A four-pronged approach to addressing a wild pig invasion in a bottomland and upland forested landscape

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A four-pronged approach to addressing a wild pig invasion in a bottomland and upland forested landscape

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Among exotic species that are capable of invading, establishing, and reaching pest status, few pose the range of impacts to biotic (e.g., competition with native species, predation, herbivory, introduction of other exotics) and abiotic (e.g., soil, hydrology) ecosystem components that can be attributed to the wild pig (Sus scrofa). Despite the presence of wild pigs throughout the southeastern United States for centuries, new invasions continue to occur in previously uninhabited and often under-investigated landscapes, including bottomland and upland forests. The recent invasion of the Sam D. Hamilton Noxubee National Wildlife Refuge (hereafter, NNWR) in east-central Mississippi represents an opportunity to understand not only a species invasion during an emergent stage, but also to improve and better inform the methods used to combat such species in forested landscapes. In recent years, the United States Fish and Wildlife Service has begun to observe direct impacts to this ecologically sensitive area which is critically important to not only migratory waterfowl but also a multitude of other faunal (e.g., amphibians, reptiles, and avian species of concern) and floral species. As a result, identifying wild pig spatial distributions (e.g., movements, occurrence) and estimating wild pig abundance in the NNWR have each increased in priority. My dissertation research has facilitated an improved
understanding of how wild pigs have invaded this novel landscape through investigations of space use, abundance, and occurrence, and will better inform and improve efficiency of future monitoring and control efforts. Understanding how this wild pig invasion relates to the NNWR landscape may also provide information that can be used to better address wild pig invasions of similar landscapes, with added value for those that are similarly characterized by sensitive ecosystems (i.e., managed for migratory waterfowl, species of concern) that are currently faced with this emerging threat. Given the universality of many of the methodological approaches undertaken in this effort, this multifaceted investigation also provides broader implications for other landscapes and exotic species of interest.
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CHAPTER I

WHAT DRIVES WILD PIG (SUS SCROFA) MOVEMENT IN BOTTOMLAND AND UPLAND FORESTS?

Abstract

The wild pig (Sus scrofa) is an exotic species that has been present in the southeastern United States for centuries yet continues to expand into new areas dominated by bottomland and upland forests, the latter of which are less commonly associated with wild pigs. Here, we aimed to investigate wild pig movement and space use attributes typically used to guide wild pig management among multiple spatiotemporal scales. Our investigation focused on a newly invaded landscape, the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA, an area dominated by bottomland and interspersed upland forests. We examined (1) estimates of core and total space use; (2) resource selection patterns to delineate use hot spots; and (3) how wild pig movements change in relation to anthropogenic pressure. Individual wild pigs (n = 10) varied in their overall movement and space use with only four wild pigs exhibiting home ranging behavior while others exhibited random walking or less discernible behavior; although, limited collar deployment terms or differential deployment periods relative to known temporal behavioral shifts may explain observed differences. Despite this, estimates of total space use among wild pigs were typically smaller at calculated core (1.2 ± 0.3 km$^2$) and 90% (4.9 ± 1.4 km$^2$) isopleths than estimates reported in other landscapes in the southeastern United States, suggesting that wild pigs were able to meet foraging, cover, and thermoregulatory needs.
within smaller areas. Generally, wild pigs selected areas closer to herbaceous, woody wetlands, fields, and perennial streams, creating corridors of use along these features within the refuge. However, selection strength varied among individuals, reinforcing the generalist, adaptive nature of wild pigs. Within this landscape, wild pigs also showed a general tendency to increase movement from fall to winter, possibly paralleling increases in hard mast availability. During this time, there were also increases in anthropogenic pressures (e.g., hunting), causing movements to become less diurnal as pressure increased. This improved understanding of space use across multiple spatiotemporal scales will better inform management strategies focusing on curbing emerging wild pig invasions in novel landscapes.

**Introduction**

Whether deliberate or accidental, human activities continue to introduce or promote exotic species in previously unaffected regions (Westphal et al., 2008; Hulme, 2009). Once introduced, exotic species can naturalize and expand when habitat requirements are met and they maintain a sustainable population (Zenni & Nunez, 2013). Improving our understanding of how these species move (e.g., spread or disperse; Kim & Mandrak, 2016; Coulter et al., 2018; Sena et al., 2021), establish home ranges (Kalb et al., 2013; Prechtel et al., 2018), and select resources (Pietrek & Gonzalez-Roglich, 2015; Walters et al., 2016; Prechtel et al., 2018) over various spatiotemporal scales in novel, previously uninvaded landscapes may aid in informing control efforts (Prechtel et al., 2018) and identifying at-risk native species, communities, or ecosystems of concern (Stohlgren & Schnase, 2006). Space use of exotic species often leads to detrimental effects on biotic (e.g., native plants, animals, invertebrates; Kenward & Holm, 1993; Stiers et al., 2011) and abiotic (e.g., soil, nutrients, water; Lankau, 2011; Chamier et al., 2012) ecosystem components, which collectively sum to provide myriad ecosystem services (e.g., wetland
ecosystems providing flood abatement, water quality improvement, and capturing and neutralizing pollutants; Clarkson et al., 2013) that are often taken for granted. The movements of exotic species may also facilitate colonization and spread of other exotic species (i.e., plants) through zoochory, representing another concern for local ecosystems (Pedrosa et al., 2019).

Advances in GPS technology continue to increase spatial accuracy and temporal resolution of data, allowing for the investigation of animal movement and space use among multiple spatiotemporal scales. Across larger spatiotemporal scales, animal movement patterns can translate into measures of total space use (e.g., home range; Börger et al., 2006a), a metric that can help elucidate the scale at which management or control should be implemented (Bengsen et al., 2012; Smith et al., 2015). At finer spatial scales (as defined in Johnson, 1980), investigating resource selection can further differentiate the amount of use various land coverages receive by a species and inform managers of a species’ life history requirements or preferences, which may include foraging, bedding, and nesting sites (Ward et al., 1998; Rumble & Gamo, 2011; Jenkins et al., 2017). Finally, our ability to identify movement patterns at various temporal scales, such as those that occur in relation to seasonal fluctuations in environmental conditions or circadian patterns, can help elucidate what alters movement and space use in relation to various mechanisms such as hunting or trapping pressure (e.g., Stillfried et al., 2015) or biological rhythms (Merrill & Mech, 2003). Because drivers of space use may shift among spatiotemporal scales, these metrics hold value for successful management of a species, and the respective importance of each metric may become increasingly apparent when tasked with controlling exotic species (Marks & Bloomfield, 2006).

The wild pig (Sus scrofa) is a successful exotic species that thrives in myriad landscapes, taking advantage of diverse food resources, water, and thermoregulatory cover (Choquenot &
Ruscoe, 2003; Fernandez-Llario, 2004), and within much of its introduced range in the United States, represents a hybridization between domestic and wild individuals (Keiter et al., 2016). Wild pigs are capable of causing ecological damage by reducing understory vegetation and impacting habitat resources of native wildlife (Gray et al., 2020; Sanders et al., 2020); disturbing soils (Boyer et al., 2020), which also disrupts normal carbon cycling (Siemann et al., 2009); altering local hydrology and water quality (Singer et al., 1984); and altering seedbanks (Pedrosa et al., 2019). Forest damage occurs through rubbing and rooting of trees (Sweitzer & Van Vuren, 2002; Gray et al., 2020), and the consumption of hard mast sources affects tree regeneration in addition to reducing food resources for native fauna (Focardi et al., 2000; Ditchkoff & Mayer, 2009). Wild pig damage patterns can vary across a landscape as their movements shift in both space (i.e., from disturbed to undisturbed areas) and time (i.e., by hour of day or season) responding to various anthropogenic disturbances (e.g., hunting pressure, Keuling et al., 2008a; roads with varying traffic intensity, Thurfjell et al., 2015). Streams and other water bodies have been positively associated with wild pig space use as well as forests, wetlands, and low elevations (Oliveira-Santos et al., 2016; Kay et al., 2017; Boyce et al., 2020). Within these areas, wild pigs often exhibit site fidelity associated with specific natural landscape features during specific times of day (e.g., diurnal and crepuscular use of forest and water bodies, respectively; Oliveira-Santos et al., 2016). High site fidelity and philopatry have also been associated with wild pigs among all sex and age classes, with a strong seasonal effect (e.g., greatest in winter and spring; Keuling et al., 2008b).

While wild pig space use has been intensively investigated in agricultural-forested matrices (Thurfjell et al., 2009; Paolini et al., 2018), grassland-shrubland dominated landscapes (Froehly et al., 2020), and grassland-forested matrices (Lavelle et al., 2018; Kramer et al., 2022),
little is known about how wild pigs might use large tracts of bottomland and upland forests in North America. Therefore, to improve our understanding of new wild pig invasions of contiguously forested landscapes and inform management and control actions, we (1) estimated the size of core and total utilization distributions; (2) quantified selection patterns in relation to various landscape features; (3) identified hot spots of space use within utilization distributions; and (4) identified daily and hourly differences in movement patterns between non-hunting and hunting seasons. We predicted wild pigs’ overall space use would reflect the species’ tendency for philopatry and site fidelity and that average utilization distribution size would be smaller than what has been reported in other studies of wild pigs located in less thermoregulatory-hospitable landscapes (e.g., grassland-shrubland; Froehly et al., 2020), yet larger than estimates reported in potentially more thermoregulatory-hospitable areas (e.g., coastal marshlands; Hartley et al., 2015). Second, we predicted wild pigs would select areas associated with water (e.g., wetlands and streams), relative to landscape features with less perceived thermoregulatory value (e.g., upland forest, shrubland, human development). These selection patterns would also manifest in the form of heterogeneities in the intensity of use within utilization distributions as specified features are also heterogeneous across a landscape. Finally, we expected wild pigs would have shorter daily movement distances and greater crepuscular or nocturnal movement when anthropogenic pressure was greatest.

**Materials and methods**

**Study site**

While the earliest reports of wild pigs in the southeastern United States date back to 1539 (Mayer & Brisbin, 1991), their distributions are increasing. For example, in Mississippi wild pig occurrences increased in coverage from 4% to 38% of the state’s total land area between 1988
and 2009 (Mississippi State University Extension Service, 2021). Investigations of wild pig space use in Mississippi have focused on movement behaviors in captive wild pigs (Dentingher, 2019), movements and survival using VHF telemetry and imagery (Hayes et al., 2009), and spatiotemporal movements in coastal areas (Hartley et al., 2015).

Comprised of 19,425 hectares of bottomland and upland forest, the Sam D. Hamilton Noxubee National Wildlife Refuge (hereafter, NNWR) was established in 1940 as a refuge and breeding ground for migratory birds and other wildlife, and has been conserved, managed, and as necessary, restored for the benefit of fish, wildlife, plant resources, and humans (United States Fish and Wildlife Service, 2017). In addition to its value for waterfowl, a variety of common native game species (e.g., white-tailed deer, Odocoileus virginianus) and several avian species of concern (e.g., red-cockaded woodpecker, Leuconotopicus borealis) use the NNWR. Observations of wild pigs and associated disturbances on the NNWR have become increasingly noticeable since 2014–2015 despite their longstanding Mississippi residency, warranting a control response effort (Taylor Hackemack, United States Fish and Wildlife Service, pers. comm.). Given this emerging invasion, the NNWR presented an interesting and unique opportunity to investigate wild pig space use to inform future control efforts on the NNWR and other areas with similar landscapes experiencing new invasions. Given the wild pig’s early age of sexual maturity (5–8 months) and high reproductive capacity (3–11 piglets across 1–2 litters/year), population growth likely cannot be controlled without a substantive annual reduction (e.g., 70%; Dzieciolowski et al., 1992; Ditchkoff et al., 2012) achieved through coordinated control measures (i.e., trapping, aerial gunning) that are informed by such investigations.
Trapping, handling, and GPS collar deployment

Between November 2020 and September 2021, we trapped unique partial sounders on the NNWR using a HogEye camera (Wildlife Dominion Management LLC, Mississippi, USA), dual-gated panel trap (Big Pig, Backwoods Solutions LLC, Mississippi, USA), and suspended corral trap (Boar Buster, Noble Research Institute LLC, Oklahoma, USA). Within each partial sounder, an adult female (\(n = 10\); mean: 68.9 ± 5.2 kg) was immobilized using an intramuscular injection of Medetomidine HCl (0.06 mg/kg), Midazolam HCl (0.3 mg/kg), and Butorphanol Tartrate (0.3 mg/kg; ZooPharm Inc., Wyoming, USA; Ellis et al., 2019). After immobilization, each female was fitted with a GPS collar (Vectronic-Aerospace Iridium, Berlin, Germany) programmed to collect relocations at a 2-h fix rate, and livestock-grade ear tags (Y-TEX, Wyoming, USA). Immobilization was reversed using Atipamezole (5.0 mg per 1.0 mg of Medetomidine). All wild pigs trapped but not GPS-collared were immediately euthanized via gunshot to the head, and all trapping and handling protocols were in accordance with NNWR guidelines (United States Fish and Wildlife Service Permit #43620-20-013) and approved by Mississippi State University Institutional Animal Care and Use Committee (Protocol #IACUC-20-022).

Analyses

We collected 12,970 GPS locations across wild pigs (375–2340 locations/female), each of which was assumed to represent a unique sounder. After ensuring locations reflected only those collected while active and on the wild pig (i.e., no locations after a collar was slipped by an animal), we cleaned GPS locations by censoring those (\(n = 5\)) that were clearly incorrect (i.e., improbable locations paired with nonsensical elevation readings). We also resampled the dataset to ensure that all retained locations followed a 2-h fix rate, leaving 12,816 GPS locations. We
modeled the distribution of step lengths (mean = 233.7 ± 2.6 m) using a gamma distribution (Fig. A.1), and linear directional movements were far less common than tortuous ones (considering a tortuosity index and net displacement; Figs. A.2–A.3). To examine overall space use, we first used non-linear least squares regression in R v. 4.1.2 (minpack.lm R package; Elzhov et al., 2016; R Core Team, 2021) to identify whether each wild pig exhibited home ranging or random walking behavior, using mean squared displacement over time. We created two models whereby the first modeled mean squared displacement as having an asymptotic relationship with time which would indicate home ranging behavior (Giuggioli et al., 2006), and the other modeled mean squared displacement in relation to a power law which would indicate random walking behavior (Bodrova & Sokolov, 2020). We fit corresponding models to each wild pig and compared them using Akaike’s Information Criterion (AIC; Akaike, 1974). As not all wild pigs exhibited home ranging behavior (Table A.1), we generated utilization distributions for each wild pig using an autocorrelated kernel density estimator (Fleming et al., 2015) at two isopleths, 90% which we used to represent a measure of total space use (Börger et al., 2006b), and a measure of core space use that we calculated for each wild pig using a threshold value beyond which the estimated area increased at a rate greater than the probability of use (Vander Wal & Rodgers, 2012).

To examine resource selection by wild pigs, we used step-selection analysis that produced a model of resource availability given a species’ movement potential over time (Thurfjell et al., 2014). Step-selection analyses assess resource selection by comparing each relocation (i.e., used) to plausible alternative relocations (i.e., available). For each used relocation, we generated 100 random available relocations by sampling step lengths from a gamma distribution and turn angles from a uniform distribution given observed movement
patterns among wild pigs (Fig. A.1). Step lengths were defined as straight-line distances between two successive fixes, while turn angles were the directional change in heading between successive steps. Thus, only movement bursts with ≥3 consecutive locations (i.e., over a minimum of 6 hours) were included in our analysis to allow for the proper calculation of turn angles. For each used and available step, we extracted information related to 9 environmental covariates expected to be related to wild pig space use that included distances to various land cover and stream types. For land cover, we used the 2016 National Land Cover Database (Dewitz, 2019), and we reclassified the 14 land cover classes present on the NNWR into 7 classes including: water (open water and barren land), developed (open spaces, low and medium intensity development), shrub, field (hay/pasture and cultivated crops), herbaceous (herbaceous cover and herbaceous wetlands), woody wetland, and upland forest (deciduous-, evergreen-, and mixed-forest). Reclassifications were based either on known discrepancies between original classification and ground knowledge (e.g., barren class exclusively located in middle of two large lakes on NNWR) or perceived functional similarity of classes on the NNWR (e.g., deciduous, evergreen and mixed forests located in upland areas) relative to wild pigs. We transformed each land cover class into its own continuous variable by calculating Euclidean distance from each land cover type in ArcGIS (Environmental Systems Research Institute, 2017). Similarly, we calculated Euclidean distances (30-m resolution) to intermittent and perennial streams using shapefiles for each stream type (Mississippi Automated Resource Information System, 1992). All environmental covariates were centered and scaled prior to analysis.

We related used and available steps (1 and 0 as our response) to our environmental covariates using conditional logistic regression, with each stratum as the used and available locations at each timepoint. Because we encountered high individual variation in availability
across individuals (i.e., relative to respective locations on the NNWR) but still desired to fit the same model across all wild pigs, we used a conditional logistic regression model with lasso regularization (Tibshirani, 1996), using the clogitL1 function from the clogitL1 R package (Reid & Tibshirani, 2014), as this allowed for elastic net penalization for model coefficients through use of a cross-validation procedure that provided a consistent method to identify an optimal model (i.e., containing beta-coefficient values at the minimum cross-validation statistic) for each wild pig. We exponentiated beta-coefficients to calculate odds ratios and used these to generate maps of predicted selection intensity (i.e., risk of selecting a location based on landscape conditions) for each wild pig within its respective utilization distribution, and we also created a population average to solve the step-selection function over the entire NNWR landscape. We generated each map using raster algebra in ArcGIS (Environmental Systems Research Institute, 2017).

Finally, we investigated possible differences in seasonality of movements as these often relate to temporally dependent influences. As we wanted to directly compare across wild pigs, we restricted our analyses to data collected between September and December as these months contained information from the greatest number of individuals (Fig. A.4). Using only days with complete information ($n = 12$ relocations/day), we calculated average distances traveled by each wild pig for each Julian day across those months. In addition, given that wild pigs will change space use patterns in relation to anthropogenic disturbance (Gaston et al., 2008; Keuling et al., 2008a; Scillitani et al., 2010), we also wanted to investigate differences in movement patterns relative to hunting pressure (i.e., pre-archery season: 1 September – 30 September; archery season: 1 October – 19 November; and firearms season: 20 November – 31 December). Therefore, we calculated average distances traveled during each hour of the day within those
time periods. We then examined average distance traveled in relation to Julian day and average distance traveled in relation to time of day in each hunting period using generalized additive mixed models using the \textit{gamm} function in the \textit{mgcv} R package (Wood & Wood, 2015).

\textbf{Results}

Woody wetlands (52.2\%) and upland forests (40.4\%) collectively dominated the NNWR, while the remaining land cover classes (e.g., water, developed) only comprised 7.4\% of the landscape. Relocations were collected from adult female wild pigs originally captured among 6 trap locations distributed across the NNWR (Fig. 1.1a) and ranged from 370 to 2317 relocations per wild pig (mean: 1281.6 ± 202.1; Fig. 1.1b). Utilization distributions were highly variable among wild pigs, with core space use ranging from 0.2–3.1 km\(^2\) (mean: 1.2 ± 0.3 km\(^2\)) and total space use ranging from 1.0–14.6 km\(^2\) (mean: 4.9 ± 1.4 km\(^2\); Table 1.1). Isopleth values used to identify cores ranged from 48–52\% (mean: 49.5\% ± 0.4\%; Table 1.1).

Most wild pigs showed selection for areas located closer to perennial streams, herbaceous, and woody wetlands (\(n = 8/10\) wild pigs for each; Table 1.2) and fields (\(n = 7/10\) wild pigs; Table 1.2). There was also a tendency across individuals for selection of areas located greater distances from upland forest (\(n = 8/10\) wild pigs; Table 1.2) and open water (\(n = 7/10\) wild pigs; Table 1.2). Selection for or against developed, shrub, and intermittent streams was weaker (Table 1.2). When individual selection tendencies were applied to utilization distributions (Fig. 1.1c), hotspots of use were localized to fields, woody wetlands, and herbaceous cover near streams. The population-level realized solution showed the same patterns as those seen in the utilization distributions across the entire NNWR landscape with most predicted use within woody wetland corridors at the center of the NNWR and the least amount of use within upland forests throughout the southwestern NNWR (Fig. 1.1d).
Finally, daily movements increased from the pre-archery to archery seasons (i.e., Julian days 244–323), before eventually appearing to plateau during the late archery season (i.e., Julian day ~310; Fig. 1.2a). Movements then declined during the firearms season (i.e., Julian days 324–366; Fig. 1.2a). Daily movement distances during the pre-archery, archery, and firearms seasons averaged 2152 ± 128 m, 3117 ± 136 m, and 2887 ± 83 m, respectively (Fig. A.5). While general similarities in hourly movement patterns (i.e., crepuscular peaks with diurnal valleys) were apparent among pre-archery, archery, and firearms seasons, movement rates during daylight hours declined during the archery and firearms seasons (Figs. 1.2b–1.2d).

**Discussion**

Wild pig movement characteristics (i.e., step lengths and turn angles) in bottomland hardwoods were noticeably shorter than those reported in more open ecoregions (350–420 m/h; Kay et al., 2017) but had similar tortuosity to other regional studies (Satter, 2023). This propensity for tortuous behavior and wild pig natural tendencies for site fidelity, however, resulted in stable space use (i.e., home ranging) for only 4 wild pigs, with the remainder exhibiting less stable or indiscernible space use patterns. Some of the uncertainty surrounding the driving force behind the lack of home ranging behavior may be attributed to limited collar deployment durations (i.e., due to battery failure, hunter harvest), which restricted our ability to identify potential timing in behavioral shifts and may have destabilized home ranging behavior. As many studies on wild pigs do not investigate movement patterns before creating home range estimates (Franckowiak & Poché, 2018; Froehly et al. 2020; Clontz et al., 2022), it is also unclear how prevalent space use instability is for this exotic species. Despite true estimates of home ranges not being delineated for several individuals, wild pigs with stable estimates of space use in our study had home ranges comparable to past estimates for wild pigs in bottomland.
hardwoods in the southeastern United States. In general, total space use in this type of landscape is larger than within coastal marshlands (i.e., 1.2 km²; Hartley et al., 2015), but smaller than estimates reported in other landscapes (e.g., shrubland-grassland; 10.47 km²; Froehly et al., 2020). Our estimates of core space use were delineated using measures specific to each individual; however, all were comparable to the standard 50% isopleth used in other studies to delineate core use (Fieberg & Kochanny, 2005; Downs & Horner, 2008), offering general reinforcement to this threshold being used to delineate a core area. Overall, while our estimates of space use were comparable to other studies in similar landscapes, which provides support for the scale at which to implement control (Kilgo et al., 2021), the lack of space use stability indicates that use of this metric to implement management may be limited to optimal periods throughout the year when wild pigs are more sessile. However, optimal periods may vary by individual or sounder, especially in the southeastern United States which is characterized by temporal inconsistencies in breeding and rearing of offspring, a factor that may contribute to the destabilization of home ranging, philopatry, and site fidelity (Keuling et al., 2008b). Because of these temporal inconsistencies, alternatives that are fixed in time relative to the timing of the planned control effort (e.g., measures of occurrence; see Chapter 4) warrant consideration, especially given varying resource availabilities that are likely to influence wild pig movement and occur across large landscapes.

When examining wild pig space use in relation to land cover and streams, we identified general consistencies in selection tendencies across individuals. These tendencies, although variable in strength, reinforced known relationships between wild pigs and areas they rely on for meeting thermoregulatory and foraging requirements (Satter, 2023). However, despite general underlying homogeneities of the NNWR landscape (i.e., approximately half of the NNWR
consisted of contiguous woody wetlands), less prominent features (i.e., herbaceous, fields, and perennial streams) were more sparsely and heterogeneously distributed, and as such were highly variable relative to their availability to individual wild pigs. Considering the life history of wild pigs as generalist and highly adaptive omnivores, the ability for certain individuals to take advantage of areas that are underrepresented or even potentially suboptimal is not surprising. It is also likely that social dynamics (i.e., territoriality) also influence how individuals and their sounders differentially use areas (Kilgo et al., 2021).

Disproportionate selection of areas characterized by woody wetlands and streams is common given the need for wild pigs to thermoregulate using available water sources (Kay et al., 2017; Clontz et al., 2022), which also supports the lack of use of upland forests as these areas may be associated with fewer thermoregulatory and foraging resources required by wild pigs (Choquenot and Ruscoe, 2003; Fernandez-Llario, 2004). While the strength of relationships to woody wetlands was noticeably weaker compared to perennial streams, this was likely due to the pervasiveness of woody wetlands within areas wild pigs were located; such abundances in availability often influence the outcome of selection analyses (Kramer et al., 2022). There is also support for wild pig use of herbaceous areas, as this evidence has focused on damage to herbaceous vegetation in otherwise forested areas in northern climates (Gray et al., 2020) and general selection patterns in the southeastern United States (Clontz et al., 2021). Given the apparent importance of herbaceous landscapes, such as herbaceous wetlands, to wild pigs, their limited spatial representation in many hardwood forests suggest they could be important areas for damage monitoring, even if difficult to access by human observers. In addition, these areas harbor not only wild pigs, but also floral and faunal species that are likely ecologically sensitive
(Weisberg et al., 2013), thereby representing areas requiring greater attention when monitoring wild pig damage and informing control efforts when accessible.

When we examined wild pig circadian patterns in relation to anthropogenic pressures in the NNWR, daily distances traveled increased as the seasons progressed from fall into winter. Space use can increase as cooling temperatures make the landscape more thermoneutral to wild pigs or in relation to the emergence of hard mast including acorns (Quercus spp.) and hickory nuts (Carya spp.; Froehly et al., 2020). However, it is notable that daily distances plateaued and then diminished during the firearms season which is typical for wild pigs that may experience increased anthropogenic pressures associated with hunting seasons (Gaston et al., 2008; Keuling et al., 2008a). This pattern is further exemplified when we examine daily circadian rhythms as there were increasingly restricted diurnal movements, a trend that is not unexpected on public lands which are also subjected to frequent anthropogenic pressures during open hunting seasons (Keuling et al., 2008a; Scillitani et al., 2010). Although general trends were similar and reflective of the life history of wild pigs (i.e., primarily crepuscular; Froehly et al., 2020), the decreases in diurnal movement distances during the archery and firearms seasons indicate that wild pigs are responding to anthropogenic pressures, even within this landscape which provides many natural refuges (e.g., inaccessible wetlands) and contains a low density of wild pigs given the relatively recent invasion of this landscape. Therefore, natural resource managers must understand wild pigs have spatiotemporal complexities (e.g., restriction of movement to only certain hours within certain landscapes) that should be considered when attempting to implement control measures such as trapping, especially during periods which are characterized by movement shifts related to anthropogenic activities, as these will likely impact efficiency and effectiveness of these measures.
Conclusions

While our investigation provides general reinforcement to earlier findings on wild pig space use in other regions, it also identified the need to investigate movement phenomena from various angles among multiple spatiotemporal scales. Seemingly, wild pigs are very flexible in their movement patterns and resource use, exhibiting individuality that may reflect generalist tendencies, and changes within individuals relative to spatiotemporally dependent external drivers further compound the challenges faced by resource managers. Thus, it is imperative that movement patterns be characterized across not only individuals but also the breadth of landscapes they can invade, and further consideration should be given to the social interactions that are also occurring within these intensively used areas (Potts et al., 2022), as this information will be critical to developing substantive and meaningful control efforts. Collectively, our findings will add to the knowledge required by natural resource managers to both control wild pigs and protect our native natural resources.

Acknowledgements

The authors would like to thank Wildlife Dominion Management, LLC (Mississippi, USA) for lending a trap used in this effort, USDA-APHIS Wildlife Services and USDA-APHIS National Wildlife Research Center for personnel support, and United States Fish and Wildlife Service personnel at the Sam D. Hamilton Noxubee National Wildlife Refuge for their general support. This research was funded by, and this publication is a contribution of, Mississippi State University’s Forest and Wildlife Research Center [McIntire-Stennis Project MISZ-085160] and Mississippi Agriculture and Forestry Experiment Station [HATCH Project MIS-085180].
### Table 1.1
Autocorrelated kernel density estimates for two utilization distribution isopleths (core and 90%) for adult female wild pigs (*Sus scrofa*; *n* = 10) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.

<table>
<thead>
<tr>
<th>Pig ID</th>
<th>Period</th>
<th>Relocations (2-h)</th>
<th>Core Isopleth</th>
<th>Core (km²)</th>
<th>90% (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>26619</td>
<td>09/14/21 – 12/02/21</td>
<td>370</td>
<td>52%</td>
<td>3.1</td>
<td>14.6</td>
</tr>
<tr>
<td>26620a</td>
<td>12/02/20 – 07/08/21</td>
<td>2317</td>
<td>49%</td>
<td>1.3</td>
<td>5.1</td>
</tr>
<tr>
<td>26626</td>
<td>08/28/21 – 02/07/22</td>
<td>1541</td>
<td>49%</td>
<td>2.5</td>
<td>9.1</td>
</tr>
<tr>
<td>26628</td>
<td>07/29/21 – 01/30/22</td>
<td>2186</td>
<td>51%</td>
<td>0.5</td>
<td>2.2</td>
</tr>
<tr>
<td>30252</td>
<td>08/28/21 – 11/17/21</td>
<td>862</td>
<td>48%</td>
<td>0.4</td>
<td>1.4</td>
</tr>
<tr>
<td>35489</td>
<td>07/26/21 – 01/09/22</td>
<td>1941</td>
<td>50%</td>
<td>0.4</td>
<td>2.0</td>
</tr>
<tr>
<td>35490a</td>
<td>03/08/21 – 10/07/21</td>
<td>1158</td>
<td>48%</td>
<td>1.3</td>
<td>4.9</td>
</tr>
<tr>
<td>35492a</td>
<td>08/12/21 – 11/18/21</td>
<td>910</td>
<td>50%</td>
<td>0.2</td>
<td>1.0</td>
</tr>
<tr>
<td>35493a</td>
<td>08/08/21 – 12/27/21</td>
<td>785</td>
<td>49%</td>
<td>1.4</td>
<td>6.4</td>
</tr>
<tr>
<td>35494</td>
<td>11/25/20 – 02/26/21</td>
<td>746</td>
<td>49%</td>
<td>0.5</td>
<td>2.1</td>
</tr>
</tbody>
</table>

a. Denotes wild pigs that exhibited home ranging behavior.
Table 1.2  Beta (β) coefficients derived from conditional logistic regression models with elastic net penalization (“lasso”) for adult female wild pigs (Sus scrofa; n = 10) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.

<table>
<thead>
<tr>
<th>Pig ID</th>
<th>βIntermittent</th>
<th>βPerennial</th>
<th>βDeveloped</th>
<th>βField</th>
<th>βHerbaceous</th>
<th>βShrub</th>
<th>βUpFor</th>
<th>βWater</th>
<th>βWWet</th>
</tr>
</thead>
<tbody>
<tr>
<td>26619</td>
<td>-</td>
<td>-0.73</td>
<td>-0.02</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.09</td>
<td>0.42</td>
<td>-0.26</td>
</tr>
<tr>
<td>26620</td>
<td>-0.21</td>
<td>-0.37</td>
<td>-</td>
<td>0.28</td>
<td>-1.66</td>
<td>0.35</td>
<td>0.51</td>
<td>-0.31</td>
<td>-0.17</td>
</tr>
<tr>
<td>26626</td>
<td>0.25</td>
<td>-0.10</td>
<td>-0.24</td>
<td>0.07</td>
<td>-0.16</td>
<td>-0.90</td>
<td>0.56</td>
<td>0.50</td>
<td>0.12</td>
</tr>
<tr>
<td>26628</td>
<td>-0.34</td>
<td>1.35</td>
<td>0.62</td>
<td>-0.38</td>
<td>-0.65</td>
<td>0.69</td>
<td>0.07</td>
<td>0.37</td>
<td>-0.07</td>
</tr>
<tr>
<td>30252</td>
<td>0.66</td>
<td>-1.24</td>
<td>-0.52</td>
<td>-0.34</td>
<td>1.32</td>
<td>1.87</td>
<td>-0.40</td>
<td>-</td>
<td>-1.01</td>
</tr>
<tr>
<td>35489</td>
<td>-0.40</td>
<td>1.29</td>
<td>0.49</td>
<td>-0.43</td>
<td>-0.56</td>
<td>0.46</td>
<td>-</td>
<td>0.41</td>
<td>-0.01</td>
</tr>
<tr>
<td>35490</td>
<td>0.74</td>
<td>-1.32</td>
<td>-0.35</td>
<td>-0.14</td>
<td>-0.18</td>
<td>-0.18</td>
<td>0.33</td>
<td>1.32</td>
<td>-1.79</td>
</tr>
<tr>
<td>35492</td>
<td>0.38</td>
<td>-2.18</td>
<td>-1.98</td>
<td>-0.88</td>
<td>-1.79</td>
<td>0.04</td>
<td>1.17</td>
<td>4.57</td>
<td>-0.45</td>
</tr>
<tr>
<td>35493</td>
<td>-0.36</td>
<td>-0.37</td>
<td>0.24</td>
<td>-0.29</td>
<td>-0.57</td>
<td>-</td>
<td>0.11</td>
<td>0.20</td>
<td>-0.27</td>
</tr>
<tr>
<td>35494</td>
<td>0.04</td>
<td>-1.48</td>
<td>0.80</td>
<td>-0.86</td>
<td>-0.81</td>
<td>-</td>
<td>0.54</td>
<td>-0.93</td>
<td>0.58</td>
</tr>
<tr>
<td>Mean</td>
<td>0.08</td>
<td>-0.52</td>
<td>-0.10</td>
<td>-0.30</td>
<td>-0.51</td>
<td>0.23</td>
<td>0.30</td>
<td>0.66</td>
<td>-0.33</td>
</tr>
</tbody>
</table>
Figure 1.1 Relocations of adult female wild pigs (*Sus scrofa*; *n* = 10) relative to successful trap locations, failed trap locations, and bait-only locations in the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA (a), individual relocations (b), individual step-selection function hotspots (c), and predicted suitability given population-averaged beta coefficients (d).
Figure 1.2  Generalized additive mixed model outputs representing daily distance traveled by adult female wild pigs (Sus scrofa; n = 10) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA as a function of Julian day (a), and 2-h step length distance as a function of hour of day during the pre-archery (b), archery (c), and firearms (d) seasons.
CHAPTER II

NO CORN, NO PROBLEM: A TEST FOR THE BEST NON-GRAIN ATTRACTANT FOR WILD PIGS

Abstract

Grain-based attractants (e.g., corn) are the standard among most wild pig (Sus scrofa) management and research efforts, but their use is not always feasible due to cost, deployment restrictions (e.g., difficulty of transporting grain into remote areas, property rules), and potential disease concerns associated with concentrating non-target species at bait sites. Attractant deployment and efficacy must therefore be considered by biologists, private landowners, and researchers given the ultimate need to use attractants to attract wild pigs. To examine the efficacy of potential non-grain attractants, we used remote camera grids to identify attractant(s) that maximized wild pig while minimizing non-target species visitation in a forested landscape in the southeastern United States. Further, we only considered non-grain attractants easy to carry (i.e., <0.5 kg and compact) and deploy (i.e., painted on tree trunks or activated scent wicks). Comparing 8 non-grain attractants among food, non-food, and control (i.e., no attractant; \( n = 11 \) visitations) treatments, we found used cooking oil (i.e., fish fryer grease; \( n = 38 \) visitations), orange marmalade (\( n = 36 \) visitations), and caramel syrup (\( n = 29 \) visitations) were most attractive to wild pigs. Although also attractive to opossums (Didelphis virginiana; \( n = 50 \) visitations),...
visitations), used cooking oil was not a significant attractant among other non-target species. In contrast, orange marmalade was attractive to raccoons (*Procyon lotor*), opossums, and gray squirrels (*Sciurus carolinensis; n = 188 combined visitations*), and caramel syrup was attractive to raccoons and opossums (*n = 137 combined visitations*). Used cooking oil is a non-grain attractant most likely to maximize wild pig visitation while minimizing non-target species attraction, support sampling of remote areas considering its ease of distribution, and warrant further consideration in wild pig management and research.

**Introduction**

Successful wildlife management and conservation depends on the ability to properly assess target species distribution, population size, and trends (Saracco et al., 2008; Kindberg et al., 2011). This is particularly important for exotic species as distributions and populations may rapidly expand in new environments due to life history characteristics that often include a wide range of environmental tolerance, a broad or generalist diet, early sexual maturity, prolific reproduction, dispersal ability, and absence of natural enemies (Ricciardi & Rasmussen, 1998; Sakai et al., 2001; Jeschke et al., 2012). The inconspicuous habits (e.g., nutria, *Myocastor coypus*; Witmer & Pitt, 2012) along with human phobia (e.g., black rat, *Rattus rattus*; Phillips, 2010) among mammalian exotics often make use of direct, invasive field methods laborious or otherwise logistically challenging (Van Rensburg et al., 1987). As a result, non-invasive methods are often used to assess distribution and population size, including those that benefit from the use of attractants (e.g., camera-trapping, hair-snaring, scent stations; Ferreras et al., 2018; Gurney et al., 2020; Holinda et al., 2020). Attractants have a variety of uses in wildlife management and research relating to exotic species including trapping (Reed et al., 2011), toxicant delivery (Engeman et al., 2006), and population abundance estimation (Amburgey et al., 2021). Although
attracting a target species is critically important in each application, minimizing non-target visitation may be of equal or greater importance especially when lethal methods and/or sensitive species are involved (Glen et al., 2007).

Wild pigs (*Sus scrofa*) are tolerant and adaptable to various environmental conditions (Barrett & Birmingham, 1994), have a generalist omnivorous diet (Ditchkoff & Mayer, 2009), early age of sexual maturity (Dzieciolowski et al., 1992), high reproductive capacity (Ditchkoff et al., 2012), and efficient dispersal ability (Snow et al., 2017); traits that facilitate population expansion and establishment. Although present in the United States since the 1500s (Lewis et al., 2019), wild pigs have increasingly presented challenges to natural resource managers, biologists, and private landowners in recent decades as populations and distributions have continued to expand (Corn & Jordan, 2017), leading to agricultural damage and control costs exceeding US $1.5 billion annually (Pimentel, 2007). Management actions often include active removal methods (e.g., trapping, shooting, and poisoning; Barrett & Birmingham, 1994; Massei et al., 2011) requiring effective attractants for luring wild pigs. However, research may also benefit from an improved understanding of attractant efficiencies. Grain (e.g., corn, wheat) is a common attractant (Lavelle et al., 2017) used in wild pig population assessments (Davis et al., 2020; Schlichting et al., 2020) and control efforts (Poche et al., 2018). However, grain loses appeal when considering its attractiveness to non-target species (a quality that can augment, for example, disease transmission; Miller et al., 2003), increased costs (Lavelle et al., 2017), and deployment feasibility in grain-restricted areas (e.g., national wildlife refuges, wildlife management areas, disease management zones) that harbor wild pig populations.

Non-grain attractants such as liquid domestic swine feed additives (e.g., apple and strawberry; Campbell & Long, 2008) and orange flavoring (Karlin & Khan, 2020) may provide
alternatives for attracting wild pigs and have been shown to be effective in some cases. For example, use of orange flavoring with grain was shown to have greater visits from wild pigs and fewer visits from non-target species such as white-tailed deer (*Odocoileus virginianus*) and raccoon (*Procyon lotor*) relative to grain-only stations (Karlin & Khan, 2020). However, non-grain attractants for wild pigs, even when used alone, can still attract non-targets (Campbell & Long, 2008). When effective, non-grain attractants may aid in reducing costs and labor required to meet management and research objectives. For example, a non-grain attractant (e.g., jar of jelly; Andelt & Woolley, 1996) may represent a cost-efficient and less labor-intensive alternative that allows for a greater deployment range into remote or otherwise access-limited areas. However, while attractants may be effective in one region or ecotype, complementary investigations in new areas are warranted considering differences among non-target communities, local climatic conditions, and the availability of food resources. Previous attractant studies have focused on wild pig populations and broader communities among countries (e.g., Australia; Elsworth et al., 2004), coastal islands (e.g., Ossabaw Island, Georgia, USA; Kavanaugh & Linhart, 2000), private lands characterized by shrub rangelands (e.g., Texas, USA; Campbell & Long, 2008; Karlin & Khan, 2020), and state-owned wildlife management areas with distinct wild pig hunting seasons (e.g., Alabama, USA; Sandoval et al., 2019). While most studies focused on food-based attractants, investigation of urine-based attractants (Sandoval et al., 2019) may also be useful, particularly on public lands (e.g., national wildlife refuges) where food-based attractants may be precluded in certain areas due to baiting, feeding, hunting seasons, or access rules and restrictions. Here, we aimed to evaluate the effectiveness of 8 commercially available, non-grain attractants for wild pigs within a forested landscape in the southeastern United States that would maximize attraction of wild pigs and minimize attraction of non-target
species. We used both food and non-food non-grain alternatives to assess potential for implementation considering access, time, and grain baiting restriction challenges for stakeholders working on public lands.

**Materials and methods**

**Study area**

We tested attractants at the Sam D. Hamilton Noxubee National Wildlife Refuge during summer 2021. The study area encompassed 19,425 ha in east-central Mississippi (Fig. 2.1) with bottomland hardwoods (i.e., woody wetlands; 52.2%) and upland forests (i.e., evergreen, deciduous, and mixed; 40.4%) collectively dominating the landscape, while remaining land cover types (e.g., water, developed) comprised the remaining 7.4% (Dewitz, 2019). In addition to the presence of wild pigs since 2014, native mammals included white-tailed deer, raccoon, bobcat (*Lynx rufus*), coyote (*Canis latrans*), nine-banded armadillo (*Dasypus novemcinctus*), opossum (*Didelphis virginiana*), gray squirrel (*Sciurus carolinensis*) and other conspicuous Rodentia. Annual precipitation totaled 162.6 cm, and average monthly low and high temperatures ranged 0.6–22.2 ºC and 12.2–32.8 ºC during the study year, respectively (National Oceanic and Atmospheric Administration, 2023). During the study period (17 June – 30 July), precipitation totaled 21.2 cm, and average low and high temperatures ranged 21.2 – 31.9 ºC, respectively (National Oceanic and Atmospheric Administration, 2023).

**Sampling design**

We detected and GPS-marked rooting and wallowing areas during previous wild pig damage surveys in 2020–2021 (see Chapter 4). Based on damage predominantly occurring within woody wetlands, we placed 5 attractant sampling areas (Fig. 2.1) within this land cover
type using ArcGIS (Environmental Systems Research Institute, 2017). A 3x3 grid was overlayed in each area and a centroid location was generated in each cell to represent the location of each treatment (Fig. 2.1). We used a grid size representing the smallest home range size reported for wild pigs in the region (0.6 km²; Hartley et al., 2015) to ensure availability of each treatment to a given wild pig with enough separation (~200 m spacing) among treatments to suggest an individual was attracted to that treatment and not an accidental “combination” of adjacent scents (Campbell & Long, 2008). Grids were also oriented to avoid perennial streams, a potentially confounding variable (i.e., as streams provide travel corridors; Beasley et al., 2014). Although each grid was monitored for 14 days, monitoring periods were staggered (i.e., grids A-B: 17–30 June 2021, grid C: 2–15 July 2021, and grids D-E: 17–30 July 2021) due to the number of available cameras (see below).

**Treatment application and monitoring**

At each sampling grid centroid, we randomly placed 9 treatments for the duration of the monitoring period as follows: used cooking oil (i.e., fish fryer grease); orange marmalade (Great Value, Arkansas, USA), strawberry jelly (Smuckers, Ohio, USA), apple jelly (Smuckers, Ohio, USA), and caramel syrup (Smuckers, Ohio, USA); Hogshine, which is a commercial grain additive (Yawt Yawt, Mississippi, USA); sow in heat urine (BoarMasters Wildlife Attractants, Idaho, USA), dominant boar urine (BoarMasters Wildlife Attractants, Idaho, USA); and a control (camera only; Fig. 2.1). Non-urine treatments consisted of a weekly application to the same tree (i.e., 192 mL, equivalent to half standard jar per application), and urine treatments consisted of a weekly application to a key wick (Wildlife Research Center, Minnesota, USA) hung from the same tree branch (i.e., 7 mL, the maximum amount that could be applied without exceeding wick absorption capacity). Initial applications and camera installations were completed on the day that
preceded monitoring (i.e., day 1 started at midnight), and second applications and camera checks (i.e., battery checks and memory card changes) occurred on day 7. Monitoring of species visitation was conducted using a motion-sensing remote camera (FORCE-20; Spypoint, Quebec, CA) located 5 m from the treatment with each camera set to capture 3-image bursts at high sensitivity without delay. During the first monitoring period, cameras were placed 1 m above ground level; however, due to flash flooding concerns within woody wetlands, camera height was increased to 1.5 m on day 2 for all cameras. Flash flooding events were brief (i.e., < 1 d) and did not appear to differentially impede wild pig or non-target visitation. We maintained the adjusted height for the remainder of the study period in every grid. All procedures were in accordance with Sam D. Hamilton Noxubee National Wildlife Refuge guidelines (United States Fish and Wildlife Service Permit #43620-20-013).

Statistical analysis

We defined a visitation event as a mammal species observation within the camera frame ≥10 minutes since the last observation of that species on camera (Karlin & Khan, 2020). Due to overdispersion of the species occurrence data from substantial non-detections, a negative binomial generalized linear model (MASS package; Venables & Ripley, 2002) was fit for each species with ≥30 visitation events in program R (R Core Team, 2021). We used our finest scale count data (i.e., visits/day for each treatment in each grid) as our response variable with attractant treatment as a predictor and the control treatment set as the base comparison. We determined statistical significance at α = 0.05.
Results

We observed 1,191 visitation events among 12 mammal species, 5 of which were included in analysis including wild pig, opossum, raccoon, gray squirrel, and white-tailed deer (Table 2.1). Remaining species included nine-banded armadillo (n = 21 visits), gray fox (*Urocyon cinereoargenteus*; n = 13 visits), bobcat (n = 7 visits), fox squirrel (*Sciurus niger*; n = 5 visits), coyote (n = 4 visits), eastern cottontail (*Sylvilagus floridanus*; n = 2 visits), and unidentified Rodentia (n = 3 visits). Among treatments, wild pig visitations were fewest for Hogshine and greatest for used cooking oil (Table 2.1; Fig. 2.2). Used cooking oil, orange marmalade, and caramel syrup collectively maximized wild pig visitation, with these treatments being 1.24, 1.19, and 0.97 times more likely to be visited than the control, respectively (Table 2.2).

For non-target species, opossums visited a variety of attractants including caramel syrup, orange marmalade, strawberry jelly, used cooking oil, apple jelly, boar urine, and Hogshine (Table 2.1) and were 1.67 to 3.39 times more likely to visit these attractants compared to the control (Table 2.2). Opossums did, however, have few visits to sow urine (Table 2.1). Raccoons had the greatest number of visits to strawberry jelly, orange marmalade, and caramel syrup and the least number of visits to boar urine (Table 2.1). Raccoons were 1.18, 1.11, and 0.69 times more likely to visit strawberry jelly, orange marmalade, and caramel syrup, respectively, compared to the control (Table 2.2). Gray squirrels had a greater number of visits to orange marmalade (1.15 times) and strawberry jelly (0.92 times) compared to the control (Table 2.1), with visits to other attractants not different compared to the control (Table 2.2). Finally, white-tailed deer showed no specific increase in attractant-specific visitation relative to the control (Tables 2.1–2.2).
Discussion

Examining a variety of non-grain wild pig attractants allowed us to determine an effective attractant for wild pigs that minimized non-target species visitations: used cooking oil. While orange marmalade demonstrated similar effectiveness in attracting wild pigs, it was also a favorite among opossums, raccoons and gray squirrels. Although each attractant has been shown to be successful in other studies, both were deployed concomitantly with grain (Higginbotham, 2012; Karlin & Khan, 2020). Thus, we show that these attractants can also be effective when used independently. While used cooking oil and orange marmalade were generally effective in attracting wild pigs throughout the duration of our study (i.e., 31.4% and 30.0% of monitoring days with ≥1 visitation, respectively), this effectiveness was most evident when comparing our total visitations to those of alternative top non-grain attractants identified elsewhere in the southeastern United States. For example, used cooking oil (38 visits/70 days = 0.54) and orange marmalade (36 visits/70 days = 0.51) in our study appeared to perform similarly well to strawberry (48 visits/100 days = 0.48) and apple scents (43 visits/100 days = 0.43; Campbell & Long, 2008), and although study methodologies differed, our work further demonstrates utility of alternative non-grain attractants that may prove useful where grain is not permitted or logistics make transporting grain infeasible, and the need for local tests of attractant efficiency.

It is curious that other attractants we used, such as strawberry and apple jelly, were ineffective in attracting wild pigs as they were identified as most attractive to wild pigs in southern Texas (Campbell & Long, 2008). Neither attractant performed well in our study, with not only weak relationships with wild pig visitation and, for strawberry jelly, also high non-target visitation (e.g., opossums, raccoons, gray squirrels). Although there is no definitive explanation for this disparity between these two areas in the southeastern United States, local conditions and
study design characteristics likely influenced wild pig preferences. For example, between Campbell and Long (2008) and this study, ecoregions (South Texas Plains shrub rangeland vs. Blackland Prairie woodland dominated by wet bottomland hardwood forests), study timing (late summer/early spring vs. mid-summer), attractant type (commercial domestic swine additives vs. simple “household” items), deployment method (soaked cotton in polyvinyl capsules vs. direct application to tree), duration between station visits and rebaiting (daily vs. weekly), and local wildlife community compositions, could have all influenced wild pig choices. As any or all of these may have played a role in generating study-based disparities, our findings demonstrate the importance of understanding relationships between attractant efficacy and wild pigs per locality, or otherwise, within the context of the above listed considerations. Even our identification of orange marmalade as an effective wild pig attractant, while promising given its general consistency with other research, should be understood within local contexts (i.e., use of orange-flavored grain in mock corral traps in a shrubland landscape in central Texas; Karlin & Khan, 2020). Meanwhile, purely grain-based strategies seem more universal in attractiveness for both target and non-target species when allowed and feasibly deployed (Lavelle et al., 2017).

Attractants tested in this study represented those that had either performed well in other wild pig research or management applications, or those that are commercially produced for the purpose of attracting wild pigs for hunting and trapping. While attractant performance varied considerably, the underlying theme of non-target visitation is important to consider. Depending on objectives and the acceptable level of non-target species collateral damage (i.e., when using toxicants or trapping), use of any of these attractants will be accompanied by some level of risk, and this study demonstrated that none of our attractants solely attracted wild pigs. However, if the aim of using the attractant is to aid in conducting research (e.g., camera trapping, non-
invasive genetic sampling), this obviously carries lesser direct risk to non-targets than lethal control (e.g., toxicant delivery; Campbell et al., 2006), even though indirect risks associated with congregating animals can persist such as wildlife disease transmission (Cartensen et al., 2011; Plummer et al., 2018).

Wild pig visitation was greatest with used cooking oil while also minimizing non-target visitation, a result that was not obtained using orange marmalade and caramel syrup which attracted primarily opossums and raccoons. While opossum visitation was also high for used cooking oil, raccoon visitation was not, an unexpected finding given associations between raccoons and fish-scented baits in oral pharmaceutical distributions (Campbell et al., 2006; Johnson et al., 2016) and the origin (i.e., fish-fryer) of the used cooking oil used during our study. Although we desired to identify an attractant which also minimized opossum visitation, this species was attracted to all treatments but sow urine, making minimizing opossum visitations difficult and potentially infeasible. Considering high levels of opossum visitation to a variety of attractants, both as a non-target (e.g., fish-scent; Campbell et al., 2006; Johnson et al., 2016) and target species (e.g., molasses; Goodwin & Ten Houten, 1991; chicken, catnip oil; Jordan & Lobb-Rabe, 2015), all within the broader context of the generalist omnivorous diet and adaptive nature of opossums to nearly any environment (Walsh et al., 2017; Greenspan et al., 2018; Hart et al., 2019), this issue was not restricted to our study area and other attractants will likely need to be investigated if the aim is to exclude opossums.

Our work continues to demonstrate the importance of investigating attractant preferences locally. While top attractants in the literature likely hold collective value when identifying or refining the suite of candidate attractants deployed in bottomland hardwoods or elsewhere in the southeastern United States, differences among local conditions and deployment characteristics in
addition to the generalist diet of wild pigs may lead to variation in attractant efficacy. Although grain-based strategies may also benefit from concomitant use of top non-grain attractants with grain, costs (e.g., $7-$10 per 22.7-kg bag of whole corn relative to $2-$3 per standard jar of non-grain attractant), deployment feasibility (e.g., difficulty of transporting grain into remote areas), and potential drawbacks (e.g., disease risks associated with concentration of non-target species such as raccoon and white-tailed deer at grain bait sites, accelerated depletion of grain by non-targets), collectively undermine the value of deploying grain in many situations and suggest the need for non-grain alternatives for research and management purposes. Combining or alternating non-grain attractants could increase visits, even repeat visits, supporting recapture rates required for abundance estimation (i.e., spatial capture-recapture methods), keeping sounders interested during trap construction, and attracting new individuals otherwise unattracted to alternative non-grain attractants. Researchers and managers are encouraged to explore such combinations and evaluate effectiveness.

In conclusion, this study effectively demonstrated the value of non-grain attractants in maximizing visitation from wild pigs, while also identifying attractants which can minimize visitations from non-targets, within bottomland hardwoods in Mississippi. More importantly, however, our efforts provide an important link to addressing and answering research questions related to wild pig populations on public lands that pose direct (i.e., regulatory) or indirect (i.e., remoteness or otherwise limited physical access) challenges to researchers and resource managers.

**Acknowledgements**

The authors would like to express their gratitude to the United States Fish and Wildlife Service personnel at the Sam D. Hamilton Noxubee National Wildlife Refuge for their support.
This research was funded by, and this publication is a contribution of, Mississippi State University’s Forest and Wildlife Research Center [McIntire-Stennis Project MISZ-085160] and Mississippi Agriculture and Forestry Experiment Station [HATCH Project MIS-085180].
Table 2.1  Total number of visitation events along with the mean number of visitation events (± standard error) in parentheses for each species and treatment across grids (n = 5) during an investigation of non-grain attractants for wild pigs (Sus scrofa) in Mississippi, USA.

<table>
<thead>
<tr>
<th>Attractant</th>
<th>Wild pig</th>
<th>Opossum</th>
<th>Raccoon</th>
<th>Gray squirrel</th>
<th>White-tailed deer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Used cooking oil</td>
<td>38 (7.6 ± 3.4)</td>
<td>50 (10.0 ± 4.0)</td>
<td>30 (6.0 ± 1.1)</td>
<td>14 (2.8 ± 1.6)</td>
<td>6 (1.2 ± 1.2)</td>
</tr>
<tr>
<td>Orange marmalade</td>
<td>36 (7.2 ± 3.8)</td>
<td>77 (15.4 ± 5.3)</td>
<td>73 (14.6 ± 3.6)</td>
<td>38 (7.6 ± 3.4)</td>
<td>3 (0.6 ± 0.4)</td>
</tr>
<tr>
<td>Caramel syrup</td>
<td>29 (5.8 ± 1.1)</td>
<td>89 (17.8 ± 4.5)</td>
<td>48 (9.6 ± 5.0)</td>
<td>21 (4.2 ± 1.2)</td>
<td>5 (1.0 ± 0.6)</td>
</tr>
<tr>
<td>Strawberry jelly</td>
<td>24 (4.8 ± 3.3)</td>
<td>52 (10.4 ± 4.3)</td>
<td>78 (15.6 ± 3.2)</td>
<td>30 (6.0 ± 3.3)</td>
<td>7 (1.4 ± 0.7)</td>
</tr>
<tr>
<td>Sow urine</td>
<td>23 (4.6 ± 1.9)</td>
<td>4 (0.8 ± 0.6)</td>
<td>38 (7.6 ± 3.2)</td>
<td>14 (2.8 ± 1.2)</td>
<td>5 (1.0 ± 0.4)</td>
</tr>
<tr>
<td>Boar urine</td>
<td>18 (3.6 ± 1.7)</td>
<td>23 (4.6 ± 4.6)</td>
<td>14 (2.8 ± 1.1)</td>
<td>13 (2.6 ± 0.9)</td>
<td>9 (1.8 ± 0.6)</td>
</tr>
<tr>
<td>Apple jelly</td>
<td>10 (2.0 ± 0.7)</td>
<td>39 (7.8 ± 3.8)</td>
<td>27 (5.4 ± 2.2)</td>
<td>21 (4.2 ± 0.7)</td>
<td>2 (0.4 ± 0.2)</td>
</tr>
<tr>
<td>Hogshine</td>
<td>9 (1.8 ± 1.3)</td>
<td>16 (3.2 ± 1.3)</td>
<td>22 (4.4 ± 2.0)</td>
<td>16 (3.2 ± 1.6)</td>
<td>10 (2.0 ± 0.9)</td>
</tr>
<tr>
<td>Control</td>
<td>11 (2.2 ± 0.8)</td>
<td>3 (0.6 ± 0.2)</td>
<td>24 (4.8 ± 3.3)</td>
<td>12 (2.4 ± 1.2)</td>
<td>5 (1.0 ± 0.4)</td>
</tr>
</tbody>
</table>
Table 2.2  Negative binomial generalized linear model $\beta$-coefficients with standard error and $z$- and $P$-values for each species and treatment relative to the control treatment during an investigation of non-grain attractants (i.e., treatments) for wild pigs (*Sus scrofa*) in Mississippi, USA. $P$-values ≤0.05 for treatments are bolded.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>$B$</th>
<th>Standard error</th>
<th>$Z$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sus scrofa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild pig</td>
<td>Apple jelly</td>
<td>-0.10</td>
<td>0.49</td>
<td>-0.19</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Boar urine</td>
<td>0.49</td>
<td>0.45</td>
<td>1.11</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>Caramel syrup</td>
<td>0.97</td>
<td>0.42</td>
<td>2.30</td>
<td>0.021</td>
</tr>
<tr>
<td></td>
<td>Hogshine</td>
<td>-0.20</td>
<td>0.50</td>
<td>-0.40</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Used cooking oil</td>
<td>1.24</td>
<td>0.41</td>
<td>3.01</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Orange marmalade</td>
<td>1.19</td>
<td>0.41</td>
<td>2.87</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Sow urine</td>
<td>0.74</td>
<td>0.43</td>
<td>1.71</td>
<td>0.09</td>
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<tr>
<td></td>
<td>Strawberry jelly</td>
<td>0.78</td>
<td>0.43</td>
<td>1.82</td>
<td>0.07</td>
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<tr>
<td>Didelphis virginiana</td>
<td>Apple jelly</td>
<td>2.57</td>
<td>0.64</td>
<td>4.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Opossum</td>
<td>Boar urine</td>
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<td>0.65</td>
<td>3.11</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Caramel syrup</td>
<td>3.39</td>
<td>0.63</td>
<td>5.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Hogshine</td>
<td>1.67</td>
<td>0.67</td>
<td>2.50</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Used cooking oil</td>
<td>2.81</td>
<td>0.64</td>
<td>4.42</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Orange marmalade</td>
<td>3.25</td>
<td>0.63</td>
<td>5.15</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Sow urine</td>
<td>0.29</td>
<td>0.80</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Strawberry jelly</td>
<td>2.85</td>
<td>0.64</td>
<td>4.49</td>
<td>&lt;0.001</td>
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<tr>
<td>Procyon lotor</td>
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<td>0.33</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>Raccoon</td>
<td>Boar urine</td>
<td>-0.54</td>
<td>0.38</td>
<td>-1.42</td>
<td>0.16</td>
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Table 2.2 (continued)

<table>
<thead>
<tr>
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<th>Treatment</th>
<th>B</th>
<th>Standard error</th>
<th>Z</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td>Caramel syrup</td>
<td>0.69</td>
<td>0.31</td>
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<td>0.024</td>
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<tr>
<td>Hogshine</td>
<td>-0.09</td>
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<td>-0.25</td>
<td>0.80</td>
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<tr>
<td>Used cooking oil</td>
<td>0.22</td>
<td>0.33</td>
<td>0.69</td>
<td>0.49</td>
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<tr>
<td>Orange marmalade</td>
<td>1.11</td>
<td>0.29</td>
<td>3.78</td>
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<td>Sow urine</td>
<td>0.46</td>
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<tr>
<td>Strawberry jelly</td>
<td>1.18</td>
<td>0.29</td>
<td>4.03</td>
<td>&lt;0.001</td>
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</table>

Sciurus carolinensis

Gray squirrel

<table>
<thead>
<tr>
<th>Treatment</th>
<th>B</th>
<th>Standard error</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple jelly</td>
<td>0.56</td>
<td>0.41</td>
<td>1.37</td>
<td>0.17</td>
</tr>
<tr>
<td>Boar urine</td>
<td>0.08</td>
<td>0.44</td>
<td>0.18</td>
<td>0.87</td>
</tr>
<tr>
<td>Caramel syrup</td>
<td>0.56</td>
<td>0.41</td>
<td>1.37</td>
<td>0.17</td>
</tr>
<tr>
<td>Hogshine</td>
<td>0.29</td>
<td>0.43</td>
<td>0.68</td>
<td>0.50</td>
</tr>
<tr>
<td>Used cooking oil</td>
<td>0.15</td>
<td>0.44</td>
<td>0.35</td>
<td>0.72</td>
</tr>
<tr>
<td>Orange marmalade</td>
<td>1.15</td>
<td>0.38</td>
<td>3.02</td>
<td>0.003</td>
</tr>
<tr>
<td>Sow urine</td>
<td>0.15</td>
<td>0.44</td>
<td>0.35</td>
<td>0.72</td>
</tr>
<tr>
<td>Strawberry jelly</td>
<td>0.92</td>
<td>0.39</td>
<td>2.35</td>
<td>0.019</td>
</tr>
</tbody>
</table>

Odocoileus virginianus

White-tailed deer

<table>
<thead>
<tr>
<th>Treatment</th>
<th>B</th>
<th>Standard error</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple jelly</td>
<td>-0.92</td>
<td>0.87</td>
<td>-1.05</td>
<td>0.29</td>
</tr>
<tr>
<td>Boar urine</td>
<td>0.59</td>
<td>0.61</td>
<td>0.96</td>
<td>0.34</td>
</tr>
<tr>
<td>Caramel syrup</td>
<td>0.00</td>
<td>0.68</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Hogshine</td>
<td>0.69</td>
<td>0.60</td>
<td>1.15</td>
<td>0.25</td>
</tr>
<tr>
<td>Used cooking oil</td>
<td>0.18</td>
<td>0.66</td>
<td>0.28</td>
<td>0.78</td>
</tr>
<tr>
<td>Orange marmalade</td>
<td>-0.51</td>
<td>0.77</td>
<td>-0.66</td>
<td>0.51</td>
</tr>
<tr>
<td>Sow urine</td>
<td>0.00</td>
<td>0.68</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Strawberry jelly</td>
<td>0.34</td>
<td>0.64</td>
<td>0.53</td>
<td>0.60</td>
</tr>
</tbody>
</table>
Figure 2.1 Location of the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA (top left), with sample area grid locations within the refuge (bottom left) and assigned treatments at grid locations (right) during an investigation of non-grain attractants for wild pigs (*Sus scrofa*).
Figure 2.2  Wild pig (*Sus scrofa*) sounder visiting a used cooking oil attractant in the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA during an investigation of non-grain attractants for wild pigs.
CHAPTER III
CAN HAIR SNARES PROVIDE A RELIABLE METHOD FOR ESTIMATING
ABUNDANCE OF AN EXOTIC UNGULATE?

Abstract

Mitigating exotic species invasions in new areas requires reliable information on abundance and source-sink dynamics to evaluate effectiveness of concomitant control efforts. Despite being present in the southeastern United States since the early 1500s, wild pigs (*Sus scrofa*) continue to invade previously unaffected areas, including the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, a bottomland and upland forested landscape with an emerging wild pig population. Considering the early stage of invasion, we designed and implemented a non-invasive hair sampling technique for wild pigs to estimate abundance and relatedness of individuals (as an indicator of gene flow between populations) within the NNWR. Following 8-week sampling periods in 2021 (*n* = 160 samples) and 2022 (*n* = 159 samples), we identified 38 and 26 unique individuals, respectively, although weekly recapture rates across years (1–8%) were too low to yield precise abundance estimates within a capture-recapture modeling framework. We also identified low levels of heterozygosity indicating high relatedness among our sample population which likely reflected lack of natural and anthropogenic barrier features to gene flow and/or a limited number of external source populations. Finally, we observed positive trends in viable samples collected relative to sampling week in each year, suggesting more optimal sampling period(s) may exist (e.g., autumn), and we acknowledge that
methodological modifications, including use of grain in more accessible areas rather than our remote approach using scent-only attractants, may increase hair snare attractiveness and thus wild pig encounters and permit increased sampling frequency. Collectively, these 3 methodological modifications (i.e., altered season, bait type, and access) provide viable pathways to increase precision for estimates of abundance. This information, when used concomitantly with ongoing monitoring and control efforts, will contribute to a more holistic understanding of this exotic species and inform management actions among new invasions and established populations.

**Introduction**

Understanding wildlife population dynamics equips natural resource managers and biologists with necessary information to effectively monitor changes in abundance and evaluate effectiveness of management or control strategies (Dolbeer, 1998). Various active and passive methods have been used to estimate the abundance of wildlife populations. Active methods traditionally have included spotlight surveys (Collier et al., 2007), aerial surveys (Hone, 2008), or capture-mark-recapture techniques, the latter of which have considerable utility in small mammal (Jung et al., 2020) and insect (Parmenter & MacMahon, 1989) applications but can become laborious or otherwise risky when directly handling larger fauna. While passive methods have most commonly involved camera-trap surveys (Rovero et al., 2013), recent advances in DNA technology have enabled non-invasive genetic sampling which has shown promise in producing precise and accurate abundance estimates within a capture-recapture framework (Gardner et al., 2009). Genetic approaches allow for an examination of heterozygosity at unique loci (Nei, 1978; Waits et al., 2001) and individual profiling through identification of specific genotypes and sex (Waits et al., 2001; Waits & Paetkau, 2005). Combined with capture histories
of individuals within a sample, abundance estimation within a capture-recapture framework becomes possible using information unobtainable by other passive techniques (Lukacs & Burnham, 2005). Such passive methods may be especially useful when tasked with addressing exotic species invasions that require population monitoring but in which post-capture release is undesirable or infeasible. Within areas occupied by exotic species, genetic investigations can allow for estimation of population size (Piggott et al., 2008), while also identifying source populations, population bottlenecks, and genetic variation (Tsutsui et al., 2000; Allendorf & Lunquist, 2003; Zalewski et al., 2010), helping to inform natural resource managers and biologists on the magnitude of emerging invasions and effectiveness of control actions (e.g., selective removal, trapping).

Among genetic non-invasive sampling approaches, fecal DNA sampling has been most common and may be especially useful considering its randomness compared to samples obtained using attractants (King et al., 2021). However, sample degradation can occur rapidly due to high temperature, humidity, and precipitation levels, reducing amplification success and increasing genotyping errors (Taberlet & Luikart, 1999; Broquet et al., 2007; Brinkman et al., 2010). While use of attractants within alternative passive sampling methods (e.g., barbed wire hair snares) may present other inherent concerns (e.g., sex- and age-related avoidance of sampling stations leading to capture bias; Wold et al., 2020), the quality of DNA collected from hair samples tends to exceed fecal samples and has become the preferred collection method for many species (Depue & Ben-David 2007; Herr & Schley, 2009; Murphy et al., 2016).

The wild pig (Sus scrofa) is an exotic species with invasion origins in the southeastern United States dating back to the 1500s (Lewis et al., 2019) with continued population expansions due to not only natural dispersal capabilities (Snow et al., 2017), but also anthropogenic support
including translocation by hunters (Hernández et al., 2018). As wild pig distributions continue to expand and population growth goes largely unchecked in many areas due to lack of natural predators (i.e., Jeschke et al., 2012) and impactful anthropogenic control measures (e.g., aerial gunning; Davis et al., 2018; trapping; Gaskamp et al., 2021), ecologically sensitive areas, including those within the United States Fish and Wildlife Service’s National Wildlife Refuge System, continue to experience emerging invasions and require reliable means for estimating and monitoring wild pig population size.

Wild pig abundance has been measured using active (e.g., hunter surveys; Massei et al., 2015; trap removal models; Davis et al., 2020) and passive methods (e.g., track counts; Engeman et al., 2013; pellet counts; Ferretti et al., 2016; camera trapping; Massei et al., 2018; fecal DNA sampling; Davis et al., 2020). Among passive methods, camera trapping can yield wild pig abundance estimates consistent with estimates derived using other passive methods, although its effectiveness increases when used on populations with visually identifiable individuals (Schlichting et al., 2020). Furthermore, this method can become expensive and laborious due to the number of cameras required, with biases induced as cost reductions produce variability (Davis et al., 2020). Another passive method, genetic sampling, has shown promise in producing precise and accurate abundance estimates within a capture-recapture framework (Kierepka et al., 2016). Although use of genetic information in wild pig investigations has focused on fecal DNA collection (Ebert et al., 2012; Kierepka et al., 2016; Davis et al., 2020), issues with sample degradation can become especially problematic in the southeastern United States which experiences less than ideal environmental conditions (e.g., high temperature, humidity, and precipitation). Also, given the association between wild pigs and woody wetland (i.e., bottomland hardwood) areas, which may exacerbate these issues, development of a method that
obtains high quality DNA samples from wild pigs for abundance estimation that does not use fecal samples is warranted. Hair DNA sampling for wild pigs remains seemingly novel despite its potential to estimate abundance and relatedness while improving understanding of wild pig invasions and better informing management decisions.

Our objectives were to (1) design and implement a hair DNA sampling technique, (2) estimate abundance of wild pigs in a landscape characterized by recent invasion, and (3) estimate genetic heterozygosity to examine relatedness relative to contributing source population(s). Non-invasive genetic sampling using hair snares, while novel for wild pigs, could be an efficient tool for improving understanding of the current magnitude of wild pig invasions and better inform management decisions within areas which may make other sampling approaches (i.e., fecal DNA) less feasible. We hypothesized that visitation of hair snares by wild pigs and estimates of abundance would relate to sex, age, and social group characteristics, with abundance estimates driven primarily by DNA sample collections from sounders (which are more philopatric and tend to exhibit greater site fidelity) relative to adult males (Keuling et al., 2008b). Therefore, adult females and their family groups would contribute most viable hair samples. We also hypothesized that the genetic structure of the sample population would be reflective of a highly related population due to its emerging status and lack of natural and anthropogenic landscape barriers, with low accompanying heterozygosity values (i.e., <0.70; Paetkau, 2003) among microsatellite loci.

**Materials and methods**

**Study area**

The Sam D. Hamilton Noxubee National Wildlife Refuge (hereafter, NNWR; Fig. 3.1) encompassed 19,425 ha in east-central Mississippi, USA with bottomland hardwoods (i.e.,
woody wetlands; 52.2%) and upland forests (i.e., evergreen, deciduous, and mixed; 40.4%) collectively dominating the landscape, while remaining land cover types (e.g., water, developed) comprised the remaining 7.4% (Dewitz, 2019). In addition to the presence of wild pigs since 2014, native mammals included white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*). Elevation ranged from 193 m to 603 m, and the Noxubee River, Cypress Creek, Loakfoama Creek, and Oktoc Creek represented major perennial streams that crossed the NNWR centrally from west to east. There were a limited number of county, refuge, and private roads (and one highway), and a few private residences represented development on the NNWR.

**Sampling sites**

We began to implement wild pig hair snares by determining the wild pig distribution across the NNWR. During 2020–2021, we used wild pig damage transects (see Chapter 4) to identify areas (i.e., 1-km² grid cells) with concentrations of rooting activity and/or wallows for deployment of hair snares (Fig. 3.1). Then, during 2021, we determined optimal, non-grain attractants using a camera grid evaluation of candidate food and urine scents in the NNWR (see Chapter 2). Optimal attractants of used cooking oil (i.e., fish fryer grease) and orange marmalade (Great Value, Arkansas, USA) adhered to area restrictions on grain deployment, supported hair snare activation in remote areas, and minimized attractiveness of hair snares to non-target species (e.g., raccoon). In 2021, an attractant was randomly assigned to each individual hair snare (i.e., both attractants used *n* = 2 times per cluster) and retained throughout the sampling period. In 2022, attractants were randomly assigned to hair snares but alternated weekly to encourage increased visitation through novelty.
We designed and deployed 20 wild pig hair snares in 2021 based on our wild pig damage transects and the following methods (Fig. 3.1). We deployed hair snares in clusters \((n = 5; \text{ Fig. 3.1})\) to prevent territorial individuals (e.g., adult males) from preventing other wild pigs from accessing hair snares and creating a demographic bias within our sample (Ebert et al., 2010). We randomly generated hair snare locations \((n = 4)\) within each 1-km\(^2\) cell in ArcGIS (Environmental Systems Research Institute, 2017) and spaced clusters >2 km to promote independence between clusters and capture genetic heterozygosity across the NNWR. For each hair snare, two strands of barbed wire were stretched around trees \((n = 2)\) and T-posts \((n = 2)\) in a square formation with a perimeter of 32 m, and a non-grain attractant was placed in a decentralized manner on three tree trunks or stumps within the square. Barbed wire strands were placed 40–50 cm and 15–20 cm above ground level to obtain samples from adult and juvenile wild pigs, respectively (Fig. 3.2). However, lower strands were only used on two randomly assigned sides for each hair snare to reduce impedance of wire crossings by adults (Fig. 3.3). Hair sampling was conducted annually during 8 weeks from August–October, 2021–2022, with hair snares checked approximately weekly. However, during 2021, hair snares in 2 clusters (i.e., Roberts, Skinner; Fig. 3.1) became inundated during week 4 by Hurricane Ida, an event that prevented sampling of those hair snares \((n = 8)\) and adversely impacted all clusters (see below). In 2022, all hair snares were sampled weekly. To evaluate hair snare effectiveness, we monitored wild pig contact and/or crossing events with barbed wire strands with a single remote camera trap (FORCE-20; Spypoint, Quebec, CA) during 2021. In 2022, however, remote cameras \((n = 4)\) were placed on each side of hair snares \((n = 7)\) with the greatest number of samples collected in 2021 to improve our understanding of wire contacts and/or crossings relative to resulting
samples, as this was an issue identified in the only other study that tested hair snares for wild pigs (Ebert et al., 2010).

**Sample collection, processing, and analysis**

All hair present on an individual barb was collected and treated as a single sample (Fig. 3.3). Samples were collected using single-use latex gloves and sterilized tweezers. We sterilized all sampling utensils and barbs between sample collections using a butane torch. All samples were stored in coin envelopes with desiccant at room temperature to prevent sample degradation. We labeled each sample with date, hair snare identification, side of collection, and barb number on that side. Hair samples were processed (i.e., DNA amplified and genotyped) by Wildlife Genetics International Incorporated (British Columbia, CA), and each sample was assessed for individual genotype using microsatellite loci \( n = 8 \) that were associated with high amplification success and heterozygosity, along with low genotyping error (e.g., allelic dropout). A sex marker was also determined using samples from collared and non-collared individuals \( n = 9 \) males, \( n = 9 \) females) trapped during GPS collar deployments in the NNWR in 2020–2021 (see Chapter 1). At each locus, number of alleles, observed heterozygosity, and expected heterozygosity were calculated to improve our understanding of genetic variability within the population. All initial multilocus genotyping efforts and evaluations of heterozygosity were conducted using trapped and hair snare-sampled individuals from the NNWR in 2020–2021.

Final genotypes were used to estimate abundance in the NNWR with conditional likelihood closed-capture models (Huggins, 1989) in Program MARK v.10.1 (White & Burnham, 1999). We used Akaike’s Information Criterion corrected for small sample size (AICc; Akaike, 1973; Sugiura, 1978) within an information theoretic approach to evaluate a candidate set of models that treated capture probabilities as constant or allowed them to vary by additive
effects of week and year, or as interactions between these terms. We also considered a linear
trend on capture probabilities in 2022 based on apparent weekly increases in the number of
viable samples collected. Weekly precipitation was also a factor of interest but could not be
investigated due to the staggered nature of sampling within each sampling week (i.e., hair snare
clusters sampled on different days each week due to labor involved, thereby leading to
differential weekly precipitation totals). However, we accounted for known flooding effects of
Hurricane Ida (i.e., 142.8 mm of rainfall; National Oceanic and Atmospheric Administration,
2023) in week 4 of 2021 by fixing its capture probability to zero in all models. We estimated
overdispersion for the global model using Fletcher $\hat{c}$ (Fletcher, 2012) and used model averaging
for derived estimates of abundance (Stanley & Burnham, 1998).

Results

In 2021, we obtained 159 hair samples (with used cooking oil: $n = 88$; orange marmalade:
$n = 71$), of which 49 samples (30.8%) were viable and yielded individual genotypes. There were
38 individuals ($n = 20$ males, $n = 18$ females) among these samples, with 31 individuals
represented by a single sample each and 7 individuals detected among 2–5 samples. However,
among these there were only 5 recaptures (i.e., individuals detected >1 sampling week). In 2022,
we obtained 160 samples (with used cooking oil: $n = 92$; orange marmalade: $n = 68$), of which
42 samples (26.3%) were viable and yielded individual genotypes. There were 26 individuals ($n$
= 15 males, $n = 11$ females) among these samples, with 16 individuals represented by a single
sample each and 10 individuals detected among 2–5 samples. Again, recaptures were rare, with
only 3 individuals detected during >1 sampling week. No individuals captured in 2021 were
recaptured in 2022. We identified noticeable trends in sample collections in both years, with
65.3% (32/49) and 71.4% (30/42) of all viable samples collected in weeks 6–8 in 2021 and 2022, respectively (Figs. B.1–B.2).

Among camera-monitored hair snares in 2022, we documented 90 wire contacts and/or crossing events, of which 52 (57.8%) yielded accompanying samples. Among all hair snares, we identified noticeable disparities between samples yielded from our top strands (2021: n = 145; 2022: n = 144) relative to our bottom strands (2021: n = 14; 2022: n = 16). Further, although we could only account for additive, interactive, and observed effects of sampling week and year in our candidate set of models, we identified differences in weekly precipitation totals during weeks that yielded viable samples relative to those that did not across individual wild pigs, although these differences were more apparent in 2021 (weeks with viable samples: 33.5 ± 3.9 mm; weeks without viable samples: 51.9 ± 2.9 mm) than 2022 (weeks with viable samples: 19.9 ± 4.9 mm; weeks without viable samples: 23.8 ± 2.1 mm; National Oceanic and Atmospheric Administration, 2023).

We detected no overdispersion using Fletcher $\hat{c}$. Our top-ranked Huggins closed-capture model, in which capture probabilities were treated as equal in all weeks except for week 4 (2021) and as a linear trend by week (2022), garnered 87.4% of model weights, with no other candidate model receiving >7.5% of remaining model weights (Tables 3.1–3.2). Model averaged estimates of abundance for 2021 ($\hat{n} = 148$; 95% CI = 80–331) and 2022 ($\hat{n} = 107$; 95% CI = 50–293) were accompanied by high variability with coefficients of variation of 0.40 and 0.52, respectively, which reflected imprecision (relative to desired coefficients of variation <0.2; Pollock et al., 1990). Across microsatellite loci (n = 8) that were most likely to accurately yield individual genotypes, observed alleles (mean: 4.1 ± 0.4), observed heterozygosity (mean: 0.64 ± 0.04), and expected heterozygosity (mean: 0.65 ± 0.04) suggested low levels of genetic diversity within the
NNWR wild pig population, especially considering these loci were the most variable within the entire genome.

**Discussion**

Visitation rates did not appear to be biased by demographic characteristics, contrasting our prediction but also appearing to avoid a related concern in the only other study that investigated feasibility of hair snare use for wild pigs (Ebert et al., 2010). While our basis for this conclusion relates to the apparent evenness of sampling by sex, it would also be plausible to attribute this finding to sampling of juvenile males within sounders rather than adults. However, considering our lack of success in sampling juvenile wild pigs of each sex via the bottom strand across both years, it is more plausible to conclude that demographic biases were not as problematic during our investigation, with our clustered distribution of hair snares potentially alleviating this issue.

Surprisingly, no individuals captured in 2021 were recaptured in 2022, an unexpected finding since hair snare locations were the same during both years. This may reflect an association of hair snares with minimal nutritional benefit (i.e., scent only) given prior experiences of wild pigs with these locations. Alternatively, both seasonal and flash flooding of the NNWR leads to displacement of wild pigs from areas within which many of our hair snares were located, and upon recession of flood waters, wild pigs may have relocated to other areas within or adjacent to the NNWR, especially given the contiguous properties of the NNWR’s woody wetlands and ability of these areas to meet foraging and thermoregulatory requirements. However, failure to detect an individual at multiple hair snare clusters, while important to our assumption of cluster independence within a single sampling year, may also undermine the
strength of this conclusion given our inability to recapture any individuals sampled during 2021 at any cluster in 2022.

We identified notable trends in sample collection both years, with most viable samples collected during the final three weeks. While we found a positive linear trend in viable samples by week in 2022, this relationship was less discernible in 2021 and may have been related to the effects of Hurricane Ida during the intermediate stages of our sampling effort. Regardless, the similarly high percentages of viable samples collected during the final weeks in each year may suggest that an optimal window for sampling exists for the NNWR, and we may have merely sampled during its commencement (i.e., during our final weeks). While possible explanations for this phenomenon could include increases in hair snare attractiveness due to accumulating effects of scent deployment or higher sample quality due to a temporal effect (i.e., more recently collected samples), we believe that these explanations are less likely to represent the observed trend, especially considering the viability of hair samples collected from trapped wild pigs (i.e., 18/18, or 100% genotyping success) which were stored in an identical manner to hair snare samples and for longer durations. Rather, temporal shifts in space use relative to increases in hard mast availability (Froehly et al., 2020) or increasing anthropogenic pressures (i.e., hunting-related; see Chapter 1) near the end of the sampling period may have led to greater numbers of individuals in remote areas within which hair snares were located. Trends could also be related to differential weekly precipitation, which is demonstrated through contrasts between successful and unsuccessful sample collections from unique individuals by week, with this pattern being more discernible in 2021 than 2022, the latter of which was comprised by generally dry conditions both preceding and during the sampling period. Our inability to detect 2021 captures in 2022 could also potentially be attributed to these conditions, given differences observed at
multiple hair snare clusters between 2021 and 2022 (i.e., moist conditions vs. drought conditions, respectively) which may have led to displacement of wild pigs in a manner comparable to flooding at the opposite extreme. Regardless of the factor or factors which yielded the consistent pattern we observed in our collection of viable samples across years, this will present an issue for not only the NNWR but other public lands which must impose baiting restrictions at a time (i.e., October 1, or the start of archery season) during which wild pigs may be most responsive to attractants, whether non-grain or grain. The low overall number of viable samples, while concerning, may also reflect the emergent status of wild pigs in the NNWR, and while our method would conceivably benefit from continued population growth, this represents a suboptimal tradeoff which will likely be accompanied by continued degradation of natural ecosystems within the NNWR.

Although the low number of individuals captured and recaptured across sampling years was concerning, our method still showed utility and potential to yield samples needed for reliable abundance estimates. For example, wire contact and/or crossing rates during our 2022 camera monitoring of hair snares were more than twice the previously reported rates (14–25%; Ebert et al., 2010), especially considering these percentages across studies represent total samples collected without regarding processing. While Ebert et al. (2010) also cited issues with behavioral biases (i.e., exclusion of subordinate individuals by territorial adult males) which led to unequal capture probabilities, our study appeared to remedy this specific issue. However, our study still identified an issue with our underlying assumption of equal capture probabilities of adults and juveniles due to difficulties in sampling the latter via the bottom strand, as evidenced by the low number of samples yielded across sampling years. Use of bottom stranding on only two sides of each hair snare may have contributed to this disparity, with juveniles simply gaining
entry to the attractant through a top strand-only side; however, this design was deliberately implemented to prevent issues in impeding wire contacts and/or crossing events by adults. While the top strand appeared to be effective in sampling adults, identifying optimal strand heights may present a challenge in the southeastern United States and other areas where wild pig breeding is asynchronous and leads to a broad spectrum of possible wild pig sizes (i.e., heights) at any given time. Because of this, the use of double stranding on all sides with a more effective attractant (i.e., grain-scent combination) may remedy our concerns of impeding adult visitation. Alternatively, our method as currently designed may be limited to estimation of the breeding population (i.e., adults).

Even when we alternated non-grain attractants on a weekly basis in 2022 to encourage repeat visitation, we failed to increase recaptures, an issue that yielded coefficients of variation which indicated imprecision in abundance estimates. We also encountered difficulties in obtaining samples generally regarded as high quality for genotyping success (i.e., \( \geq 3 \) guard hairs with roots; D. Paetkau, pers. comm.), with few of our samples (i.e., 10.7% and 16.3% in 2021 and 2022, respectively) meeting this criterion, suggesting the passive nature of our method may become problematic when less enticing attractants are deployed. To remedy this issue, we cautiously encourage use of grain-based attractants while still complementing grain with non-grain attractants (e.g., orange flavor) to improve association of hair snares with nutritional (i.e., caloric) benefit and to enhance attractiveness, respectively. Given the ability of wild pigs to rapidly deplete grain, an increase in sampling frequency and bait replenishment (e.g., twice weekly) would be afforded by distributing hair snares closer to roads and trails and may collectively improve success in obtaining samples of higher quantity and quality (i.e., greater number of hairs/sample that were not exposed to environmental conditions long enough to
degrade). This improvement, in turn, could plausibly yield the numbers of captures and recaptures needed to generate more precise abundance estimates. While these modifications were not feasible in our study, which required use of non-grain attractants in remote or otherwise inaccessible areas for grain deployment, these next steps appear to be warranted and should maximize the usefulness of this technique.

Consistent with our prediction, the wild pig population showed a high level of relatedness evidenced by low heterozygosity, even among the most variable microsatellite loci used for individual genotyping; a finding that could potentially be attributed to the NNWR population’s emerging invasion status and/or lack of natural and anthropogenic barrier features to prevent gene flow. This was further reinforced when considering the spatial representativeness of wild pigs trapped or hair-snared across the NNWR that were used to generate heterozygosity estimates. For example, because the NNWR represents a recent invasion (i.e., 2014–present), low genetic variation could potentially be attributed to a founder effect. Wild pigs that represent the primary source of the NNWR invasion are believed to be those which gradually dispersed to the NNWR from one or more nearby properties that introduced wild pigs in the 1980s. Given the apparent attractiveness of the NNWR to wild pigs through its capacity to meet foraging (e.g., moist, easy-to-root soils) and thermoregulatory requirements (i.e., majority of the NNWR is woody wetlands containing a network of perennial streams which may act as corridors), increases in genetic variation may eventually be possible if wild pigs immigrate into the NNWR from other nearby source populations connected via such corridor features. The lack of substantive barrier features, whether anthropogenic (e.g., major highways, residential development) or natural (e.g., rugged terrain, large rivers), may facilitate such future invasions, and lack of substantive lethal pressures imposed on wild pigs in the NNWR (i.e., incidental take
of ~100 wild pigs/year during native game hunting seasons; T. Carpenter, USFWS, pers. comm.) may further exacerbate this issue.

Considering the successes relating to our design and implementation of this novel technique for wild pigs which include improvements in sample-yielding wire contacts and crossings, insights into optimal sampling timing, and reduction in behavioral biases, we encourage continued use of this method, especially considering these additional minor modifications may yield reliable abundance estimates within the sampling area and allow for extrapolation to a broader scale given other information, such as occurrence, which may be obtained using other non-invasive techniques (see Chapter 4). Ultimately, these steps will allow natural resource managers and biologists to monitor population abundance changes through time, information which may prove especially useful when used concomitantly with coordinated control efforts.

Acknowledgements

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Table 3.1  Capture probabilities ($p$) from top-ranked Huggins closed-capture model of wild pig (*Sus scrofa*) abundance in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in 2021–2022.

<table>
<thead>
<tr>
<th>Year</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>Lower Confidence Interval (95%)</th>
<th>Upper Confidence Interval (95%)</th>
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</thead>
<tbody>
<tr>
<td>2021</td>
<td>$p$ (Weeks 1–3, 5–8)</td>
<td>0.04</td>
<td>0.02</td>
<td>0.02</td>
<td>0.09</td>
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<tr>
<td></td>
<td>$p$ (Week 4)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<td>2022</td>
<td>$p$ (Week 1)</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.03</td>
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<td></td>
<td>$p$ (Week 2)</td>
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<td>0.01</td>
<td>0.00</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>$p$ (Week 3)</td>
<td>0.02</td>
<td>0.01</td>
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</tr>
<tr>
<td></td>
<td>$p$ (Week 4)</td>
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<td>0.01</td>
<td>0.01</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>$p$ (Week 5)</td>
<td>0.03</td>
<td>0.02</td>
<td>0.01</td>
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<td></td>
<td>$p$ (Week 6)</td>
<td>0.04</td>
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<td>0.01</td>
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<td></td>
<td>$p$ (Week 7)</td>
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<td>0.03</td>
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<td></td>
<td>$p$ (Week 8)</td>
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<td>0.05</td>
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1. Week 4 in 2021 was fixed to zero to account for effects of Hurricane Ida.
Table 3.2  Results from candidate set of Huggins closed-capture models investigating additive, interactive, and other effects of year and/or week on capture probability of wild pigs (*Sus scrofa*) on the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in 2021–2022. Year-specific effects (“.” and “T”) reflect constant and linear trend effects, respectively.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc Weights</th>
<th>Parameters (K)</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>2021 (.), 2022 (T)</td>
<td>315.08</td>
<td>0.00</td>
<td>0.874</td>
<td>3</td>
<td>373.54</td>
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<tr>
<td>Week</td>
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<td>4.92</td>
<td>0.075</td>
<td>8</td>
<td>368.22</td>
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<tr>
<td>Year+Week</td>
<td>321.93</td>
<td>6.85</td>
<td>0.028</td>
<td>9</td>
<td>368.08</td>
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<tr>
<td>Year*Week</td>
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<td>0.017</td>
<td>15</td>
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<tr>
<td>Null</td>
<td>326.04</td>
<td>10.96</td>
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<td>388.54</td>
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<tr>
<td>Year</td>
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<td>12.82</td>
<td>0.001</td>
<td>2</td>
<td>388.38</td>
</tr>
</tbody>
</table>

1. Week 4 in 2021 was fixed to zero across all models to account for effects of Hurricane Ida.
Figure 3.1 Distribution of hair snares ($n = 20$) and clusters ($n = 5$) within 1-km$^2$ grid cells with observed wild pig ($Sus scrofa$) damage in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) during 2021–2022.
Figure 3.2  Hair snare corral design used for genetic sampling of wild pigs (*Sus scrofa*) in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in 2021–2022. Two sides were single upper stands and the other two sides were double-stranded, and although only trees are shown, a combination of two trees and two T-posts were used as corners for each hair snare.
Figure 3.3  Adult wild pig (*Sus scrofa*) contacting barbed wire hair snare in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR), with accompanying hair sample.
CHAPTER IV
IMPLEMENTING AND EVALUATING A RAPID ASSESSMENT TOOL FOR DETECTING AND MAPPING WILD PIGS (*Sus scrofa*) IN A NEWLY INVADED LANDSCAPE

Abstract

As exotic species colonize new areas, rapid assessment tools may provide necessary information for prioritizing management efforts. Given logistical limitations associated with large landscapes, investigation of sampling effort relative to assessment accuracy is necessary to improve method efficiency and adoption. We used 500-m X 20-m belt transects (*n* = 184) within a systematic survey of wild pig (*Sus scrofa*) rooting and wallowing damage in 2020–2021, along with species distribution models, to predict where wild pig presence would most likely occur throughout a large national wildlife refuge recently invaded by wild pigs. Considering time and effort requirements for sampling 19,425 ha, we also subsampled data to understand when model accuracy faltered. Using all transect data from the first sampling year, approximately 25% of the refuge was predicted to have wild pigs in association with woody wetlands and perennial streams. Random subsampling showed that accurate predictions ceased when <70% of the original dataset was used. However, when cells were chosen based on wild pig land use tendencies, data requirements could be reduced by 46.7%. In the subsequent year, transects were used to validate model predictions and test the monitoring tool’s sensitivity over time. All but one cell (98%; 48/49) predicted to have wild pig occurrence had detected wild pig damage, whereas only 71% (35/49) of cells predicted to not have wild pig occurrence had no damage in the subsequent year. Cells predicted to not have wild pigs, but which had damage in the
subsequent year, were located adjacent to areas with damage or along refuge boundaries. Our work shows that a simple, efficient monitoring tool (i.e., transects) combined with predictive modeling can reliably identify areas with a high likelihood of wild pig presence to rapidly inform control efforts and improve monitoring efficiency. However, sampling efforts must still be sufficient enough so that landscape heterogeneity is adequately captured within a predictive modeling framework. Additionally, areas located on the periphery of predicted occurrence areas or boundaries may require greater monitoring, even if they don’t fit landscape-based criteria identified within an assessment, considering exotic species expansion.

**Introduction**

Exotic species expansion or establishment often leads to direct consequences for native biodiversity and ecosystem health (Keller et al., 2011). Recent explosions in floral and faunal invasions in recent decades are often attributed to intentional introductions (e.g., recreational hunting; Nogueira-Filho et al., 2009) or related to expanding globalization (Hulme, 2009; Keller et al., 2011). Regardless of the introduction mechanism, exotic species may naturalize and expand if they survive, reproduce, and maintain a sustainable population (Zenni & Nunez, 2013). This leads to diverse impacts on natural and anthropogenic systems (Arim et al., 2006; Keller et al., 2011) including the displacement, exclusion, or elimination of native species (Porter & Savignano, 1990; Kenward & Holm, 1993), the degradation of natural systems (Carlsson et al., 2004; Weidenhamer & Callaway, 2010), and the loss of agricultural productivity (Pimentel et al., 2005). Therefore, new monitoring and assessment tools need to reliably predict where species impacts are most likely to occur, with an emphasis on accomplishing this before establishment leads to uncontainable ecological disasters (e.g., Wiles et al., 2003).
Identifying and implementing monitoring measures in response to exotic species has proven challenging for resource managers. Monitoring tools can have difficulty in maintaining stride with changing distributions, a problem that is exacerbated among large landscapes faced with resource limitations (e.g., funding, personnel, time; Delaney et al., 2008). To address these concerns, rapid assessment has been promoted as a best practice for detecting exotic species early (Reaser et al., 2020). Rapid assessment relies on efficiency (i.e., reduced cost, labor, time) and effectiveness, as these will ultimately determine success or failure of control programs (Morisette et al., 2020; Reaser et al., 2020). Relative to direct methods of detecting an exotic species (e.g., camera grids; Aschim & Brook, 2019), indirect methods such as looking for sign on transects (Plumptre, 2000) may establish an initial baseline of species presence information and direct monitoring approaches for exotic species while strategically allocating limited resources (Morisette et al., 2020). If proven to be both efficient and effective, indirect methods can aid in identifying, predicting, and validating exotic species spatiotemporal distributional changes during annual monitoring efforts. A considerable knowledge gap exists, however, regarding method efficacy when used in this context, with emphasis on the amount of data required to reliably assess an emerging invasion.

Species distribution models have multiple ecological applications and have been used to identify priority areas for avian biodiversity conservation (e.g., Moradi et al., 2019), determine habitat suitability and connectivity for recolonizing carnivores (e.g., Boudreau et al., 2021), and improve understanding of the distribution of marine vegetation (e.g., Tyberghein et al., 2012). They have also been used to predict exotic mammal distribution and density (e.g., Lewis et al., 2017; Pittiglio et al., 2018). This extensive usage among myriad of objectives, the intensity of this technique’s validation and calibration (Hao et al., 2020), and its prior performance in
spatially predicting exotic species occurrence, make it a candidate for informing local management, control, and monitoring efforts. When used during emerging stages of invasion, it may also help prioritize management areas, better informing resource allocation and control efforts.

Wild pigs (*Sus scrofa*) are one of the most harmful exotic species worldwide, producing billions of dollars in damage and disease risk to agriculture annually (Pimentel, 2007; Rolesu et al., 2007), as well as damaging native ecosystems through rooting and wallowing activities that disturb seed banks, soils, native vegetation, and hydrology (Singer et al., 1984; Pedrosa et al., 2019; Gray et al., 2020). In North America, wild pigs thrive as generalist omnivores that can invade, establish, and persist in myriad landscapes (e.g., agroecosystems; Kramer et al., 2022; riparian and bottomland areas, deciduous forests; Clontz et al., 2021). Although wild pigs have been present in the southeastern United States since the 1500s (Lewis et al., 2019), increases in population size and expansion had gone relatively unnoticed until the mid-1980s (Corn & Jordan, 2017). Since this time, wild pig expansion has been aided by prolific reproductive capacity (Comer & Mayer, 2009), natural dispersal capabilities (e.g., 12.6 km/year geographic range increase; Snow et al., 2017) and human translocation of wild pigs into new areas (Hernández et al., 2018). As such, understanding how landscape features (e.g., bottomland and upland forests, streams; Beasley et al., 2014) relate to wild pig occurrence in areas of emerging invasion may better predict wild pig distribution and inform monitoring and control efforts (Gaskamp et al., 2018; Reaser et al., 2020). For example, in recently invaded areas, an initial census of occurrence could identify landscape features related to wild pig presence, and a subsequent investigation of subsampling census intensity may improve efficiency (i.e., reduction in cost, labor, time; Delaney et al., 2008). Once understood, effective subsampling (e.g., through
spatially balanced sampling; Brown et al., 2015) would allow for detection and prediction of wild pig distributions in recently invaded areas before populations become unmanageable, even in large, expansive landscapes. Information from the initial assessment can also be compared to future assessments to assess spatiotemporal changes. In tandem, these assessments would provide necessary information to refine a methodologically sound, effective, and efficient long-term sampling protocol.

In Mississippi, domesticated wild pigs have been present since the early 1500s and invasion during the previous century has become accelerated by hybridization with Eurasian wild pigs released for hunting purposes (Hamrick et al., 2011). Wild pig populations have expanded from 4% to 38% of the state’s total land area between 1988 and 2009 (Mississippi State University Extension Service, 2021), not only in agricultural landscapes but also those that are natural and likely more ecologically sensitive (e.g., wetlands; Engeman et al., 2007). Within federally protected forested lands recently colonized by wild pigs, we aimed to 1) use an initial transect census of wild pig occurrences (i.e., damaged areas) to facilitate understanding of landscape features which promote wild pig presence, 2) evaluate at what level subsampling impeded our ability to predict wild pig presence, and 3) validate the ability of transect-based knowledge to persist throughout time in an invasion area. Considering the recent invasion of this area and wild pig life history characteristics, we predicted wild pig presence would be clustered among areas containing perennial streams, woody wetlands, and deciduous forest. Additionally, we predicted transect efficacy would diminish rapidly using a random (i.e., uninformed) subsampling approach, but that a subsampling approach accounting for landscape features associated with occurrence and non-occurrence of wild pigs would represent a more efficient alternative.
Materials and methods

Study area

The United States Fish and Wildlife Service’s (USFWS) Sam D. Hamilton Noxubee National Wildlife Refuge (hereafter, NNWR) encompassed 19,425 ha in east-central Mississippi, USA. The NNWR consisted of mostly bottomland hardwoods, upland hardwoods, pine forest, mixed forest, grasslands, and wetlands (MacGown et al., 2012). Valued for waterfowl conservation, the NNWR was also inhabited by multiple native game species and 6 avian species of concern such as the red-cockaded woodpecker (*Leuconotopicus borealis*) and wood stork (*Mycteria americana*). Elevation ranged from 193 m to 603 m, and the Noxubee River, Cypress Creek, Loakfoama Creek, and Oktoc Creek crossed the NNWR centrally from west to east. A limited number of county, refuge, and private roads (and one highway), and a few private residences represented development on the NNWR. Observations of wild pigs and associated damage (e.g., rooting areas, wallows) only became increasingly noticeable since 2014–2015 despite their longstanding residency in Mississippi.

Identification of wild pig occurrences

Between August 2020 and April 2021, we used 20-m X 500-m belt transects (*n* = 184) to identify wild pig rooting areas and wallows (i.e., damage sites as a proxy for their occurrence) across the NNWR. We first overlayed a 1-km² grid over a NNWR boundary shapefile (USFWS, 2022) in ArcGIS (Environmental Systems Research Institute, 2017). At all grid cell centroids, we applied a circular buffer with a 500-m radius and then generated 2 random integers between 0° and 359° per grid cell to determine compass bearings for 2 transect lines starting at the centroid and ending when intersecting the 500-m buffer. The first transect represented the default transect to be completed, while the second transect was used only when the first encountered another
property boundary. If both transects had accessibility issues, we retained the first transect and redirected the transect for its remaining length using randomly generated directions (left, right) and bearings (15–75°). Given the time required to complete a full census by a single observer, we grouped transects into geographic subsets of ≤6-cell blocks, with subsets randomly ordered for completion, with a priority on interior blocks due to winter inundation of many interior areas, either naturally or intentionally for waterfowl management. Each transect was walked by the same observer who photographed and GPS-marked (Garmin 60CSx, Garmin Ltd, Kansas, USA) all wild pig rooting areas and wallows within 10 m of the transect line.

**Predictor variables**

We used 12 environmental variables expected to be related to wild pig presence including elevation and distance to land cover and stream features. For elevation, we resampled a 10-m digital elevation model (Mississippi Automated Resource Information System, 2007) to the same resolution as our land cover dataset (i.e., 30 m). For land cover, we used the 2016 National Land Cover Database (Dewitz, 2019). Of the original 20 land cover classes available, 14 were present on the NNWR. We reclassified these into 9 classes including: water (open water and barren land), developed (open spaces, low and medium intensity), shrub, field (hay/pasture and cultivated crops), herbaceous (herbaceous cover and herbaceous wetlands), woody wetland, and deciduous-, evergreen-, and mixed-forest. Reclassifications were based either on known discrepancies between original classification and ground knowledge (e.g., barren class exclusively located in middle of two large lakes on the NNWR), or perceived functional similarity of classes on the NNWR (e.g., open fields) relative to wild pigs. We transformed each land cover class into its own continuous variable by calculating Euclidean distance from each land cover type. Similarly, we calculated Euclidean distances (at a 30-m resolution) to
intermittent and perennial streams using shapefiles for each stream feature (Mississippi Automated Resource Information System, 1992). All predictor variable data was centered and scaled prior to analysis.

**Modeling predicted wild pig presence**

We used all rooting and wallow locations as presence points within a species distribution modeling framework (Elith et al., 2011). As species distribution models require presence points compared to absences (which are rarely recorded for distribution modeling; Phillips et al., 2009), we created a 20-m buffer around each surveyed transect and randomly generated 100 pseudo-absences for each presence location within the buffers. Presence locations were buffered by 10 m prior to generating pseudo-absences so that they did not overlap. Presence and pseudo-absence locations, along with environmental variables, were then used within a Maximum Entropy (MaxEnt) model to generate a predicted wild pig presence distribution. We removed elevation and mixed forest predictors due to multicollinearity issues with woody wetland and evergreen forest ($r = 0.78$ and $r = 0.87$, respectively). Woody wetland was retained rather than elevation given the previously documented value of woody wetlands for wild pig foraging and thermoregulation (Paolini et al., 2018). Similarly, evergreen forest was retained rather than mixed forest given spatial associations to each other within upland areas of the NNWR, and the ability to examine evergreen forest relative to two distinct and pure deciduous forest classes (i.e., upland deciduous and woody wetlands) already retained and which likely accounted for the affinity of broadleaf vegetation by wild pigs for thermoregulation. We calibrated the model using 80% of the data and evaluated model fit and stability using the remaining 20% (i.e., 5-fold validation). Model fit was assessed by quantifying the area under the curve of a receiver operating characteristic plot (AUC-ROC) and true skill statistic (TSS; sensitivity – specificity
+1) using the ROCR R package (Sing et al., 2005). We assessed stability as models having good fits (AUC-ROC and TSS values closer to 1 than 0.5 and 0, respectively; Allouche et al., 2006) and contributions from the same top 4 predictors across all folds. Occurrence was predicted (predict R function) as a range of values from 0 (low likelihood) to 1 (high likelihood) across the NNWR. We then transformed the continuous prediction to a binary format (non-occurrence/occurrence) using a likelihood threshold that maximized model sensitivity plus specificity using the ROCR R package (Liu et al., 2013).

**Evaluation of subsampling approaches**

Because cost, labor, and time required to complete a full census may collectively undermine its utility for rapid assessment, as in our large study area, we tested the influence of subsampling on model results by reducing the number of sampled grid cells in 10% increments (e.g., 90%, 80%, etc.) from the full census. We randomly sampled cells for inclusion and reran our above model using reduced sampling intensities until models could no longer be deemed either having good fit or stability per our 5-fold validation procedure. We again generated predictive maps in both continuous and binary form at each increment and used binary map outputs at all stable levels (including 100%) to determine mean and standard error for the top predictor variables relating to predicted wild pig presence or absence.

As an alternative to random subsampling, we used information from the top predictors in our binary map outputs to identify 1-km² grid cells most likely to have only the presence or absence of wild pigs (i.e., 0 or 1) and omitted cells with confounding predictor values. Because the number of predicted absence cells (n = 86) exceeded the number of predicted presence cells (n = 49), we randomly sampled the former to ensure equal numbers of each cell type (i.e., 50% presence cells, 50% absence cells), and repeated the same modeling and evaluation procedures
within these cells, including incremental subsampling, until model stability was lost. Predictor data extraction, species distribution modeling, and model evaluation analyses were conducted using R v. 4.1.2 (R Core Team, 2021).

**Field validation**

Because we identified a need to not only evaluate subsampling approaches but also overall effectiveness of using transects to reliably detect, monitor, and predict wild pig presences and absences, the 98 cells with presence-only or absence-only predictions were resurveyed between August and October 2022. We retained our original transect, including any required transect redirection (i.e., leading to the same end point), and randomly generated 2 new bearings for the second transect following procedures used during the full census. This permitted evaluation of the same transect across multiple years and the sensitivity of varying transect direction.

**Results**

Woody wetlands (52.2%) and upland forests (i.e., evergreen, deciduous, and mixed; 40.4%) collectively dominated the NNWR landscape, while the remaining classes (e.g., water, developed) made up the remaining 7.4%. We completed 184 transects (Fig. 4.1a) during the initial census that yielded 303 damage observations ($n = 285$ rooting areas, $n = 18$ wallows; Fig. 4.1b). Of these transects, 69 contained $\geq 1$ damage observation, with a mean distance of 122.7 m between the transect origin and the first detection of damage (range: 1.3 – 445.1 m). Using the full suite of transect data, models had an AUC-ROC $\geq 0.82$ and TSS $\geq 0.54$ across all 5-fold validation runs and maintained predictor stability (Table 4.1). Predictors most influential to wild pig occurrence likelihood were areas located greater distances from evergreen forest and
developed lands and closer to woody wetlands and perennial streams (Table 4.2). About 47.1 km², or 25.2%, of the NNWR was predicted to have a high likelihood of occurrence of wild pigs (i.e., above a likelihood threshold of 0.44; Fig. 4.1c; Table 4.1).

Models also had high predictive performance and remained stable across all 5-folds when we randomly subsampled cell information from 100% to 70%. At 90%, 80% and 70%, models had similar AUC-ROC and TSS values to the full census, the same top predictors, and similar average distances to top contributing variables (Tables 4.1–4.3). However, at 60% (i.e., 111 cells), while AUC-ROC and TSS values remained comparable to those at higher sampling levels, our fourth top predictor, “developed”, was surpassed by “deciduous” during multiple validations (Tables 4.1, 4.2). Based on the full census and stable subsamples (i.e., 90%, 80%, and 70%), grid cells predicted to have wild pigs present were those with an average distance ≤1.9 m to woody wetlands, ≤305.7 m to perennial streams, ≥598.0 m to evergreen forest, and/or ≥826.5 m to developed lands (Table 4.3). When we subsampled using a balanced presence and absence cell approach (i.e., 98 cells), models had high predictive performance and stability across all 5-fold validation model runs at 100% and 90% before losing stability at 80% (i.e., 80 cells), despite comparable AUC-ROC and TSS values even at this subsampling level (Tables 4.1, 4.4).

Cells surveyed the following year had 196 total transects (i.e., double observer; n = 2/cell) that yielded 119 damage observations (n = 112 rooting areas, n = 7 wallows; Fig. 4.1d). Among predicted presence cells, 48/49 cells (96/98 transects; 98.0%) had damage in 2022, with a mean distance of 45.4 m between transect origin and first observed damage (i.e., not including completed 500-m transects; n = 2). Predicted presence cells were not sensitive to varying transect direction, as all 49 cells yielded consistent results (i.e., both had or did not have damage). Among predicted absence cells, 35/49 cells (71.4%), or 75/98 transects (76.5%), had absence of
damage, with a mean distance of 159.5 m between transect origin and first observed damage in cells that had damage. Predicted absence cells showed greater sensitivity to varying transect direction with only 44/49 cells (89.8%) returning a consistent result. For the cells that were predicted to have absences that actually had damage, 12/14 (85.7%) shared a border (i.e., side or corner) with predicted presence cells, while the remaining 2 cells were located on the NNWR border with unknown (i.e., non-surveyed) wild pig status on adjacent lands. Overall, 83/98 cells (84.7%), or 171/196 transects (87.3%), were validated relative to their respective predictions.

Discussion

Our findings supported our first prediction that wild pig damage would be concentrated in land cover types typically used by wild pigs including woody wetlands (i.e., bottomland hardwoods) and perennial streams. Although deciduous forest did not have a strong relationship with damage, which is atypical for wild pigs (Singer et al., 1984), this class composed only 1.5% of the landscape and was concentrated primarily in an upland section of the NNWR that was not occupied by wild pigs. Wild pigs rely on deciduous forests near water, not only for foraging, but also thermoregulation, nesting, and bedding sites (Choquenot & Ruscoe, 2003; Fernandez-Llario, 2004), and upland deciduous forests in our study area were devoid of water sources to meet these needs. Although wild pig damage-density relationships often are non-linear (Davis et al., 2018), the identification of areas predicted to have wild pig occurrence (and therefore their associated damages) may be indicative of areas meeting multiple life history requirements, even without readily available density or abundance estimates (see Chapter 3).

Our findings suggest that baseline data provided the means for choosing cells that contained landscape characteristics related to a species’ occurrence, and that this could better inform a rapid assessment approach over random subsampling. Indeed, we identified a reduction
in effort of 30% \((n = 129/184 \text{ transects})\) prior to losing model stability when randomly
subsampling cells, but we were able to reduce effort by 46.7% \((n = 98/184 \text{ transects})\) when
choosing cells with features that were preferred and not preferred by wild pigs. Although we
retained these 98 cells for field validation the following year, our models suggested this could be
reduced to 51.1% \((n = 90/184 \text{ transects})\) while still achieving predictive stability. As a result,
rather than randomly sampling across a large landscape, using characteristics known to hold
value to a species when selecting areas for sampling may be more informative. While a
systematic sampling framework was used on the NNWR to obtain baseline occurrence
information, other types of occurrence data such as expert opinion (Markov et al., 2022), citizen
science data (McCaffrey, 2005), and common non-invasive sampling techniques (e.g., camera
traps and hair snares; Monterroso et al., 2014) might also be used in a similar fashion to what
was done here, especially when resources are limited. Regardless, identifying a balance between
efficiency and effectiveness of monitoring will likely rely on the ability to accurately model
occurrence during early stages of invasion and how that translates to reduced efforts to maintain
knowledge before full establishment occurs (Morisette et al., 2020; Reaser et al., 2020).

We used a likelihood-based threshold to obtain a binary prediction of presence-absence
that could help define our top predictors. Inevitably, use of different thresholds (e.g., equal
sensitivity and specificity; Freeman & Moisen, 2008) may have yielded differences in calculated
averages of predictor values and impacted which cells were chosen. While our likelihood
threshold is commonly used in species distribution models as it is based on a model’s ability to
make robust predictions relative to competing alternatives (Liu et al., 2013), threshold use can
depend on other objectives. For example, an agency may not want to consider places where there
are \( \leq 10\% \) of a species’ occurrences and therefore use a 10\text{th} percentile threshold (Escalante et al.,
While, for wild pigs in our study, resulting predictor values did not vary considerably across sampling intensities (Table 4.3 relative to Table 4.1; Figs. C.1–C.2), use of various thresholds could lead to substantive changes in how sampling protocols may be defined. This issue of model discrimination is common in species distribution modeling, and it is imperative to, at minimum, be aware of the implications of using various likelihood thresholds (Chivers et al., 2014).

Our findings supported our prediction that we could use transects as a reliable means of monitoring, especially in areas predicted to have wild pig presence. This support was most evident with our field validation in the subsequent year where all but one predicted presence cell were validated on both transects, suggesting that a simple and efficient monitoring tool (i.e., transects) can be used in tandem with predictive modeling to reliably identify where wild pigs are most likely to occur. These areas may represent those in which coordinated control efforts (i.e., corral trapping, aerial gunning) should be concentrated (Gaskamp et al., 2018). Given consistent agreement between transects in each cell, coupled with relatively short distances required to detect damage within them, reduction in sampling effort (i.e., transect number or length) may be feasible during subsequent monitoring events once a reliable baseline is established. While we had good validation where wild pigs were predicted to occur, this support was not as strong for cells where they were predicted to be absent, as some cells had damage observed in the following season. However, detection of wild pig damage in these areas was not necessarily alarming, as all but two predicted absence cells with damage during validation were adjacent to a predicted presence cell. Wild pig dispersal capabilities, generalist adaptive life history, and the spatiotemporal resolution of our survey method (i.e., 1-km² resolution, 16 months between survey periods) could all aid in explaining wild pig expansion into neighboring
cells. The 2 cells not adjacent to cells with observed damage were located on the border of the NNWR and considering our census did not extend outside this boundary we have no way of knowing if there is also wild pig expansion into the NNWR from adjacent lands. Therefore, areas located on the periphery of damaged areas, or on borders, may represent those in need of greater allocation of monitoring, even if they do not meet the landscape-derived criteria for species presence or absence.

For exotic species that create noticeable landscape damage, damage observed in new areas may become an increasingly apparent issue when populations are not subjected to substantive control measures. On the NNWR, lethal control of wild pigs has been mainly limited to incidental take during native game hunting seasons (i.e., ~100 wild pigs/year, T. Carpenter, USFWS, pers. comm.). Because recreational hunting has not been demonstrated as a viable control method for wild pigs and may exacerbate an existing invasion by causing spatiotemporal shifts of wild pigs into less accessible areas (Scillitani et al., 2010), an increase in the damage detected between years was not surprising and may reflect a population that will continue to expand if substantive control efforts are not undertaken.

Conclusions

Given the formidable threat exotic species pose to ecosystems and native biodiversity, it is likely that efforts to refine methods used to monitor and rapidly assess invasions will continue. Our work has both critically evaluated and demonstrated the ability of our approach to aid in reducing effort, including ease of implementation and cost-effectiveness, without sacrificing reliability, while also permitting replicability of the method as a viable long-term solution for monitoring invasions. Indeed, current collaboration on state-owned wildlife management areas in Mississippi already shows how integrating transect monitoring and species distribution modeling
can be effective, not only in landscapes that vary considerably from our study area (i.e., predominantly upland forest), but also how this assessment tool can be used to assess distributions before and after control efforts (A. Ballard, Mississippi Department of Wildlife, Fisheries and Parks, pers. comm.). Given the universality of this rapid assessment tool that combines simple-to-use field techniques and robust analytical procedures, we advocate that it be considered a viable option in the toolkit for natural resource managers, biologists, and others tasked with addressing exotic species.

**Acknowledgements**

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**Tables**

Table 4.1  
Area under the curve of a receiver operating characteristic (AUC-ROC), true skill statistic (TSS), and likelihood threshold values across models created from either the full transect census with random subsampling (left) or models created from the subsample of grid cells predicted to have presence or absence of wild pig (*Sus scrofa*) occurrence (right) in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.

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Table 4.2 Percent contribution of predictor variables for the total census and random subsampling across 5-fold validation procedures for predicting wild pig (*Sus scrofa*) occurrence in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Results are shown from 100% to 60% cells sampled (i.e., point of model instability).

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Table 4.3  Mean and standard error (SE) for the top 4 contributing predictors used to identify validation cells for predicting wild pig (*Sus scrofa*) occurrence in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Values were quantified for each predictor using binary model likelihood threshold outputs across stable sampling intensities (i.e., 70–100%). All values are shown in meters.

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Table 4.4  Percent contribution of predictor variables for chosen presence and absence cells for wild pigs (*Sus scrofa*) in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA, including a decreasing number of grid cells sampled across 5-fold validation procedures. Results are shown from 100% to 80% cells sampled (i.e., point of model instability).

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Figure 4.1  Systematic grid across the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) with completed census transects of wild pig (*Sus scrofa*) damage (a), continuous predicted occurrence distribution (b), binary predicted occurrence distribution (c), and observed damage relative to completed validation transects, chosen predicted presence cells, and chosen predicted absence cells (d).
REFERENCES


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APPENDIX A

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER I
Table A.1  Summary of two competing non-linear least squares movement models (i.e., home ranging, random walking) for adult female wild pigs (*Sus scrofa*; *n* = 10) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.

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</table>
Figure A.1 Distribution of step lengths (m) for adult female wild pigs (*Sus scrofa*; *n* = 10) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.
Figure A.2  Tortuosity/straightness indices for adult female wild pigs (Sus scrofa) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Pig 35489 is not shown due to its similarity to pig 26628 reflective of the merging of their remnant sounders.
Figure A.3  Net displacement for adult female wild pigs (*Sus scrofa*) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Pig 35489 is not shown due to its similarity to pig 26628 reflective of the merging of their remnant sounders.
Figure A.4  Number of complete cases ($n = 12$ relocations/day) relative to Julian day for adult female wild pigs ($Sus$ $scrofa$) trapped in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.
Figure A.5  Mean daily distances traveled by wild pigs (*Sus scrofa*) relative to Julian day during the pre-archery, archery, and firearms seasons in the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA.
APPENDIX B

SUPPLEMENTAL FIGURES FOR CHAPTER III
Figure B.1  Number and proportion of viable wild pig (*Sus scrofa*) hair samples collected by sampling week during 2021 in the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA.

Figure B.2  Number and proportion of viable wild pig (*Sus scrofa*) hair samples collected by sampling week during 2022 in the Sam D. Hamilton Noxubee National Wildlife Refuge in Mississippi, USA.
APPENDIX C

SUPPLEMENTAL FIGURES FOR CHAPTER IV
Figure C.1  Comparison of continuous predictive maps of wild pig (*Sus scrofa*) occurrence across 100% (a), 90% (b), 80% (c), 70% (d), and 60% (e) sampling intensities across the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Maps reflect outputs from the first cross-validation runs (i.e., k-fold = 1) in Table 4.1.
Figure C.2  Comparison of binary predictive maps of wild pig (*Sus scrofa*) occurrence across 100% (a), 90% (b), 80% (c), 70% (d), and 60% (e) sampling intensities across the Sam D. Hamilton Noxubee National Wildlife Refuge (NNWR) in Mississippi, USA. Maps reflect outputs from the first cross-validation runs (i.e., k-fold = 1) in Table 4.1.