fall season performed better than the control sites. For strawberry, these findings match a previous study in Texas that also found strawberry scent to be attractive to wild pigs (Campbell and Long, 2008). However, an additional study showed that strawberry baits did not perform well (Campbell and Long, 2009). For creosote bush oil, there have been similarly mixed results on whether related substances (e.g., birchwood tar and creosote tar) were attractive to wild pigs (Elsworth et al., 2004; Massei et al., 2021), but have also shown utility in deterring non-targets (Elsworth et al., 2004). All other scents performed similarly or worse than the control sites during all seasons, indicating that wild pigs were not attracted to any other scents that we could detect.

Table 4
Parameter estimates and 95 % credible intervals (CIs) for a post hoc model evaluating the effects of landscape on the likelihood of visitation by wild pigs in South Carolina and Texas, USA during 2020–2021.

	Parameter Estimates		
Predictor variable	Median	Lower CI	Upper CI
SOUTH CAROLINA			
Fall	3.169*	0.770	5.711
Spring	-2.457	-5.547	0.512
Distance to road	0.011*	0.004	0.019
Distance to stream	0.000*	0.000	0.001
Proportion of shelter	-0.001	-0.024	0.023
Fall × distance to road	-0.013*	-0.022	-0.003
Spring × distance to road	-0.013*	-0.022	-0.003
Fall × distance to stream	-0.001	-0.001	0.000
Spring × distance to stream	-0.001	-0.001	0.000
Fall × proportion of shelter	-0.017	-0.044	0.009
Spring × proportion of shelter	0.039*	0.008	0.071
TEXAS			
Fall	0.873	-0.309	2.081
Spring	-0.807	-2.162	0.531
Distance to road	0.003	-0.006	0.013
Distance to stream	-0.002*	-0.004	-0.001
Proportion of shelter	0.005	-0.006	0.017
Fall × distance to road	-0.002	-0.014	0.010
Spring × distance to road	-0.003	-0.017	0.011
Fall × distance to stream	0.001*	0.000	0.002
Spring × distance to stream	0.002*	0.001	0.004
Fall × proportion of shelter	0.001	-0.010	0.013
Spring × proportion of shelter	-0.005	-0.017	0.008

[*] Indicates a statistically and biologically significant relationship.

Considering the advanced olfactory senses of wild pigs, a plethora of commercially available attractants have been developed specifically for wild pigs (Lavelle et al., 2017), and scent attractants are often recommended to attract wild pigs (Engeman et al., 2013). Thus, the limited effectiveness of scent attractants in attracting wild pigs in our study was unexpected. However, two previous studies in the UK and USA also found that wild pigs appeared to visit control sites as frequently or more frequently than sites with attractants (Wathen et al., 1988; Massei et al., 2021), and another study found that no attractants increased consumption of baits by wild pigs (Elsworth et al., 2004). This evidence suggests that most scent attractants are not sufficient for increasing the visitation of free-ranging wild pigs to an area. This is especially remarkable considering most attractants also did not increase visitation by season or by sex. We expected more responses related to food availability or reproductive seasons because of the well-established behaviors of wild pigs (Mayer and Brisbin, 2009). We did find increased visitation to all sites (regardless of scent attractant) during the fall season in both study locations, which indicated a seasonal behavior that could be exploited for controlling wild pigs. The reason for increased visitation during the fall is uncertain, but could be related to increased space-use during dryer periods (Kay et al., 2017; Gray et al., 2020), for reproductive behaviors (Gray et al., 2020), or in response to hunting pressure (Calenge et al., 2002). Regardless, attracting wild pigs to trapping or toxic baiting sites may be most efficient during the fall season.

The most influential factor for increasing visitation by wild pigs appeared to be the site location. The random effect of Site ID was in every top model, and improved model fit whenever included. Our post hoc analysis revealed some aspects of location that may explain why visitation was higher in some locations. In South Carolina, sites closer to roads were visited most during the winter. Our sites were constrained to be near roads (i.e., ≤150 m), therefore these results indicate that wild pigs may have been directly using the roads. These results are corroborated by previous studies that have shown wild pigs select roads for traveling in certain seasons (Clontz et al., 2021), and linear features of landscapes (Snow et al., 2021). During the winter in Texas, wild pigs visited sites closer to water flowlines which would represent places in this arid environment with moisture for rooting, wallowing, or foraging behaviors (Gray et al., 2020). Overall, our findings suggest that prioritizing locations where wild pigs concentrate their movements would be more effective than relying on scent attractants to attract wild pigs from afar. As suggested in previous studies (Lavelle et al., 2018; Snow and VerCauteren, 2019), if wild pigs are not visiting targeted sites within a few days (i.e., 5–7 days), we recommend moving sites to new locations nearer to where wild pigs are concentrating their activity, rather than relying on scent attractants to pull them in.

A primary limitation of our study is that wild pigs may have responded to our scent attractants, but we could not detect their responses using remote cameras aimed directly at the treatments. For example, wild pigs could have approached but stayed out of camera view once they realized there was no reward. A solution for this would be to use GPS collars on wild pigs to test for responses that occurred farther away from the sites. Alternatively, offering a pile of whole-kernel corn or similar food bait at the sites could overcome the issue of no

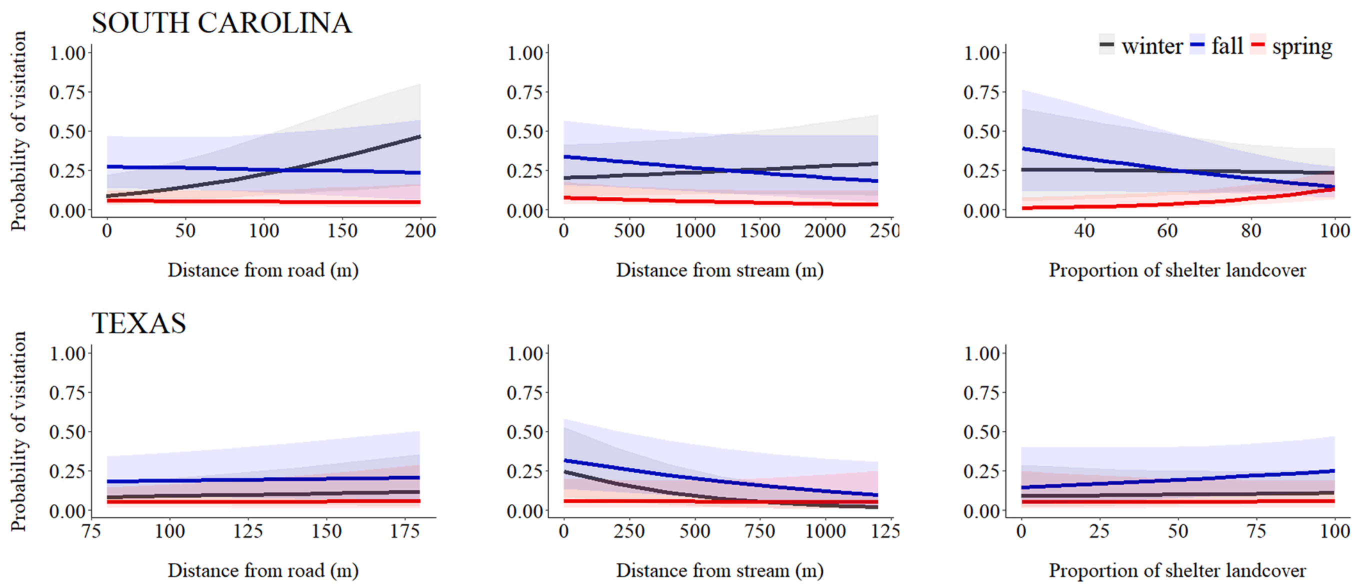

Fig. 3. Predicted probabilities of visitation by wild pigs based on seasonal and landscape metrics in South Carolina and Texas, USA during 2020–2021.

reward, but would confound the effects of a scent attractant. Additionally, a controlled experiment on captive wild pigs could also be useful for comparing preferences to scents. Another limitation is that we do not know how far away our scent treatments could be detected by wild pigs. We tried to overcome this by having adequate sample size to account for site-to-site variation, but the effects of site-to-site variation seemed to be a major driver of visitation, overwhelming any potential effects of scent. For example, localized wind conditions could have dispersed scents better at particular sites which we did not measure. Wild pigs are known to reliably visit bait sites from distances averaging 1–1.5 km (McRae et al., 2019; Snow and VerCauteren, 2019), therefore we expect they should have detected our scent attractants from greater-than-localized distances. Further, considering that we did not detect differences in the speeds at which wild pigs visited the sites, we expect the lack of response was due to the ineffectiveness of the scents rather than our study design.

5. Conclusions

Out of 60 scent attractants tested, we did not identify a panacea attractant that could be used to effectively attract wild pigs across seasons and regions in the US. Most scents tested did not attract wild pigs, except for strawberry extract and creosote bush oil, but only during the fall season in Texas. We recommend that managers attempting to control populations of wild pigs by attracting them to focal sites for removal (e.g., trapping, toxic baiting, shooting) prioritize choosing the best locations rather than relying on scent attractants to attract wild pigs from afar. If wild pigs are not visiting sites, we recommend moving the sites to new locations rather than deploying different scents. Next steps of this research could focus on using GPS collars to determine if scent attractants brought wild pigs close to sites (just not in front of remote cameras. Also, combining scent attractants with rewards for wild pigs (e.g., consumable baits) to see if a combination could be more effective at attracting wild pigs from farther and faster.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The research was supported by the United States Department of Agriculture. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official US Government determination or policy. Mention of commercial products or companies does not represent an endorsement by the US government. Contributions of C.A. Kupferman and J.C. Beasley were partially supported by the Department of Energy Office of Environmental Management under Award Number DE-EM0005228 to the University of Georgia Research Foundation. We thank J. Benavidez, H. Bontrager, K. Brumm, S. Cook, C. Dawson, S. Graber, B. Maiersperger, I. Messer, A. Murray, A. Neal, A. Plascencia, and A. Stift for assisting with data collection. We thank anonymous reviewers for their comments on this manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2022.105705.

References

Ballari, S.A., Cuevas, M.F., Ojeda, R.A., Navarro, J.L., 2015. Diet of wild boar (Sus scrofa) in a protected area of Argentina: the importance of baiting. Mamm. Res. 60, 81–87.

Barrios-Garcia, M.N., Ballari, S.A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol. Invasions 14, 2283–2300.

Beasley, J.C., Ditchkoff, S.S., Mayer, J.J., Smith, M.D., Vercauteren, K.C., 2018. Research priorities for managing invasive wild pigs in North America. J. Wildl. Manag. 82, 674–681.

Bieber, C., Ruf, T., 2005. Population dynamics in wild boar Sus scrofa: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J. Appl. Ecol. 42, 1203–1213.

Broom, D.M., Fraser, A.F., 2007. Domestic animal behaviour and welfare. CABI, Wallingford, UK, p. 438.

Brunjes, P.C., Feldman, S., Osterberg, S.K., 2016. The pig olfactory brain: a primer. Chem. Senses 41, 415–425.

Calenge, C., Maillard, D., Vassant, J., Brandt, S., 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game and Wildlife. Sci. (Fr.) 19, 281–301.

Campbell, T.A., Long, D.B., 2008. Mammalian visitation to candidate feral swine attractants. J. Wildl. Manag. 72, 305–309.

Campbell, T.A., Long, D.B., 2009. Strawberry-flavored baits for pharmaceutical delivery to feral swine. J. Wildl. Manag. 73, 615–619.

Campbell, T.A., Long, D.B., Shriner, S.A., 2013. Wildlife contact rates at artificial feeding sites in Texas. Environ. Manag. 51, 1187–1193.

Choquenot, D., Kilgour, R.J., Lukins, B.S., 1993. An evaluation of feral pig trapping. Wildl. Res. 20, 15–21.

Clontz, L.M., Pepin, K.M., VerCauteren, K.C., Beasley, J.C., 2021. Behavioral state resource selection in invasive wild pigs in the Southeastern United States. Sci. Rep. 11, 1–14.

Comer, C.E., Mayer, J.J., 2009. Wild pig reproductive biology. Wild pigs: biology, damage, control techniques, and management. In: Mayer, J.J., Brisbin Jr., I.L. (Eds.), SRNL-RP-2009-00869. Savannah River National Laboratory, Aiken, South Carolina, pp. 51–75.

Elsworth, P., Mitchell, J., Parker, R., 2004. Evaluation of attractants and toxins for improved target specificity in the control of feral pigs, Report to the National Feral Animal Control Program.(Department of Natural Resources and Mines: Inglewood.), Queensland Government Natural Resources and Mines, Department of Natural Resources and Mines. Inglew. Qld 4387 28.

Engeman, R., Massei, G., Sage, M., Gentle, M., 2013. Monitoring wild pig populations: a review of methods. Environ. Sci. Pollut. Res. 20, 8077–8091.

Ferretti, F., Coats, J., Cowan, D.P., Pietravalle, S., Massei, G., 2018. Seasonal variation in effectiveness of the boar-operated system to deliver baits to wild boar. Pest Manag. Sci. 74, 422–429.

Gabor, T.M., Hellgren, E.C., Silvy, N.J., 2001. Multi-scale habitat partitioning in sympatric suiforms. J. Wildl. Manag. 65, 99–110.

Gaskamp, J.A., Cathey, J.C., Higginbotham, B., Bodenchuk, M.J., 2019. Wild pigs in south-central North America. In: VerCauteren, K.C., Beasley, J.C., Ditchkoff, S.S., Mayer, J.J., Roloff, G.J., Strickland, B.K. (Eds.), Invasive wild pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA, pp. 347–368.

Gieling, E.T., Nordquist, R.E., van der Staay, F.J., 2011. Assessing learning and memory in pigs. Anim. Cogn. 14, 151–173.

Gray, S.M., Roloff, G.J., Montgomery, R.A., Beasley, J.C., Pepin, K.M., 2020. Wild pig spatial ecology and behavior. In: VerCauteren, K.C., Beasely, J., Ditchkoff, S.S., Mayer, J., Roloff, G.J., Strickland, B.K. (Eds.), Invasive wild pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA, pp. 33–56.

Hannes, G., Heinz-Ulrich, R., 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J. Wildl. Manag. 68, 939–946.

Hesselbarth, M.H., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42, 1648–1657.

Hone, J., 1990. How many feral pigs in Australia. Wildl. Res. 17, 571–572.

Ivan, J.S., Newkirk, E.S., 2016. CPW Photo Warehouse: a custom database to facilitate archiving, identifying, summarizing and managing photo data collected from camera traps. Methods Ecol. Evol. 7, 499–504.

Karlin, M.L., Khan, H.A., 2020. Determining feral pig (Sus scrofa) attractant selection preference and response to mock corral traps. Texas Journal of Science 72, Article 1.

Kay, S.L., Fischer, J.W., Monaghan, A.J., Beasley, J.C., Boughton, R., Campbell, T.A., Cooper, S.M., Ditchkoff, S.S., Hartley, S.B., Kilgo, J.C., Wisely, S.M., Wyckoff, A.C., VerCauteren, K.C., Pepin, K.M., 2017. Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Mov. Ecol. 5, 14.

Keiter, D.A., Davis, A.J., Rhodes, O.E., Cunningham, F.L., Kilgo, J.C., Pepin, K.M., Beasley, J.C., 2017. Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. Sci. Rep. 7, 9446.

Lavelle, M.J., Snow, N.P., Fischer, J.W., Halseth, J.M., VanNatta, E.H., VerCauteren, K.C., 2017. Attractants for wild pigs: current use, availability, needs, and future potential. Eur. J. Wildl. Res. 63, 86.

Lavelle, M.J., Snow, N.P., Halseth, J.M., VanNatta, E.H., Sanders, H.N., VerCauteren, K.C., 2018. Evaluation of movement behaviors to inform toxic baiting strategies for invasive wild pigs (*Sus scrofa*). Pest Manag. Sci. 74, 2504–2510.

Lewis, J.S., Corn, J.L., Mayer, J.J., Jordan, T.R., Farnsworth, M.L., Burdett, C.L., VerCauteren, K.C., Sweeney, S.J., Miller, R.S., 2019. Historical, current, and potential population size estimates of invasive wild pigs (*Sus scrofa*) in the United States. Biol. Invasions 21, 2373–2384.

Lewis, J.S., Farnsworth, M.L., Burdett, C.L., Theobald, D.M., Gray, M., Miller, R.S., 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Sci. Rep. 7, 44152.

Lindgren, F., Rue, H., 2015. Bayesian spatial modelling with R-INLA. J. Stat. Softw. 63, 1–25.

Martino, S., Rue, H., 2009. Implementing approximate Bayesian inference using Integrated Nested Laplace Approximation: A manual for the inla program, Department of Mathematical Sciences, NTNU, Norway, http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.431.9452&rep=rep1&type=pdf, pp. 1–72.

Massei, G., Cowan, D.P., Coats, J., 2021. A novel method for detecting wild boar presence. Hum. Interact. 15, 14.

Massei, G., Roy, S., Bunting, R., 2011. Too many hogs? A review of methods to mitigate impact by wild boar and feral hogs. Hum. Wildl. Interact. 5, 79–99.

Mayer, J., Brisbin, I.L. (Eds.), 2009. Wild pigs: biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, USA.

Mayer, J.J., Beasley, J.C., Boughton, R.K., Ditchkoff, S.S., 2019. Wild pigs in southeastern North America. In: VerCauteren, K.C., Beasley, J.C., Ditchkoff, S.S., Mayer, J.J., Roloff, G.J., Strickland, B.K. (Eds.), Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA, pp. 369–402.

Mayer, J.J., Brisbin, I.L., 1986. A note on the scent-marking behavior of two captive-reared feral boars. Appl. Anim. Behav. Sci. 16, 85–90.

McClure, M.L., Burdett, C.L., Farnsworth, M.L., Lutman, M.W., Theobald, D.M., Riggs, P.D., Grear, D.A., Miller, R.S., 2015. Modeling and mapping the probability of occurrence of invasive wild pigs across the contiguous United States. PloS One 10, e0133771.

McIlroy, J., Gifford, E., 2005. Are oestrous feral pigs, *Sus scrofa*, useful as trapping lures? Wildl. Res. 32, 605–608.

McIlroy, J., Gifford, E., Forrester, R., 1993. Seasonal patterns in bait consumption by feral pigs (Sus scrofa) in the Hill Country of South-Eastern Australia. Wildl. Res. 20, 637–651.

McRae, J.E., Schlichting, P.E., Snow, N.P., Davis, A.J., VerCauteren, K.C., Kilgo, J.C., Keiter, D.A., Beasley, J.C., 2019. Factors affecting bait site visitation: area of influence of baits Wildl. Soc. Bull. 44, 362–371.

Sandoval, N., Williams, B.L., Ditchkoff, S.S., Smith, M.D., 2019. Relative efficacy of a urinebased lure for attracting wild pigs. J. Southeast. Assoc. Fish. Wildl. Agencies 6, 156–160.

Schley, L., Roper, T.J., 2003. Diet of wild boar Sus scrofa in Western. Eur. Part. Ref. Consum. Agric. Crops Mamm. Rev. 33, 43–56.

Seigler, D.S., Ebinger, J.E., Kerber, A., 2007. Characterization of thorn-scrub woodland communities at the Chaparral wildlife management area in the south Texas Plains, Dimmit and La Salle Counties, Texas. Phytologia 89, 241–257.

Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21, 3940–3941.

Snow, N.P., Halseth, J.M., Glow, M.P., Lavelle, M.J., Fischer, J.W., VanNatta, E.H., VerCauteren, K.C., 2021. Daily and landscape influences of species visitation to toxic bait sites for wild pigs. Wildl. Soc. Bull. 45, 109–120.

Snow, N.P., Halseth, J.M., Lavelle, M.J., Hanson, T.E., Blass, C.R., Foster, J.A., Humphrys, S.T., Staples, L.D., Hewitt, D.G., VerCauteren, K.C., 2016. Bait preference of free-ranging feral swine for delivery of a novel toxicant. PLoS One 11, e0146712.

Snow, N.P., Jarzyna, M.A., VerCauteren, K.C., 2017. Interpreting and predicting the spread of invasive wild pigs. J. Appl. Ecol. 54, 2022–2032.

Snow, N.P., Miller, R.S., Beasely, J., Pepin, K.M., 2020. Wild pig population dynamics. In: VerCauteren, K.C., Beasely, J., Ditchkoff, S.S., Mayer, J., Roloff, G.J., Strickland, B.K. (Eds.), Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA, pp. 57–82.

Snow, N.P., VerCauteren, K.C., 2019. Movement responses inform effectiveness and consequences of baiting wild pigs for population control. Crop Prot. 124, 104835.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van der Linde, A., 2014. The deviance information criterion: 12 years on. J. R. Stat. Soc.: Ser. B: Stat. Methodol. 485–493.

Sullivan, S.R., 2015. Management and impacts of wild hogs (*Sus scrofa*) in South Carolina (M.S. Thesis). Clemson University, South Carolina, USA, p. 103 (M.S. Thesis).

Sundman, E.R., Gabler, N.K., Millman, S.T., Stalder, K.J., Karriker, L.A., Johnson, A.K., 2022. The use of attractants to stimulate Neonatal Piglet interest in rope enrichment. Animals 12, 211.

VerCauteren, K.C., Beasley, J.C., Ditchkoff, S.S., Mayer, J.J., Roloff, G.J., Strickland, B.K. (Eds.), 2019. Invasive Wild Pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA, p. 477.

Wathen, G., Thomas, J., Farmer, J., 1988. European Wild Hog Bait Enhancement Study. Final Report, University of Tennessee, College of Veterinary Medicine.

Webster, S.C., Beasley, J.C., 2019. Influence of lure choice and survey duration on scent stations for carnivore surveys. Wildl. Soc. Bull. 43, 661–668.

White, D.L., Gaines, K.F., 2000. The Savannah River Site: site description, land use, and management history. Stud. Avian Biol. 21, 8–17.