MULTI-SCALE RESOURCE USE OF WILD PIGS IN THE RED HILLS REGION OF NORTH FLORIDA AND SOUTH GEORGIA, USA

by

CHRISTOPHER ANTHONY TERRAZAS

(Under the Direction of Michael T. Mengak)

ABSTRACT

Wild pigs *(Sus scrofa*) are a prolific invasive species that have spread across the world and inflicted severe damage in their introduced range. Wild pig management has developed in response to a precipitous increase in abundance. Interpreting wild pig resource selection at multiple scales of use can improve future removal and management efforts. I used GPS data from wild pigs to understand resource selection at two spatial scales (home range and within home range). Wild pigs preferred forested wetland and upland hardwood habitats, especially those that have experienced longer intervals without prescribed fire. I also used GPS data to assess fine-scale bedding site selection. Wild pigs preferred to construct beds within forests with a lower basal area and more dense understory vegetation from 1-1.25 m above ground. Future management could use these insights to prioritize removal and habitat modification to mitigate wild pig damage.

INDEX WORDS: Bedding site selection, habitat use, invasive species, prescribed fire, resource selection, *Sus scrofa*, wild pigs

MULTI-SCALE RESOURCE USE OF WILD PIGS IN THE RED HILLS REGION OF NORTH FLORIDA AND SOUTH GEORGIA, USA

by

CHRISTOPHER ANTHONY TERRAZAS

BS, Abraham Baldwin Agricultural College, 2019

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2023

MULTI-SCALE RESOURCE USE OF WILD PIGS IN THE RED HILLS REGION OF NORTH FLORIDA AND SOUTH GEORGIA, USA

by

CHRISTOPHER ANTHONY TERRAZAS

Major Professor:	Michael T. Mengak
Committee:	Kim Sash
	L. Mike Conner
	James C. Beasley

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
December 2023

DEDICATION

To my wife, Kelsey. Thank you for loving and supporting me through everything. Thank you for helping me work on my stand-up comedy. You could've laughed at the unfunny jokes, but you didn't.

ACKNOWLEDGEMENTS

I would like to thank my thesis advisor, Dr. Michael T. Mengak, for pushing me to think critically and talking with me through all the ideas, good and bad. I would also like to thank my graduate committee, Kim Sash, Dr. Mike Conner, and Dr. James Beasley for their advice and support throughout this process. I would like to thank the USDA for funding this project. I would also like to thank Eric Staller from Tall Timbers Research Station for playing a significant role in receiving the grant, and for coming out and helping with collaring pigs. I thank all the Wildlife Services personnel for assisting with capture and handling pigs for my project. I would like to thank the several landowners in the Red Hills for allowing us to use their properties for our research. Also, I would like to thank the technicians that helped collect data for this project, including Evan Williams, Garrett Wong, Katie Pabody.

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS v

LIST OF TABLES viii

LIST OF FIGURES x

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW 1

Literature Cited 10

2 FIRE HISTORY AND WILD PIG (*SUS SCROFA*) RESOURCE SELECTION IN NORTH FLORIDA AND SOUTH GEORGIA, USA 23

Abstract 24

Introduction 24

Methods 28

Results 30

Discussion 31

Management Implications 33

Literature Cited 34

3 WILD PIG (*SUS SCROFA*) BEDDING SITE SELECTION IN NORTH FLORIDA AND SOUTH GEORGIA, USA 45

Abstract 46

Introduction 47

Methods......50

Results......52

Discussion......52

Management Implications......55

Literature Cited......55

4 CONCLUSION......66

LIST OF TABLES

Page

Table 2.1: Individual data for GPS collared wild pigs in the Red Hills region of North Florida and South Georgia, USA. Home ranges were calculated using a 95% fixed kernel density estimator. Collared pigs were monitored between December 2021 and April 2023. Fix rates were changed from 2-hour to 1-hour for 4 individuals in March 2022...41

Table 2.2: Results from a generalized linear mixed model to evaluate wild pig 3rd order resource selection in the Red Hills region of North Florida and South Georgia, USA between December 2021 and April 2023. Land cover represents the Euclidean distance (m) to the nearest patch of those cover types. Relative selection strength (RSS) is the exponentiated β coefficient estimate. Because land cover is distance based, RSS values are to be interpreted inversely, where selection is less than 1 and avoidance is greater than 1 42

Table 3.1: Individual data for GPS collared wild pigs in the Red Hills region of North Florida and South Georgia, USA between December 2021 and April 2023. Fix rates were changed from 2-hour to 1-hour for 4 individuals in March 2022....................61

Table 3.2: Descriptive statistics of data collected for a generalized linear model to evaluate wild pig bedding site selection in the Red Hills region near Tallahassee, Florida, USA between December 2021 and April 2023. Vertical cover represents precent obstruction estimated across a vertical gradient on a modified vegetation

profile board....62

Table 3.3: Results from a generalized linear model to evaluate wild pig bedding site selection in the Red Hills region near Tallahassee, Florida, USA between December 2021 and April 2023. Relative selection strength (RSS) is the exponentiated β coefficient estimate. RSS values less than 1 signify that increasing covariate values results in decreasing relative probability of use. Vertical cover represents percent obstruction across a vertical gradient on a modified vegetation profile board....63

LIST OF FIGURES

Page

Figure 2.1: Land Cover/Land Use map of the Red Hills region between Thomasville, Georgia and Tallahassee, Florida, USA. Study sites are outlined in black 40

Figure 2.2: Relative probability of use by wild pigs in the Red Hills region, USA plotted against distance to open water in two seasons based on low (January-April) and high (May-December) forage availability between December 2021 and April 2023. Error bars represent 95% confidence bands 43

Figure 2.3: Relative probability of use for bedding by wild pigs in the Red Hills region near Tallahassee, Florida, USA plotted against distance to planted pine in the high forage season (May-December) across four yearly intervals without fire................44

Figure 3.1: Land Cover/Land Use map of the Red Hills region between Thomasville, Georgia and Tallahassee, Florida, USA. Study sites are outlined in black 60

Figure 3.2: Relative probability of use for bedding by wild pigs in the Red Hills region near Tallahassee, Florida, USA plotted against basal area. Error bars represent 95% confidence bands… 64

Figure 3.3: Relative probability of use for bedding by wild pigs in the Red Hills region near Tallahassee, Florida, USA plotted against percent vertical obstruction at 1 – 1.25 m above ground (cover). Error bars represent 95% confidence bands 65

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The deliberate or unintended movement of organisms by humans has introduced species to environments outside of their natural range (Essl et al. 2020). These novel environments often lack ecological regulators that prevent introduced organisms from establishing populations or outcompeting native species. When this occurs, invasive species thrive in newly found environments, often with devastating impacts on native ecosystems (Barrios-Garcia and Ballari 2012, Simberloff 2013). Invasive species also negatively impact industries like forestry and agriculture (Pimentel et al. 2000, Lovett et al. 2016, Strickland et al. 2020). The economic impact of invasive species, while difficult to estimate, is substantial and threats to human health are of equal concern (Simberloff 2013).

Invasive wild pigs (*Sus scrofa*), hereafter "wild pig(s)" are called many names including feral pigs, wild boar, and wild hogs (Keiter et al. 2016). Wild pigs are considered one of the "100 world's worst" invasive species (GISD 2023). Outside of their native range in Eurasia and Northern Africa, wild pigs occupy every continent except Antarctica and populations are projected to continue expanding (McClure et al. 2015, Lewis et al. 2017). Wild pigs were introduced to North America as early as the 16th century by Spanish explorers (Mayer and Brisbin 2009). These individuals were initially brought as livestock and ranged freely around settlements (Mayer 2018). Subsequent voyages and later introductions of Eurasian wild boar compounded this issue, bolstering the wild pig invasion across the continent (Mayer and Brisbin 2008). In the mid-20th century, most free-range practices in the contiguous United States (USA) were outlawed. Unfortunately, illegal human transport of wild pigs accelerated their expansion across the country (Hernández et al. 2018). Sport hunting is a common pastime in the USA and has incentivized the translocation of wild pigs to new areas for hunting (Tabak et al. 2017). Populations increased precipitously in the 1990s and nation-wide abundance likely exceeds 6.9 million individuals in more than 31 states (Bevins et al. 2014, Lewis et al. 2019, USDA 2022)

Humans are not the only factor supporting the expansion of wild pigs in the USA. A high reproductive output and lack of natural predators allow them to continue spreading (Bieber and Ruf 2005, Mayer and Brisbin 2009). Juvenile females reach sexual maturity before one year of age, at a mass of 30kg (Chinn et al. 2022). Once sexually mature, females can have more than one litter per year, on average producing 5.3 fetuses per sow (95% CI = 4.8-5.7) (Snow et al. 2020). This estimate was calculated by synthesizing 27 studies across North America and variation in fetuses per sow was hypothesized to be a result of fluctuating ovulatory rates (Snow et al. 2020). Females with piglets combine to form matriarchal groups, or sounders, that can represent multiple generations while adult males often travel alone (Kaminski et al. 2005, Mayer et al. 2020).

Wild pigs are dietary generalists, which allows them to exploit a range of environments when searching for food (Ballari and Barrios-Garcia 2014). The primary foraging method exhibited by wild pigs is rooting, a process in which they dig their snouts into the ground to turn up food items in the soil (Mayer 2009, Gray et al. 2020*b*). Rooting disrupts soil chemistry and alters vegetative dynamics in the understory (Singer et al. 1984, Gray et al. 2020*a*). Damage from rooting can result in increased species richness of understory vegetation although negative impacts far outweigh the perceived good (Arrington et al. 1999, Hensel et al. 2021). Gray et al. (2020*a*) found conflicting results in which wild pig rooting reduced herbaceous species diversity, but these results may vary due to differences in the dynamics of forest and wetland systems. Regardless, rooting negatively impacts vegetative communities by altering natural cycles, especially when repeatedly disturbed (Sharp and Angelini 2019).

Damage from wild pigs is not limited to rooting; biological and environmental factors drive wild pigs to behave in additionally destructive ways such as wallowing, rubbing, and tusking (Graves 1984, Bracke 2011). Wallowing, a behavior in which wild pigs cover their bodies in mud, is the more damaging of the three and poses a greater threat to native species due to the increased potential for disease transmission (Bracke 2011, Eckert et al. 2019). Disease spread is a particularly serious threat because wild pigs can carry 34 disease-causing pathogens that are transmissible to livestock, native wildlife, and humans (Miller et al. 2017). Rubbing and tusking, behaviors in which pigs rub against or dig their tusks into trees, primarily serve to remove ectoparasites and debris (Gray et al. 2020*b*). Rubbing and tusking, albeit not as impactful as wallowing, still pose a threat to tree health (Gray et al. 2020*b*).

Because rooting is a foraging behavior, wild pig damage is largely driven by the availability of food sources. Plant matter makes up a vast majority of wild pig diets, but their monogastric digestive system limits their ability to digest cellulose (Elston et al. 2005). The diet composition of wild pigs can shift seasonally to account for access to energy-rich foods, for instance exploiting hard mast availability in the fall (Henry and Conley 1972, Wood and Brenneman 1980). Selective uptake of seeds can impact oak species recruitment and alter canopy composition in later generations (Siemann et al. 2009). This study found that wild pigs exhibited a preference for large-seeded species whereas Gray et al. (2020*a*) found no preference for seed size. Newly recruited or recently planted seedlings are at risk of wild pig damage, including cherry bark oak (*Quercus pagoda*) and longleaf pine (*Pinus palustris*) (Fern et al. 2020). A single wild pig can destroy more than 400 planted longleaf pine seedlings in a day (Hopkins 1947). In other plantation forestry operations like pecan (*Carya illinoinensis*) orchards, wild pigs have been documented to decrease harvest efficiency by 34% (Boyer et al. 2020). Given the threat of losses within the industry, successful forest management and restoration depend on the management of this invasive pest (Campbell and Long 2009).

Agricultural crops, when available, can serve as another primary food source and driver of range expansion (McCann et al. 2003, Schley and Roper 2003, Snow et al. 2017). Damage to crops is often cited as the largest contributor to losses associated with wild pigs. A recent estimate in 12 US states found that damage costs approximately $272 million per year across 6 commonly planted crops (McKee et al. 2020). In rural Tennessee, a survey reported that costs associated with wild pigs exceeded $28 million annually; $13 million of which was attributed to agricultural damage (Poudyal et al. 2017). Corn (*Zea mays*) and peanuts (*Arachis hypogaea*) incur the highest losses and most damage occurs immediately after planting and later when plants mature (Anderson et al. 2016, Boyce et al. 2020). Damage to crops can increase when fields are in closer proximity to forests and riparian areas. This is likely due to the juxtaposition of habitats that wild pigs select for (Kay et al. 2017, Clontz et al. 2021).

During seasons in which protein-rich forage is less abundant, wild pigs can resort to consuming vertebrates (Wilcox and Van Vuren 2009). Ground nesting birds including northern bobwhite (*Colinus virginianus*) and wild turkey (*Meleagris gallopavo*) are susceptible to nest depredation by wild pigs (Rollins and Carrol 2001, Sanders et al. 2020). Several species of native mammals and herpetofauna have been documented in the opportunistic diet of wild pigs (Singer et al. 1984, Jolley et al. 2010). These species were mostly fossorial though arboreal species were also consumed when on the ground seeking warmer refugia (Jolley et al. 2010). Wild pigs have also been documented depredating the nests of several species of endangered marine turtles (McDonough et al. 2022).

Negative impacts on native species are not limited to predation or consumption. Native wildlife in the Southeastern USA like eastern gray squirrels (*Sciurus carolinensis*) and northern raccoons (*Procyon lotor*) can exhibit shifts in activity patterns in pig-invaded areas (Dykstra et al. 2023). Wild pigs and other mast-consuming species including white-tailed deer (*Odocoileus virginianus*), wild turkey, and black bear (*Ursus americanus*) share overlapping diets, increasing the risk of competition for resources (Mayer et al. 2020).

Natural resource managers have employed a range of tactics to combat the invasion of wild pigs (West et al. 2009). In contrast to successful eradication on islands across the world, the coterminous USA is unlikely to ever be free of wild pigs (Katahira et al. 1993, Lombardo and Faulkner 2000, Parkes et al. 2010, Cox et al. 2022). As a result, management strategies prioritize mitigating damage (Massei et al. 2011). Intensive wild pig removal can improve water quality and reduce agricultural damage across a treated landscape (Gaskamp et al. 2018, Bolds et al. 2022). Removal methods include corral trapping, ground shooting, aerial gunning, dog hunting, and the Judas method (West et al. 2009, Campbell and Long 2009). Each approach has advantages and limitations relative to seasonality, cost, and location (Campbell and Long 2009). Aerial gunning from a helicopter can remove many pigs in a short time, but its success depends on a sparse canopy (Massei et al. 2011). This vegetative structure occurs more commonly in states like Texas than in the southeastern USA (West et al. 2009, Campbell et al. 2010). For population and damage reduction, whole-sounder trapping with corral traps is recognized as the most effective (Lewis et al. 2020). While many attractants are utilized to habituate and lure wild pigs to a potential trapping site, no single lure or bait is as important as the location at which the attractant is placed (Lavelle et al. 2017, Snow et al. 2022). Intuitively, placing attractants in habitats that wild pigs frequent will yield greater success (Snow et al. 2022).

The use of toxicants deployed from pig-specific feeders is an emerging field of study highlighting two compounds: sodium nitrite and warfarin (Poché et al. 2018, Beasley et al. 2021, Snow et al. 2021). No states currently allow the use of toxicants due to concerns about non-target impacts and unknown efficacy. A recent stakeholder survey in Alabama found that hunters, farmers, and forest owners generally supported the use of toxicants if used properly and do not threaten human health or water quality (Williams et al. 2021). The future of toxicant use in the USA is promising and could be a useful addition to the current assortment of wild pig removal methods.

Each method can be valuable on its own, though calculated implementation of multiple tactics over time can increase the efficiency of a management program (McCann and Garcelon 2008, West et al. 2009). For example, once most pigs are trapped, more active and intense measures can be taken to remove individuals from low densities (Cox et al. 2022). When high-energy food sources like agricultural crops and hard mast are available, baiting and trapping can be inadequate, prompting the need for more dynamic strategies (Wilcox et al. 2004).

Implementing a strategic removal program is critical because wild pigs can respond negatively to removal pressure, especially after multiple unsuccessful attempts (Massei et al. 2011). Fischer et al. (2016) found that wild pigs in southern Missouri shifted home ranges and increased diurnal movement after repeated removal attempts. However, in Alabama wild pigs used smaller home and core ranges during seasons of high hunting pressure (Gaston et al. 2008). This highlights the importance of immediate removal to prevent the dispersal of targeted groups and reduce the potential for trap shyness (Saunders et al. 1993, Fischer 2016). The need for adaptive management accounting for seasonality and location is a testament to the behavioral plasticity exhibited by wild pigs. A commonly overlooked facet of wild pig management is post-removal monitoring, which can help prevent subsequent recolonization and damage (Lewis et al. 2020, Massei et al. 2011). In cases where removal is restricted, like densely populated areas, exclusionary fencing of valuable natural resources is a viable option although cost can be limiting (Massei et al. 2011).

Identifying drivers of wild pig resource selection across multiple spatial scales is critical for highlighting areas for future monitoring and management. Given their physiological needs, thermoregulatory cover, and proximity to water are the most-limiting habitat factors for wild pigs in the southeastern USA (Gaston et al. 2008, Friebel and Jodice 2009, Clontz et al. 2021). This relationship has been documented across the world (Schlichting et al. 2016, Froese et al. 2017, Kramer et al. 2022, Risch et al. 2022). In a primarily temperate region like the southeast USA, wild pigs adapt their efforts to further exploit resources when climatic conditions permit such movements (Baber and Coblentz 1986, Franckowiak et al. 2018). For instance, cooler and wetter seasons allow pigs to move more freely across the landscape (Singer et al. 1981). In warmer and drier seasons, dense bottomlands and riparian areas are selected for, because pigs lack the physiological ability to thermoregulate (Kay et al. 2017, Franckowiak et al. 2018). This is not always the case, because anthropogenic influences like hunting pressure can lead to smaller home ranges in the wet season (Hayes et al. 2009). Seasons can also be defined in the context of forage availability (Clontz et al. 2021). In this case, pigs move less when food is in greater abundance and disperse to more diverse areas when sources are limited.

Differences in movement and home range size between males (larger) and females (smaller) are evident, given the dispersing behavior of males and physical limitations on females when farrowing (Singer et al. 1981, Friebel and Jodice 2009, Clontz et al. 2021). Variability in estimated movement and home range can be due to differing spatial and temporal scales (Kay et al. 2017). In the southeastern United States, home range sizes of wild pigs generally average 4-5 km^2, although differences within the region are evident (Mayer et al. 2020). This emphasizes the need for studies that investigate multiple scales to identify patterns that might not be visible across the spatial or temporal extent of a study. Froehly et al. (2020) applied this to wild pig behavior, finding that trapping success could increase during cooler seasons when food is less abundant. Multi-scale studies allow researchers to identify the behavioral states of animals and associate those states with landscape features and seasons (Clontz et al. 2021, Gray et al. 2022). These behavioral associations to habitat characteristics allow natural resource managers to fine-tune monitoring and removal efforts based on season and predicted behaviors like resting and foraging (Clontz et al. 2021). To delineate suitable habitat for a particular species, researchers commonly study resource selection at the 3rd order which falls within an animal's home range (Johnson 1980). This order, or spatial scale, is used most frequently because it can be used to highlight habitat characteristics to be manipulated by managers to promote or reduce a species' success.

At a finer spatial scale, bedding (or resting) site selection is understudied and can provide valuable insight into prioritizing the placement of attractants for trapping and toxicants (Ditchkoff and Bodenchuk 2020). Gaston et al. (2008) noted that while tracking wild pigs in Alabama, many pigs were pushed out from bedding sites next to blown down trees and recommended that removal be focused near those structures. In South Carolina, wild pig beds were also found adjacent to structures like fallen logs or dense vegetation (Mayer et al. 2002). To our knowledge, surrounding forest vegetation has not been used to assess fine scale resting site selection. These characteristics could be used to prioritize trapping efforts and inform land management decisions.

Given the variability in wild pig home range and resource selection across their invasive range, the need for region-specific studies increases as they continue to expand their distribution (Garza et al. 2018). The Red Hills region between Tallahassee, Florida and Thomasville, Georgia, USA, encompasses 176,000 ha of privately-owned lands managed primarily for northern bobwhite hunting and ecosystem management. This region is known for supporting vast expanses of the longleaf pine-wiregrass (*Aristida* sp.) ecosystem and includes one of the few remaining old-growth longleaf pine forests in the world. The Red Hills also accommodates a variety of threatened and endangered species, including the highest density of red-cockaded woodpeckers (*Picoides borealis*) on private lands in the world. The Red Hills is dominated by old-field vegetation with loblolly (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) filling a majority of the open canopy.

Prescribed fire is a commonly used forest management practice in the region that supports native wildlife habitat and reduces hazardous forest fuels (Block et al. 2016). In the Red Hills, prescribed fire is applied on a 1–3-year frequency in the uplands. Unfortunately, downslope ecotones around forested wetlands and riparian areas are excluded from fire on some properties, creating a hard boundary between burned and unburned habitats. This exclusion from fire has allowed mid-story hardwood species to encroach upslope toward firebreaks and exclude valuable grasses and forbs that once dominated the understory (Brockway and Lewis 1997). Dense mid-story vegetation around bottomland areas can serve as valuable refugia for wild pigs and the historic suppression of fire in the region may increase that cover (Nowacki and Abrams 2008).

The goal of this study was to improve wild pig monitoring and removal strategies by evaluating resource use in the Red Hills, an area in which wild pigs have not been studied. To achieve this, my objectives included: 1) Assessing fine-scale resting site selection using surrounding vegetation characteristics and 2) Evaluating 3rd-order resource selection relative to fire history and other factors (natural and anthropogenic) to prioritize removal efforts.

LITERATURE CITED

Anderson, A., C. Slootmaker, E. Harper, J. Holderieath, and S. A. Shwiff. 2016. Economic estimates of feral swine damage and control in 11 US states. Crop Protection 89:89–94.

Arrington, D. A., L. A. Toth, and J. W. Koebel. 1999. Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. Wetlands 19:535–544.

Baber, D. W., and B. E. Coblentz. 1986. Density, home range, habitat use, and reproduction of feral pigs on Santa Catalina Island. Journal of Mammalogy 67:512–525.

Ballari, S. A., and M. N. Barrios-Garcia. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. Mammal Review 44:124–134.

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

Beasley, J. C., L. M. Clontz, A. Rakowski, N. P. Snow, and K. C. VerCauteren. 2021. Evaluation of a warfarin bait for controlling invasive wild pigs (*Sus scrofa*). Pest Management Science 77:3057–3067.

Bevins, S. N., K. Pedersen, M. W. Lutman, T. Gidlewski, and T. J. Deliberto. 2014. Consequences associated with the recent range expansion of nonnative feral swine. BioScience 64:291–299.

Bieber, C., and T. Ruf. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed food resources. Journal of Applied Ecology 42:1203–1213.

Block, W. M., L. M. Conner, P. A. Brewer, P. Ford, J. Hauffer, A. Litt, R. E. Masters, L. R. Mitchell, and J. Park. 2016. Effects of prescribed fire on wildlife and wildlife habitat in selected ecosystems of North America. The Wildlife Society Technical Review 16–01. The Wildlife Society, Bethesda, Maryland, USA.

Bolds, S. A., B. G. Lockaby, l. Kalin, S. S. Ditchkoff, M. D. Smith, and K. C. VerCauteren. 2022. Wild pig removal reduces pathogenic bacteria in low-order streams. Biological Invasions 24:1453–1463.

Boyce, C. M., K. C. VerCauteren, and J. C. Beasley. 2020. Timing and extent of crop damage by wild pigs (*Sus scrofa* Linnaeus) to corn and peanut fields. Crop Protection 133:e105131. https://doi.org/10.1016/j.cropro.2020.105131

Boyer, K. S., W. S. Fairbanks, C. Rohla, and S. L. Webb. 2020. Surficial soil damage by wild pigs (*Sus scrofa*) decreases pecan harvest efficiency. Crop Protection 128:e104992. https://doi.org/10.1016/j.cropro.2019.104992

Bracke, M. B. M. 2011. Review of wallowing in pigs: description of the behaviour and its motivational basis. Applied Animal Behaviour Science 132:1–13.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167-183.

Campbell, T. A., and D. B. Long. 2009. Feral swine damage and damage management in forested ecosystems. Forest Ecology and Management 257:2319–2326.

Campbell, T. A., D. B. Long, and B. R. Leland. 2010. Feral swine behavior relative to aerial gunning in Southern Texas. Journal of Wildlife Management 74:337–341.

Chinn, S. M., P. E. Schlichting, T. J. Smyser, C. F. Bodwen, and J. C. Beasley. 2022. Factors influencing pregnancy, litter size, and reproductive parameters of invasive wild pigs. Journal of Wildlife Management 86:e22304. https://doi.org/10.1002/jwmg.22304

Clontz, L. M., K. M. Pepin, K. C. VerCauteren, and J. C. Beasley. 2021. Behavioral state resource selection in invasive wild pigs in the Southeastern United States. Scientific Reports 11:e6924. https://doi.org/10.1038/s41598-021-86363-3

Cox, F. S., S. R. Horn, W. M. Bannister, and N. M. Macdonald. 2022. A local eradication pilot study of methods for feral pig eradication in Auckland Island. New Zealand Journal of Ecology 46:e3490. https://doi.org/10.20417/nzjecol.46.3490

Ditchkoff, S. S., and M. J. Bodenchuk. 2020. Management of wild pigs. Pages 175-197 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Dykstra, A. M., C. Baruzzi, K. VerCauteren, B. Strickland, and M. Lashley. 2023. Biological invasions disrupt activity patterns of native wildlife: an example from wild pigs. Food Webs 34:e00270. https://doi.org/10.1016/j.fooweb.2022.e00270

Eckert, K. D., D. A. Keiter, and J. C. Beasley. 2019. Animal visitation to wild pig (*Sus scrofa*) wallows and implications for disease transmission. Journal of Wildlife Diseases 55:488–493.

Elston, J. J., E. A. Klinsek, and D. G. Hewitt. 2005. Digestive efficiency of collared peccaries and wild pigs. The Southwestern Naturalist 50:515–519.

Essl, F., B. Lenzner, S. Bacher, S. Bailey, C. Caphina, C. Daehler, S. Dullinger, P. Genovesi, C. Hui, P. Hulme, J. M. Jeschke, S. Katsanevakis, I. Kühn, B. Leung, A. Liebhold, C. Liu, H. Maclsaac, L. Meyerson, M. Nuñez, A. Pauchard, P. Pyšek, W. Rabitsch, D. Richardson, H. Roy, G. Ruiz, J. Russell, N. Sanders, D. Sax, R. Scalera, H. Seebens, M. Springborn, A. Turbelin, M. van Kleunen, B. van Holle, M. Winter, R. Zenni, B. Mattsson, and N. Roura-Pascual. 2020. Drivers of future alien species impacts: an expert-based assessment. Global Change Biology 26:4880–4894.

Fern, M. P., J. B. Armstrong, R. J. Barlow, and J. S. Kush. 2020. Ecological factors influencing wild pig damage to planted pine and hardwood seedlings. Human-Wildlife Interactions 14:228–238.

Fischer, J. W., D. McMurty, C. R. Blass, W. D. Walter, J. Beringer, and K. C. Vercauteren. 2016. Effects of simulated removal activities on movements and space use of feral swine. European Journal of Wildlife Research 62:285–292.

Franckowiak, G. A., S. Torres-Poché, and R. M. Poché. 2018. Activity patterns by feral hogs in the Texas panhandle. American Midland Naturalist 180:233–245.

Friebel, B. A., and P. G. R. Jodice. 2009. Home range and habitat use of feral hogs in Congaree National Park, South Carolina. Human-Wildlife Conflicts 31:49–63.

Froehly, J. L., N. R. Beane, D. E. Evans, K. E. Cagle, and D. S. Jachowski. 2020. Using multi-scale behavioral investigations to inform wild pig (*Sus scrofa*) population management. PLoS ONE 15:e0228705. https://doi.org/10.1371/journal.pone.0228705

Froese, J. G., C. S. Smith, P. A. Durr, C. A. McAlpine, and R. D. van Klinken. 2017. Modelling seasonal habitat suitability for wide-ranging species: invasive wild pigs in northern Australia. PloS ONE 12:e0177018. https://doi.org/10.1371/journal.pone.0177018

Garza, S. J., M. A. Tabak, R. S. Miller, M. L. Farnsworth, and C. L. Burdett. 2018. Abiotic and biotic influences on home-range size of wild pigs (*Sus scrofa*). Journal of Mammalogy 99:97–107.

Gaskamp, J. A., K. L. Lee, T. A. Campbell, N. J. Silvy, and S. L. Webb. 2018. Damaged caused to rangelands by wild pig rooting activity is mitigated with intensive trapping. Cogent Environmental Science 4:e1540080. https://doi.org/10.1080/23311843.2018.1540080

Gaston, W., J. B. Armstrong, W. Arjo, and H. L. Stribling. 2008. Home range and habitat use of feral hogs (*Sus scrofa*) on Lowndes County WMA, Alabama. National Conference on Feral Hogs. Missouri Department of Conservation, 13–15 April 2008, St. Louis, Missouri, USA.

Global Invasive Species Database [GISD]. 2023. 100 of the world's worst invasive alien species. <http://www.iucngisd.org/gisd/100_worst.php>. Accessed on 23 February 2023.

Graves, H. B. 1984. Behavior and ecology of wild and feral swine (*Sus scrofa*). Journal of Animal Science 58:482–492.

Gray, S. M., J. M. Humphreys, R. A. Montgomery, D. R. Etter, K. C. VerCauteren, D. B. Kramer., and G. J. Roloff. 2022. Behavioral states in space and time: understanding landscape use by and invasive mammal. Journal of Wildlife Management 86:e22211. https://doi.org/10.1002/jwmg.22211

Gray, S. M., G. J. Roloff, D. B. Kramer, D. R. Etter, K. C. VerCauteren, and R. A. Montgomery. 2020. Effects of wild pig disturbance on forest vegetation and soils. Journal of Wildlife Management 84:739–748.

Gray, S. M., G. J. Roloff, R. A. Montgomery, J. C. Beasley, and K. M. Pepin. 2020. Wild pig spatial ecology and behavior. Pages 33–56 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Hayes, R., S. Riffell, R. Minnis, and B. Holder. 2009. Survival and habitat use of feral hogs in Mississippi. Southeastern Naturalist. 8:411–426.

Henry, V. G., and R. H. Conley. 1972. Fall foods of European wild hogs in Southern Appalachia. Journal of Wildlife Management 36:854–860.

Hensel, M. J. S., B. R. Silliman, E. Hensel, and J. E. K. Byrnes. 2021. Feral hogs control brackish marsh plant communities over time. Ecology 0:e03572. https://doi.org/10.1002/ecy.3572

Hernández, F. A., B. M. Parker, C. L. Pylant, T. J. Smyser, A. J. Piaggio, S. L. Lance, M. P. Milleson, J. D. Austin, and S. M. Wisely. 2018. Invasion ecology of wild pigs (Sus scrofa) in Florida, USA: the role of humans in the expansion and colonization of an invasive wild ungulate. Biological Invasions 20:1865–1880.

Hopkins, W. 1947. Hogs or logs? Southern Lumberman 175:151–153.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jolley, D. B., S. S. Ditchkoff, B. D. Sparklin, L. B. Hanson, M. S. Mitchell, and J. B. Grand. 2010. Estimate of herpetofauna depredation by a population of wild pigs. Journal of Mammalogy 91:519–524.

Kaminski, G., S. Brandt, E. Baubet, and C. Baudoin. 2005. Life-history patterns in female wild boars (*Sus scrofa*): mother-daughter postweaning associations. Canadian Journal of Zoology 83:474–480.

Katahira, L. K., P. Finnegan, and C. P. Stone. 1993. Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes National Park. Wildlife Society Bulletin 21:269–274.

Kay, S. L., J. W. Fisher, A. J. Monaghan, J. C. Beasley, R. Boughton, T. A. Campbell, S. M. Cooper, S. S. Ditchkoff, S. B. Hartley, J. C. Kilgo, S. M. Wisely, A. C. Wyckoff, K. C. VerCauteren, and K. M. Pepin. 2017. Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Movement Ecology 5:e14. https://doi.org/10.1186/s40462-017-0105-1

Keiter, D. A., J. J. Mayer, and J. C. Beasley. 2016. What is in a “common” name? A call for consistent terminology for nonnative *Sus scrofa*. Wildlife Society Bulletin 40:348–387.

Kramer, C. J., M. R. Boudreau, R. S. Miller, R. Powers, K. C. VerCauteren, and R. K. Brook. 2022. Summer habitat use and movements of invasive wild pigs (*Sus scrofa*) in Canadian agro-ecosystems. Canadian Journal of Zoology 100:494–506.

Lavelle, M. J., N. P. Snow, J. W. Fischer, J. M. Halseth, E. H. VanNatta, and K. C. VerCauteren. 2017. Attractants for wild pigs: current use, availability, needs, and future potential. European Journal of Wildlife Research 63:e86. https://doi.org/10.1007/s10344-017-1144-z

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

Lewis, J. S., M. L. Farnsworth, C. L. Burdett, D. M. Theobald, M. Gray, and R. S. Miller. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Scientific Reports 7:e44152. https://doi.org/10.1038/srep44152

Lewis, A. A., B. L. Williams, M. D. Smith, and S. S. Ditchkoff. 2020. Shifting to sounders: whole sounder removal eliminates pigs. Wildlife Society Bulletin 46:e1260. https://doi.org/10.1002/wsb.1260

Lombardo, C. A., and K. R. Faulkner. 2000. Eradication of feral pigs (*Sus scrofa*) from Santa Rosa Island, Channel Islands National Park, California. Pages 300–306 *in* Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, 29 March–1 April 1999, Santa Barbara, California, USA.

Lovett, G. M., M. Weiss, A. M., Liebhold, T. P. Holmes, B. Leung, K. F. Lambert, D. A. Orwig, F. T. Campbell, J. Rosenthal, D. G. McCullough, R. Wildvoa, M. P. Ayres, C. D. Canham, D. R. Foster, S. L. LaDeau, and T. Weldy. 2016. Nonnative forest insects and pathogens in the United States: impacts and policy options. Ecological Applications 26:1437–1455.

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

Mayer, J. J. 2009. Wild pig damage: overview of wild pig damage. Pages 221–246 *in* J. J. Mayer and I. L. Brisbin, editors. Wild pigs: biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, USA.

Mayer, J. J. 2018. Introduced wild pigs in North America: History, problems, and management. Pages 299-312 *in* M. Melletti and E. Meijaard, editors. Ecology, evolution, and management of wild pigs and peccaries: implications for conservation. Cambridge University Press, United Kingdom.

Mayer, J. J., J. C. Beasley, R. K. Boughton, and S. S. Ditchkoff. 2020. Wild pigs in Southeastern North America. Pages 369–402 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Mayer, J. J., and I. L. Brisbin. 2008. Wild pigs in the United States: their history, comparative morphology, and current status. University of Georgia Press, Athens, USA.

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

Mayer, J. J., F. D. Martin, and I. L. Brisbin. 2002. Characteristics of wild pig farrowing nests and beds in the upper Coastal Plain of South Carolina. Applied Animal Behaviour Science 78:1–17.

McCann, B., D. K. Davie, and G. A. Feldhamer. 2003. Distribution, habitat use, and morphotypes of feral hogs (*Sus scrofa*) in Illinois. Transactions of the Illinois State Academy of Science 96:301–311.

McCann, B. E., and D. K. Garcelon. 2008. Eradication of feral pigs from Pinnacles National Monument. Journal of Wildlife Management 72:1287–1295.

McClure, M. L., C. L. Burdett, M. L. Farnsworth, M. W. Lutman, D. M. Theobald, P. D. Riggs, D. A. Grear, and R. S. Miller. 2015. Modeling and mapping probability of occurrence of invasive wild pigs across the contiguous United States. PloS ONE 10:e0133771. https://doi.org/10.1371/journal.pone.0133771

McDonough, M. T., S. S. Ditchkoff, M. D. Smith, and K. C. Vercauteren. 2022. A review of the impacts of invasive wild pigs on native vertebrates. Mammalian Biology 102:279–290.

McKee, S., A. Anderson, K. Carlisle, and S. A. Schwiff. 2020. Economic estimates of invasive wild pig damage to crops in 12 US states. Crop Protection 132:e105105. https://doi.org/10.1016/j.cropro.2020.105105

Miller, R. S., S. J. Sweeney, C. Slootmaker, D. A. Greer, P. A. Di Salvo, D. Kiser, and S. A. Schwiff. 2017. Cross-species transmission potential between wild pigs, livestock, poultry, wildlife, and humans: implications for disease risk management in North America. Scientific Reports 7:e7821. https://doi.org/10.1038/s41598-017-07336-z

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58:123–138.

Parkes, J. P., D. S. L. Ramsey, N. Macdonald, K. Walker, S. McKnight, B. S. Cohen, and S. A. Morrison. 2010. Rapid eradication of feral pigs (*Sus scrofa*) from Santa Cruz Island, California. Biological Conservation 143:634–641.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.

Poché, R. M., D. Poché, G. Franckowiak, D. J. Somers, L. N. Briley, B. Tseveenjav, and L. Polykova. Field evaluation of low-dose warfarin baits to control wild pigs (*Sus scrofa*) in North Texas. PloS ONE 13:e0206070. https://doi.org/10.1371/journal.pone.0206070

Poudyal, N. C., C. Caplenor, O. Joshi, C. Maldonado, L. I. Muller, and C. Yoest. 2017. Characterizing the economic value and impacts of wild pig damage on a rural economy. Human Dimensions of Wildlife 22:538–549.

Risch, D. R., S. Honarvar, and M. R. Price. 2022. Environmental drivers of seasonal shifts in abundance of wild pigs in a tropical island environment. Ecological Processes 11:e55. https://doi.org/10.1186/s13717-022-00395-9

Rollins, D., and J. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. Wildlife Society Bulletin 29:39–51.

Sanders, H. N., D. G. Hewitt, H. L. Perotto-Baldivieso, K. C. VerCauteren, and N. P. Snow. 2020. Invasive wild pigs as primary nest predators for wild turkeys. Scientific Reports 10:e2625. https://doi.org/10.1038/s41598-020-59543-w

Saunders, G., B. Kay, and H. Nicol. 1993. Factors affecting bait uptake and trapping success for feral pigs (*Sus scrofa*) in Kosciusko National Park. Wildlife Research 20:653–665.

Schley, L., and T. J. Roper. 2003. Diet of wild boar, *Sus scrofa*, in Western Europe, with particular preference to consumption of agricultural crops. Mammal Review 33:43–46.

Schlichting, P. E., S. R. Fritts, J. J. Mayer, P. S. Gibson, and C. B. Dabbert. 2016. Determinants of variation in home range of wild pigs. Wildlife Society Bulletin 40:487–493.

Sharp, S. J., and C. Angelini. 2019. The role of landscape composition and disturbance type in mediating salt marsh resilience to feral hog invasion. Biological Invasions 21:2857–2869.

Siemann, E., J. A. Carrillo, C. A. Gabler, R. Zipp, and W. E. Rogers. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management 258:546–553.

Simberloff, D. 2013. Invasive species: what everyone needs to know. Oxford University Press, United Kingdom.

Singer, F. J., D. K. Otto, A. R. Tipton, and C. P. Hable. 1981. Home ranges, movements, and habitat use of European wild boar in Tennessee. Journal of Wildlife Management 45:343–353.

Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. Journal of Wildlife Management 48:464–473.

Snow, N. P., M. A. Jarzyna, and K. C. VerCauteren. 2017. Interpreting and predicting the spread of invasive wild pigs. Journal of Applied Ecology 54:2022–2032.

Snow, N. P., C. A. Kupferman, M. J. Lavelle, K. M. Pepin, M. H. Melton, W. J. Gann, K. C. VerCauteren, and J. C. Beasley. 2022. No panacea attractant for wild pigs (*Sus scrofa*), but season and location matter. Applied Animal Behaviour Science 254:e105705. https://doi.org/10.1016/j.applanim.2022.105705

Snow, N. P., R. S. Miller, J. C. Beasley, and K. M. Pepin. 2020. Wild pig population dynamics. Pages 57–82 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Snow, N. P., J. D. Wishart, J. A. Foster, L. D. Staples, and K. C. VerCauteren. 2021. Efficacy and risks from a modified sodium nitrite toxic bait for wild pigs. Pest Management Science 77:1616–1625.

Strickland, B. K., M. D. Smith, and A. L. Smith. 2020. Wild pig damage to resources. Pages 143-174 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Tabak, M. A., A. J. Piaggio, R. S. Miller, R. A Sweitzer, and H. B. Ernest. 2017. Anthropogenic factors predict movement of an invasive species. Ecosphere 8:e01844. https://doi.org/10.1002/ecs2.1844

United States Department of Agriculture [USDA]. 2022. History of feral swine in the Americas: distribution maps. <https://www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/operational-activities/feral-swine/sa-fs-history>. Accessed 01 March 2023.

West, B. C., A. L. Cooper, and J. B. Armstrong. 2009. Managing wild pigs: A technical guide. Human-Wildlife Interactions Monograph 1:1–55.

Wilcox, J. T., E. T. Aschehoug, C. A. Scott, and D. H. Van Vuren. 2004. A test of the Judas technique as a method for eradicating feral pigs. Transactions of the Western Section of The Wildlife Society 40:120–126.

Wilcox, J. T., and D. H. Van Vuren. 2009. Wild pigs as predators in oak woodlands of California. Journal of Mammalogy 90:114-118.

Williams, E. A., C. A. Lepczykm and W. Morse. 2021. Stakeholder perspectives towards the use of toxicants for managing wild pigs. PloS ONE 16:e0246457. https://doi.org/10.1371/journal.pone.0246457

Wood, G. E., and R. E. Brenneman. 1980. Feral hog movements and habitat use in coastal South Carolina. Journal of Wildlife Management 44:420–427.

CHAPTER 2

FIRE HISTORY AND THIRD ORDER WILD PIG (*SUS SCROFA*) RESOURCE SELECTION IN NORTH FLORIDA AND SOUTH GEORGIA, USA

Terrazas, C., K. Sash, and M. T. Mengak. *To be submitted to Wildlife Society Bulletin*

ABSTRACT

Invasive species management depends on a thorough understanding of species behavior, ecology, and natural history. Species-habitat relationships become increasingly complex when habitats are altered by humans and natural disturbances. Invasive wild pig (*Sus scrofa*) management has prioritized exploiting behaviors to improve removal efforts but has not focused on how natural disturbances interact with these behaviors. Interpretating the association between wild pigs and disturbance is critical because resource availability fluctuates in the presence of disturbances like fire. We used a 3rd order resource selection function (logistic regression) framework to interpret the interaction between prescribed fire history and wild pig movement across two seasons based on forage availability. Our results suggest that wild pigs use habitats similar to populations across the southeastern USA but prefer habitats having longer intervals without fire. Our results can improve the ability to target areas susceptible to wild pig invasion and provide cause to reintroduce fire to fire suppressed environments.

KEY WORDS

Disturbance, invasive species, prescribed fire, resource selection, *Sus* scrofa, wild pigs

INTRODUCTION

Wild pigs (*Sus scrofa*) are an invasive species that threaten a variety of environments, organisms, and industries across the world (Barrios-Garcia and Ballari 2012). Although native to Eurasia and North Africa, wild pigs occupy every continent except Antarctica and their distribution is projected to continue expanding (McClure et al. 2015, Lewis et al. 2017). Since their introduction to North America in the 1500s by Spanish explorers, wild pigs have expanded across the continent by both natural and anthropogenic means (Mayer and Brisbin 2008, Hernández et al. 2018). In the United States, wild pigs can negatively impact native wildlife, including the opportunistic consumption of small mammals and herpetofauna as well as the depredation of game bird nests (Singer et al. 1984, Jolley et al. 2010, Sanders et al. 2020). Along with potential impacts to native wildlife, industries like agriculture and forestry are also susceptible to wild pig damage given their destructive feeding behavior known as rooting (Hopkins 1947, Boyer et al. 2020). Rooting is a process in which pigs dig their snouts into the ground to turn up food items in the soil (Mayer 2009). The cost of wild pig damage and control is difficult to estimate, however a recent study found that damage to 6 types of crops across 12 US states costs farmers nearly $272 million per year (McKee et al. 2020).

To reduce damage from wild pigs, managers utilize a combination of methods including night shooting, aerial gunning, whole-sounder removal, and the judas technique (West et al. 2009, Massei and Bunting 2011, Ditchkoff and Bodenchuk 202). These methods, while potentially successful alone, are most effective when used in concert with each other as circumstances change throughout a removal program. As wild pigs may become more wary of traps or shift behavior due to pressure, more active measures like night shooting can be employed (Massei and Bunting 2011, Fischer et al. 2016). A commonality among all methods is a dependence on the detection of pigs, and removal often occurs in response to detection. Proactive measures like exclusionary fencing of natural resources are viable but can be costly (Massei and Bunting 2011).

A critical component of invasive species management, especially with wild pigs, is an understanding of resource selection. By exploiting habits exhibited by invasive species, wildlife managers and researchers can target areas prone to invasion and employ measures to reduce damage. Resource selection is a hierarchical process in which species/habitat relationships exist at multiple specific spatial scales (Johnson 1980). Suitable habitat is commonly defined at the 3rd

order, which describes decisions animals make relative to availability within home ranges. Highlighting this scale of selection allows researchers to make predictions of animal habitat use to promote valuable native species or mitigate damage caused by invasives (Clontz et al. 2021). Wild pigs can quickly adapt to new environments given their generalist diet and variable habitat selection (Ballari and Barrios-Garcia 2014). Resource selection exhibited by wild pigs varies by region but is restricted mostly by thermoregulatory cover and proximity to water (Gaston et al. 2008, Friebel and Jodice 2009, Clontz et al. 2021). Forage, including crops, in the southeastern United States varies spatiotemporally which causes a subsequent shift in wild pig movement and space use (Wood and Brenneman 1980, Boyce et al. 2020). Regionally distinct wild pig removal efforts depend on a detailed understanding of local resource use to prioritize areas for monitoring and management (Garza et al. 2018).

In the southeastern USA, dense vegetative cover is critical for wild pigs because they lack the physiological ability to thermoregulate (Kay et al. 2017). Thickets of viny species like muscadine (*Vitis sp.*) or trees including sweetgum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*) offer shade from the sun during the heat of the day. Prescribed fire, a commonly used forest management practice in the Southeast, is often applied to reduce the accumulation of these species and promote native wildlife habitat (Block et al. 2016). This includes the regular top-killing of hardwoods to limit their growth. These species, and others, thrive in the absence of fire and accumulate in shaded, fire-suppressed forests (Nowacki and Abrams 2008). Upland pine communities regularly experience fire every 1-3 years, although riparian edges and upland hardwood communities have longer fire return intervals, allowing for mesophytic species to encroach upslope (Nowacki and Abrams 2008). Dense vegetative cover in these fire-excluded areas often occurs near water and could provide valuable refugia for wild pigs. We sought to evaluate the relationship between prescribed fire history and 3rd order wild pig resource selection to improve management strategies for wild pigs. Habitat modification, including the reintroduction of prescribed fire to a fire-suppressed landscape, could be a useful management tool for limiting wild pig invasion and promoting native wildlife habitat.

STUDY AREA

Our study was conducted on 8 private quail plantations within Leon and Jefferson counties, Florida, and Thomas County, Georgia USA (Figure 2.1). Known as the Red Hills region, this area falls between Thomasville, Georgia and Tallahassee, Florida and is bordered to the east and west by the Aucilla and Ochlocknee rivers, respectively. The Red Hills region encompasses 176,000 hectares of primarily private lands managed for northern bobwhite (*Colinus virginianus*) hunting and ecosystem management. Most of the Red Hills is comprised of old field loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) regeneration with old growth and second growth longleaf pine (*P. palustris*)-wiregrass *(Aristida sp.*) mixed throughout. Given the topographic gradient within the Red Hills, hardwood and bottomland habitat consist of upland oak (*Quercus sp.*) and hickory (*Carya sp.*) forests leading downslope into forested wetlands comprised of cypress (*Taxodium sp.*) and tupelo (*Nyssa sp.*). Agricultural fields, although small (<6 hectares), are scattered throughout most properties. Field plantings varied across our study area depending on management goals, but managers in the region avoided planting corn (*Zea mays*) in recent years due to losses attributable to pigs. Fields are harrowed annually and intermittently left fallow to grow in annual weeds to support northern bobwhite and wild turkey (*Meleagris gallopavo*) brood habitat. Prescribed fire was regularly applied in the uplands on 2-year intervals to promote wildlife habitat and reduce hazardous fuels (Sisson et al.

2017). Historic fire suppression of riparian and upland hardwood communities has occurred in portions of the region, allowing for mesophytic vegetation to envelop the midstory.

METHODS

Wild Pig GPS-Collaring and Monitoring

Trapping was conducted by US Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) Wildlife Services during intensive removal efforts in the region. Corral-style traps were baited with corn and monitored with cellular cameras (Ditchkoff and Bodenchuk 2020). We physically restrained individuals within traps and fitted them with Vectronic-Aerospace Vertex™ Lite GPS collars (Vectronic-Aerospace, Berlin, Germany). For each individual captured, we recorded the sex, approximate age (sub-adult or adult), overall condition, and morphological measurements (head length, body length, heart girth). To maintain handling efficiency and reduce cost, we did not anesthetize captured pigs but used only physical restraint. For safety concerns, we collared only individuals that were visually estimated to weigh less than 45 kg. GPS collars recorded location fixes at 2-hour intervals between December 2021 and March 2022 and we later increased to 1-hour intervals in March 2022 until April 2023. To reduce location bias, we removed GPS fixes that were not 3D validated (four or more satellites acquired). We also censored location data within the first 3 days of deployment to account for any post-capture behavioral shifts. We conducted all capture and handling methods in compliance with the Tall Timbers Institutional Animal Care and Use Committee (IACUC # 2023-003).

Landscape Classification and Home Range

We used a 30 m resolution land cover raster data layer for the Red Hills region provided by Tall Timbers Research Station (TTRS) Geospatial Laboratory to define available vegetative communities within our study area. We classified land cover data into seven distinct groups: urban, open water, fields/agriculture/pasture, upland pine, upland hardwood, planted pine, and forested wetland. Land cover raster models were reclassified into distance-based variables using the Euclidean Distance tool in ArcGIS pro (Esri, Redlands, CA, USA). This created 7 separate raster data models representing the Euclidean distance from every raster cell to the nearest patch of each land cover type (Conner et al. 2003). GPS locations within the land cover of interest were recorded as 0 m. Land cover data included primary and secondary roads in the urban category, allowing us to interpret it as distance to roads because our study area was entirely rural containing few small communities especially within home ranges. We used 30 m resolution fire history data delineated by Teske et al. (2021) from Landsat burned area products developed by Hawbaker et al. (2020). We used time since previous fire (TSF), in years, to evaluate the relationship between wild pig habitat use and prescribed fire. We classified fire history data by years since the last fire occurred from 1994 to 2022. We reclassified cells with no data as "29" to indicate no fire had been detected since 1994.

We used a 95% fixed kernel density estimate (KDE) to map utilization distribution (UD) for each individual and construct home ranges using the adehabitatHR package in program R (R Core Team 2022, Calenge 2023). We used an ad-hoc "href" bandwidth estimator and a bivariate normal "bivnorm" kernel. Home ranges were separated into two distinct seasons based on low and high forage availability: January-April and May-December, respectively (Clontz et al. 2021). Because we separated home ranges by forage availability, we were able to evaluate selection based on forage availability within our model. To sample available habitat, we systematically sampled points every 30 m within seasonal home ranges to match the resolution of our raster data and provide an accurate estimate of 3rd order availability (Benson 2013).

Statistical Analyses

We used a resource selection function framework to evaluate wild pig resource selection (Manly et al. 2002). We used a generalized linear mixed-effects model (GLMM) with a binary response variable and logit link to predict probability of use relative to available habitat within seasonal home ranges. Only used and available locations within home ranges were used in our analysis. To make useful comparisons between effect sizes, we standardized each continuous variable to have a mean of 0 and a standard deviation of 1. We used variance inflation factors (VIFs) to account for multicollinearity in our model and removed covariates that had a VIF > 4. To account for the effect of variation among individuals, we included a random effect for animal ID. We fit a single global generalized linear mixed effects model (GLMM) rather than using model selection because we were interested in evaluating the effect of each variable rather than achieving parsimony. We included interaction terms within our model between TSF and distance to each land cover type, as well as between forage season and the distance to each land cover type. We used lme4 package in the statistical computing software R 4.2.1 for all analyses (Bates et al. 2015, R Core Team 2022)

RESULTS

From December 2021 to November 2022, we collared 13 wild pigs (7 male, 6 female) (Table 2.1). Between 15 December 2021 and 04 April 2023, we collected 58,973 cleaned and filtered GPS fixes. We monitored individuals between 48 and 315 days (Table 2.1). Mean 95% home range size across individuals was 11.39 km^2 (95% CI: 7.05, 15.73). Mean male home range ($\bar{x}$ = 15.66 km^2; 95% CI: 9.79, 21.52) was larger than female home range size ($\bar{x}$ = 6.41 km^2; 95% CI: 2.63, 9.04). Wild pigs in our study area were found nearer to forested wetlands, upland hardwoods, and fields while avoiding planted pines and upland pines regardless of season

(Table 2.2). Wild pigs selected habitats closer open water in the high forage season but further from them in the low forage season (Table 2.2). Roads were used proportionally to availability in the low forage season, but then were avoided in the high forage season (Table 2.2). TSF interacted significantly with each land cover type except upland hardwood. Increasing TSF increased probability of use within forested wetlands, both pine communities, and near roads. Conversely, increasing TSF decreased relative probability of use in fields and wetlands (Table 2.2).

DISCUSSION

We did not observe seasonal variation in wild pig resource selection relative to forage availability, contrary to Clontz et al. (2021). Distance to open water was the only covariate that indicated a change from selection to avoidance between seasons (Figure 2.2). Wild pigs showed no preference or avoidance for roads in the low forage season but then strongly avoided them in the high forage season. This could be due to the presence of managers in the area frequently using roads or simply that roads are typically further from water. Wild pig selection for areas near water is well-documented in the Southeast in which pigs rely more heavily on water in the warmer months for thermoregulation (Kay et al. 2017, Franckowiak et al. 2018, Gray et al. 2020). Forested wetlands were preferred year-round, which could also be a function of the available cover near water.

We expected to identify seasonal shifts in selection for fields where pigs used them more frequently in the high forage season and avoided them in the low forage season, although we found no such relationship. Contrary to other regions in the southeastern coastal plain, agricultural fields in the Red Hills are often left fallow and disked in December or January to promote ragweed (*Ambrosia artemisiifolia)* and support northern bobwhite brood habitat (Harper

2007). Although ragweed may provide dense cover from the sun later in the growing season, there is no added incentive given its lack of nutritional value for wild pigs. Discing involves turning up the soil, in a similar fashion to wild pig rooting, which could increase access to food items within the soil column and increase use in those areas. Fields were preferred year-round, which could also be due to another commonly used habitat management method in the Red Hills, supplemental feeding. Supplemental feeding occurs throughout the year and involves spreading sorghum (*Sorghum bicolor*) seed across a predetermined feed trail on a bi-weekly basis (Wellendorf et al. 2017). Feed lines often weave through pine uplands and around fields which could provide a valuable year-round food source for wild pigs, thus increasing their selection for those habitats during times when fields are not planted.

We also expected to find temporal variation in wild pig resource selection in upland hardwood habitats in which use was more probable when hard mast was available in the early winter (Henry and Conley 1972). Our results did not support our predictions, because selection was similar throughout the year. Preference for upland hardwood habitats was slightly greater in the high forage season, though not significant. In 2022, hard mast was more abundant and more persistent than normal which could have increased preference for upland hardwood habitats for longer than expected (USDA WS trappers, personal communication). Avoidance of both pine communities was evident regardless of season. Upland pine habitats in the Red Hills are often open canopy forests with relatively low basal area which allowed abundant sunlight to reach the ground and could exceed temperatures that pigs can tolerate.

Fire history significantly interacted with all habitat variables except distance to upland hardwood. Fire exclusion allows dense midstory vegetation to accumulate and can provide thermal cover for wild pigs. Upland and planted pine habitats were mostly avoided by pigs in our study area, except in areas with a longer time since fire (Figure 2.3). Areas like these in the Red Hills are often too hot for wild pigs during the summer months given their more open canopy and often grassy understory. Unfortunately, some upland and planted pine communities have been long excluded from fire, and the grassy understory has been replaced with dense hardwoods like sweetgum and various oak species. Although these species do not regularly reach the canopy, fire-suppressed pine forests are often dense with these species in the midstory and allow wild pigs to use these areas during warmer periods. Most upland pine communities in the Red Hills lack intact native ground cover given the agricultural history in the region and are primarily old-field forests comprised of loblolly/shortleaf pine woodlands. Forested wetlands, the most-used habitat by wild pigs, were used more frequently with increasing TSF. Forested wetlands and riparian edges have a longer fire return interval than upland pine savannas, therefore, prescribed fires should be allowed to creep into these areas and naturally extinguish when conditions allow. Unfortunately, firebreaks limit the ability for fire to naturally spread into the bottomland landscape, leaving it to become overgrown.

Our study indicates that prescribed fire history impacts wild pig resource selection and could be used to closely monitor areas susceptible to wild pig invasion. Wetlands and upland pine forests in the Red Hills provide valuable habitat for a suite of threatened and endangered plants and animals that are susceptible to the impact of wild pigs. Many of these species, including gopher frogs (*Lithobates capito*) and striped newts (*Notophalmus perstriatus*), rely on fire in weedy wetlands (Roznik and Johnson 2017). Maintaining a more natural fire regime could reduce wild pig use and limit potential damage while also promoting the necessary habitat for imperiled native species.

MANAGEMENT IMPLICATIONS

Our results suggest that wild pigs selected areas in which fire has been excluded from the landscape. Although managers in the Red Hills region regularly use fire to promote northern bobwhite habitat, ecotones between riparian areas and upland pine communities are left in the "fire shadow" and provide valuable refugia for wild pigs. The benefits of returning uplands and bottomland hardwoods to a more natural fire regime do not only include those relative to native flora and fauna but could also help mitigate wild pig use.

LITERATURE CITED

Ballari, S. A., and M. N. Barrios-Garcia. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. Mammal Review 44:124–134.

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

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Lme4: Linear mixed-effects models using 'Eigen' and S4. Version 1.1-30. https://cran.r-project.org/web/packages/lme4/index.html.

Benson, J. F. 2013. Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. Methods in Ecology and Evolution 4:244–251.

Block, W. M., L. M. Conner, P. A. Brewer, P. Ford, J. Hauffer, A. Litt, R. E. Masters, L. R. Mitchell, and J. Park. 2016. Effects of prescribed fire on wildlife and wildlife habitat in selected ecosystems of North America. The Wildlife Society Technical Review 16–01. The Wildlife Society, Bethesda, Maryland, USA.

Boyce, C. M., K. C. VerCauteren, and J. C. Beasley. 2020. Timing and extent of crop damage by wild pigs (*Sus scrofa* Linnaeus) to corn and peanut fields. Crop Protection 133:e105131. https://doi.org/10.1016/j.cropro.2020.105131

Boyer, K. S., W. S. Fairbanks, C. Rohla, and S. L. Webb. 2020. Surficial soil damage by wild pigs (*Sus scrofa*) decreases pecan harvest efficiency. Crop Protection 128:e104992. https://doi.org/10.1016/j.cropro.2019.104992

Calenge, C. 2023. adehabitatHR: Home Range Estimation. Version 0.4.21. https://cran.r-project.org/web/packages/adehabitatHR/index.html.

Clontz, L. M., K. M. Pepin, K. C. VerCauteren, and J. C. Beasley. 2021. Behavioral state resource selection in invasive wild pigs in the Southeastern United States. Scientific Reports 11:e6924. https://doi.org/10.1038/s41598-021-86363-3

Conner, L. M., M. D. Smith, and L. W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. Ecology 84:526–531.

Ditchkoff, S. S., and M. J. Bodenchuk. 2020. Management of wild pigs. Pages 175-197 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Fischer, J. W., D. McMurty, C. R. Blass, W. D. Walter, J. Beringer, and K. C. Vercauteren. 2016. Effects of simulated removal activities on movements and space use of feral swine. European Journal of Wildlife Research 62:285–292.

Franckowiak, G. A., S. Torres-Poché, and R. M. Poché. 2018. Activity patterns by feral hogs in the Texas panhandle. American Midland Naturalist 180:233–245.

Friebel, B. A., and P. G. R. Jodice. 2009. Home range and habitat use of feral hogs in Congaree National Park, South Carolina. Human-Wildlife Conflicts 31:49–63.

Garza, S. J., M. A. Tabak, R. S. Miller, M. L. Farnsworth, and C. L. Burdett. 2018. Abiotic and biotic influences on home-range size of wild pigs (*Sus scrofa*). Journal of Mammalogy 99:97–107.

Gaston, W., J. B. Armstrong, W. Arjo, and H. L. Stribling. 2008. Home range and habitat use of feral hogs (*Sus scrofa*) on Lowndes County WMA, Alabama. National Conference on Feral Hogs. Missouri Department of Conservation, 13–15 April 2008, St. Louis, Missouri, USA.

Gray, S. M., G. J. Roloff, R. A. Montgomery, J. C. Beasley, and K. M. Pepin. 2020. Wild pig spatial ecology and behavior. Pages 33–56 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Harper, C. A. 2007. Strategies for managing early succession habitat for wildlife. Weed Technology 21:932–937.

Hawbaker, T. J., M. K. Vanderhoof, G. I. Schmidt, Y. J. Beal, J. J. Picotte, J. D. Takacs, J. T. Falgout, and J. L. Dwyer. 2020. The Landsat burned area algorithm and products for the United States. Remote Sensing of the Environment 244:e111801. https://doi.org/10.1016/j.rse.2020.111801

Henry, V. G., and R. H. Conley. 1972. Fall foods of European wild hogs in Southern Appalachia. Journal of Wildlife Management 36:854–860.

Hernández, F. A., B. M. Parker, C. L. Pylant, T. J. Smyser, A. J. Piaggio, S. L. Lance, M. P. Milleson, J. D. Austin, and S. M. Wisely. 2018. Invasion ecology of wild pigs (Sus scrofa) in Florida, USA: the role of humans in the expansion and colonization of an invasive wild ungulate. Biological Invasions 20:1865–1880.

Hopkins, W. 1947. Hogs or logs? Southern Lumberman 175:151–153.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jolley, D. B., S. S. Ditchkoff, B. D. Sparklin, L. B. Hanson, M. S. Mitchell, and J. B. Grand. 2010. Estimate of herpetofauna depredation by a population of wild pigs. Journal of Mammalogy 91:519–524.

Kay, S. L., J. W. Fisher, A. J. Monaghan, J. C. Beasley, R. Boughton, T. A. Campbell, S. M. Cooper, S. S. Ditchkoff, S. B. Hartley, J. C. Kilgo, S. M. Wisely, A. C. Wyckoff, K. C. VerCauteren, and K. M. Pepin. 2017. Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Movement Ecology 5:e14. https://doi.org/10.1186/s40462-017-0105-1

Lewis, J. S., M. L. Farnsworth, C. L. Burdett, D. M. Theobald, M. Gray, and R. S. Miller. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Scientific Reports 7:e44152. https://doi.org/10.1038/srep44152

Manly, B. J., L. Mcdonald, D. L. Thomas, T. L. Mcdonald. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kulwer Academic Publishers, Norwell, Massachusetts, USA.

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

Mayer, J. J. 2009. Wild pig damage: overview of wild pig damage. Pages 221–246 *in* J. J. Mayer and I. L. Brisbin, editors. Wild pigs: biology, damage, control techniques and management. Savannah River National Laboratory, Aiken, South Carolina, USA.

Mayer, J. J., and I. L. Brisbin. 2008. Wild pigs in the United States: their history, comparative morphology, and current status. University of Georgia Press, Athens, USA.

McClure, M. L., C. L. Burdett, M. L. Farnsworth, M. W. Lutman, D. M. Theobald, P. D. Riggs, D. A. Grear, and R. S. Miller. 2015. Modeling and mapping probability of occurrence of invasive wild pigs across the contiguous United States. PloS ONE 10:e0133771. https://doi.org/10.1371/journal.pone.0133771

McKee, S., A. Anderson, K. Carlisle, and S. A. Schwiff. 2020. Economic estimates of invasive wild pig damage to crops in 12 US states. Crop Protection 132:e105105. https://doi.org/10.1016/j.cropro.2020.105105

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58:123–138.

R Core Team 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roznik, E. A., and S. A. Johnson. 2017. Gopher frogs, burrows, and fire: interactions in the longleaf pine ecosystem. University of Florida Institute of Food and Agricultural Sciences Extension Publication WEC 250, Gainesville, USA.

Sanders, H. N., D. G. Hewitt, H. L. Perotto-Baldivieso, K. C. VerCauteren, and N. P. Snow. 2020. Invasive wild pigs as primary nest predators for wild turkeys. Scientific Reports 10:e2625. https://doi.org/10.1038/s41598-020-59543-w

Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. Journal of Wildlife Management 48:464–473.

Sisson, D. C., E. Staller, and W. E. Palmer. 2017. Habitat Management. Pages 33–57 *in* W. E Palmer and D. C. Sisson, editors. Tall Timbers' Bobwhite Quail Management Handbook. Tall Timbers Press, Tallahassee, Florida, USA.

Teske, C., M. K. Vanderhoof, T. J. Hawbaker, J. Noble, and J. K. Heirs. 2021. Using the landsat burned area products to derive fire history relevant for fire management and conservation in the state of Florida, Southeastern USA. Fire 4:e26. https://doi.org/10.3390/fire4020026

Wellendorf, S. D., W. E. Palmer, and A. M. Bostick III. 2017. Effects of supplemental feeding on breeding season home ranges and resource selection of northern bobwhites. National Quail Symposium Proceedings 8:187–195.

West, B. C., A. L. Cooper, and J. B. Armstrong. 2009. Managing wild pigs: A technical guide. Human-Wildlife Interactions Monograph 1:1–55.

Wood, G. E., and R. E. Brenneman. 1980. Feral hog movements and habitat use in coastal South Carolina. Journal of Wildlife Management 44:420–427.

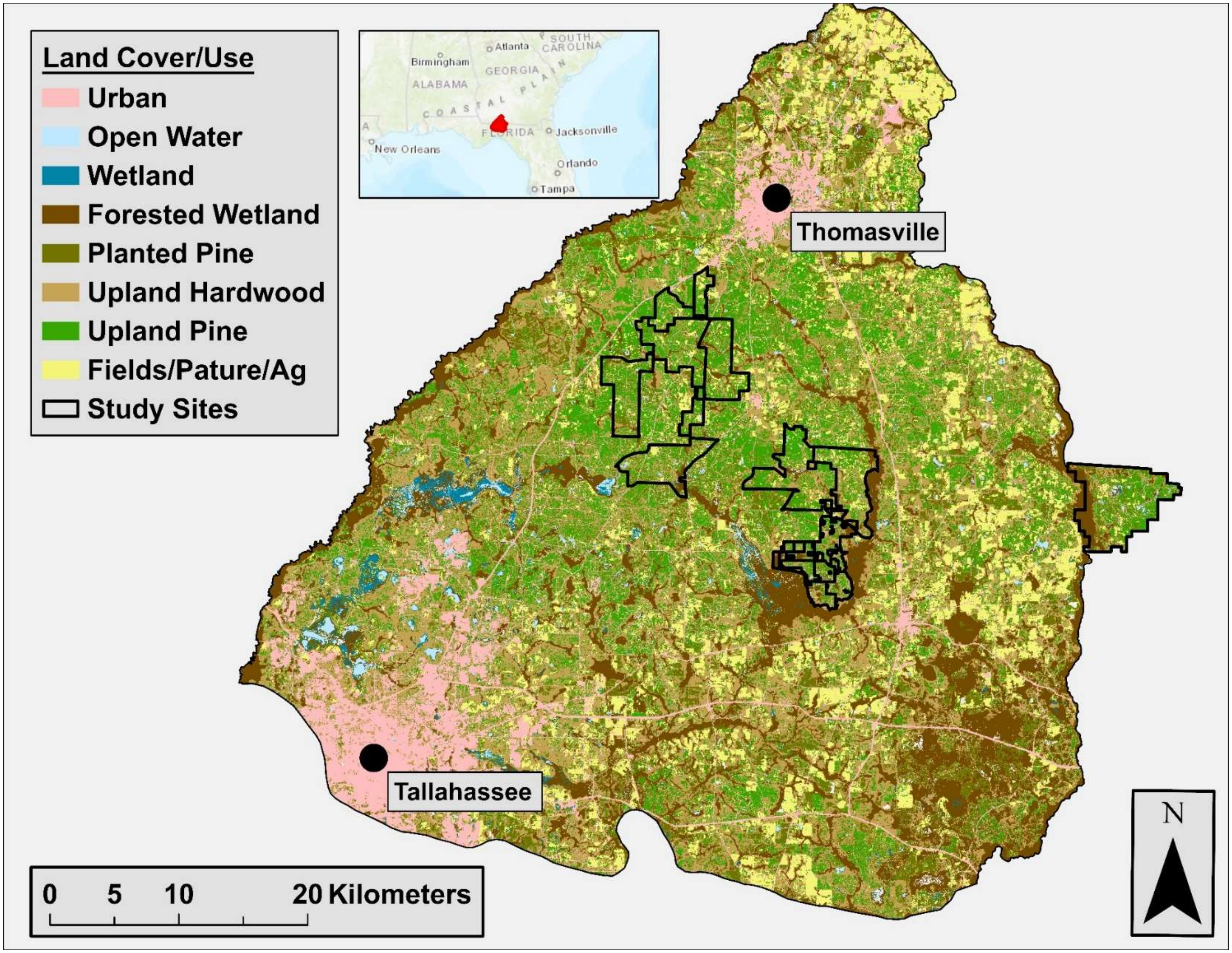

Figure 2.1. Land Cover/Land Use map of the Red Hills region between Thomasville, Georgia and Tallahassee, Florida, USA. Study sites are outlined in black

Table 2.1 Individual data for GPS collared wild pigs in the Red Hills region of North Florida and South Georgia, USA. Home ranges were calculated using a 95% fixed kernel density estimator. Collared pigs were monitored between December 2021 and April 2023.

ID	Sex	Property	Age	Home Range (km^2)	Fix Rate (hr)[a]	Length (days)	Number of Locations
W1	Male	Dekle	Sub-adult	1.61	2	48	576
W2	Male	Livingston Place	Adult	16.55	2,1	313	6570
W3	Male	Elsoma	Adult	20.86	2,1	109	1990
W4	Male	Meander	Sub-adult	24.13	1	260	6197
W5	Male	Mays Pond	Sub-adult	9.88	1	163	3941
W6	Male	Mays Pond	Adult	14.32	1	246	6037
W8	Male	Warbick Farms	Sub-adult	22.27	1	245	5900
Y26	Female	Livingston Place	Adult	5.24	2,1	314	6624
Y28	Female	Elsoma	Adult	3.88	2,1	215	4602
Y29	Female	Kelly Pond	Sub-adult	2.75	1	268	6697
Y30	Female	Warbick Farms	Sub-adult	11.20	1	187	4512
Y31	Female	Loveridge	Sub-adult	2.02	1	108	2306
Y36	Female	Warbick Farms	Adult	13.37	1	130	3021

[a] Fix rates were changed from 2-hour 1-hour for 4 individuals.

Table 2.2. Results from a generalized linear mixed model to evaluate wild pig 3rd order resource selection in the Red Hills region of North Florida and South Georgia, USA between December 2021 and April 2023.

Land cover[a]	Interaction	β	95 % CI Lower	95 % CI Upper	RSS[b]	$P < 0.05$
Forested wetland	Low forage	-0.528	-0.556	-0.501	0.590	*
	High forage	-0.452	-0.513	-0.392	0.636	*
	Time since fire	-0.118	-0.135	-0.101	0.889	*
Fields	Low forage	-0.223	-0.249	-0.197	0.800	*
	High forage	-0.179	-0.230	-0.128	0.836	*
	Time since fire	0.312	0.292	0.332	1.366	*
Upland pine	Low forage	0.538	0.495	0.582	1.713	*
	High forage	0.658	0.573	0.743	1.931	*
	Time since fire	-0.672	-0.706	-0.639	0.511	*
Upland hardwood	Low forage	-0.196	-0.225	-0.166	0.822	*
	High forage	-0.264	-0.324	-0.205	0.768	*
	Time since fire	0.019	-0.003	0.041	1.019	
Planted pine	Low forage	0.328	0.304	0.352	1.388	*
	High forage	0.047	-0.004	0.098	1.048	*
	Time since fire	-0.096	-0.111	-0.081	0.908	*
Open water	Low forage	0.172	0.152	0.191	1.187	*
	High forage	-0.142	-0.185	-0.100	0.867	*
	Time since fire	0.170	0.158	0.182	1.185	*
Roads	Low forage	0.004	-0.020	0.027	1.004	
	High forage	0.130	0.078	0.181	1.138	*
	Time since fire	-0.058	-0.072	-0.043	0.944	*

[a] Euclidean distance (m) to the nearest patch of those cover types.
[b] Relative selection strength (RSS) is the exponentiated β coefficient estimate. Because land cover is distance based, RSS values are to be interpreted inversely, where selection is less than 1 and avoidance is greater than 1.

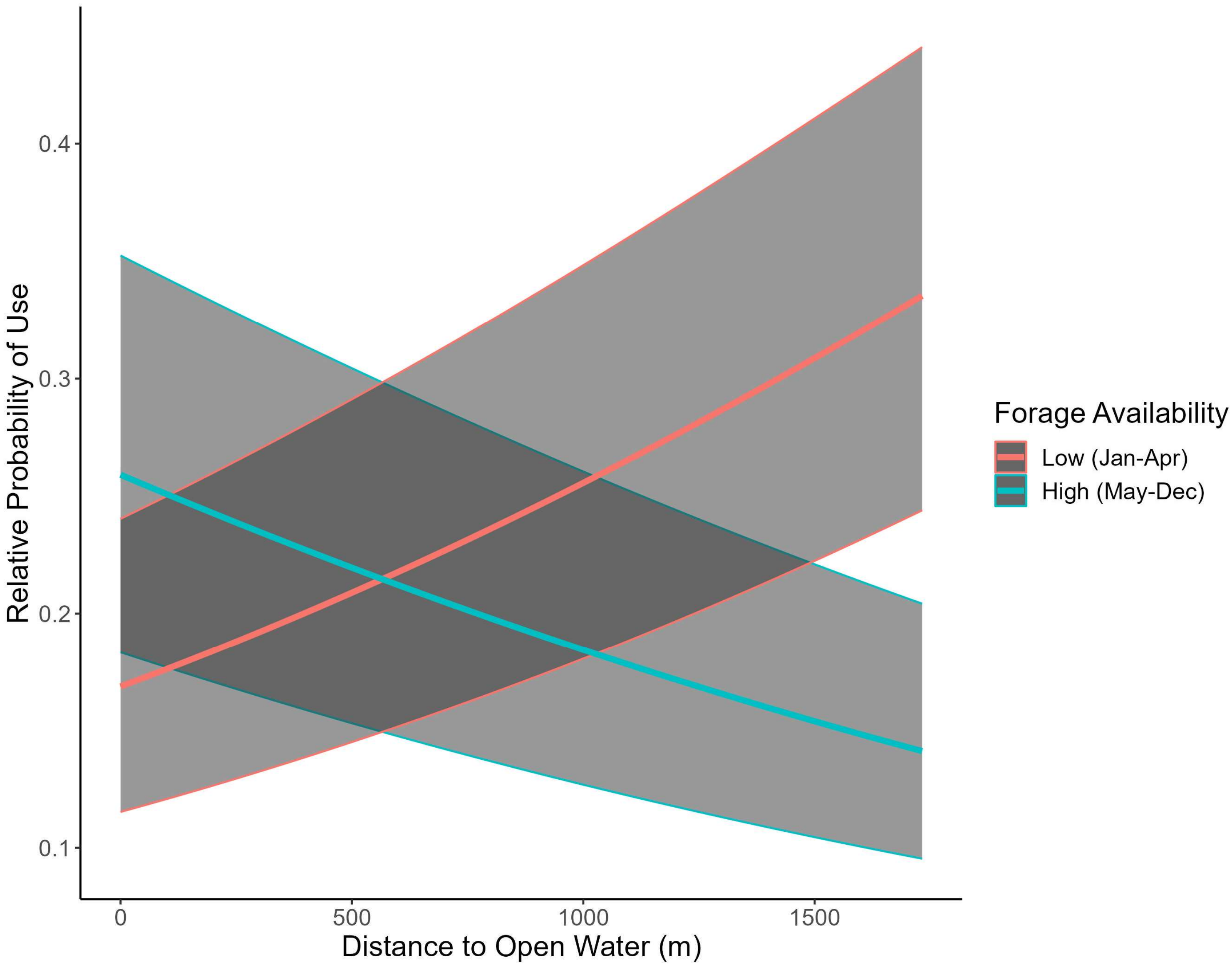

Figure 2.2. Relative probability of use by wild pigs in the Red Hills region, USA plotted against distance to open water in two seasons based on low (January-April) and high (May-December) forage availability. Error bands represent 95% confidence intervals.

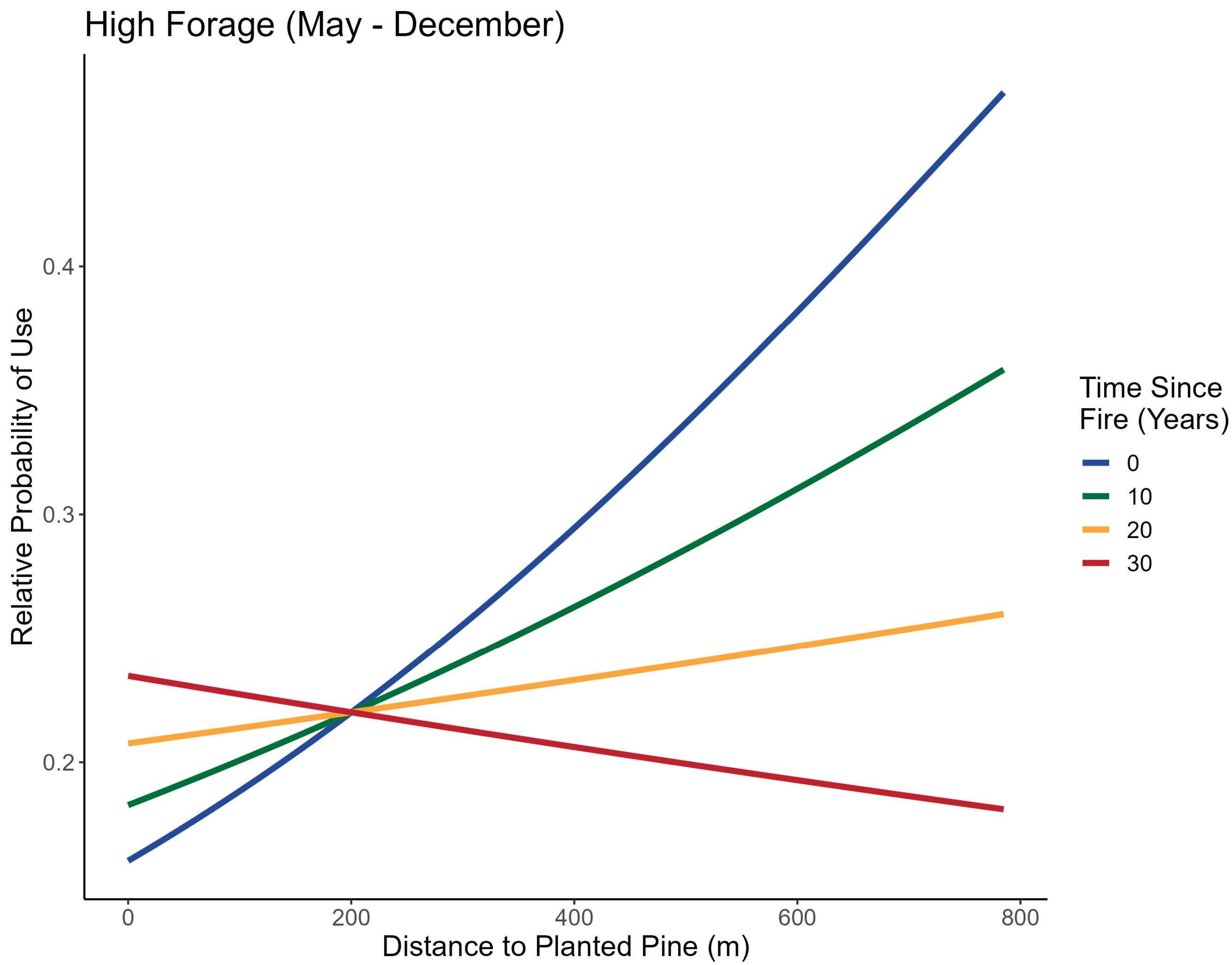

Figure 2.3. Relative probability of use by wild pigs in the Red Hills region, USA plotted against distance to planted pine in the high forage season (May-December) across four yearly intervals without fire.

CHAPTER 3

WILD PIG (*SUS SCROFA*) BEDDING SITE SELECTION IN THE RED HILLS REGION OF NORTH FLORIDA AND SOUTH GEORGIA, USA

Terrazas, C., K. Sash, and M. T. Mengak. *To be submitted to Wildlife Society Bulletin.*

ABSTRACT

Invasive wild pig (*Sus scrofa*) management has concurrently developed with their increasing distribution in past decades. Management techniques have prioritized abating economic damage through various methods of control. Corral trapping, the most common, involves habituating pigs to bait and ultimately luring sounders into a trap for removal. Bait location is critical with bait typically placed between areas that pigs frequent like bedding and foraging grounds. Wild pigs leave behind a significant amount of evidence of foraging through their distinct rooting behavior. However, bedding cover is more difficult to identify due to the cryptic tendency of animals to hide while resting. Wild pig resource selection is well-documented throughout North America, but bedding cover selection is relatively understudied and could provide valuable insights into their ecology and management. We used GPS data from 13 wild pigs to identify and evaluate bedding sites and their surrounding vegetative structure. Logistic regression analysis of use-availability data revealed that wild pigs constructed beds located in lower basal area forest patches. Increasing vertical cover from 1 to 1.25 m above the ground increased the likelihood of pigs using an area for bedding. Our model did not suggest that canopy cover and ground cover composition of forbs, grasses, bare ground, or woody vegetation impacted the probability of a pig bedding at a particular site. Interpreting the relationship between invasive species behavior and fine-scale resource use can help managers increase the efficiency of removal efforts.

KEY WORDS

Bedding sites, invasive species, resource selection, resting cover, *Sus* scrofa, wild pigs

INTRODUCTION

Wild pigs (*Sus scrofa*) are a prolific invasive species across the world that inflict significant damage to native ecosystems, agriculture, and native wildlife while posing threats to human health (Barrios-Garcia and Ballari 2012, Miller et al. 2017). Wild pig populations have increased throughout North America since their introduction in the 1500s by Spanish explorers (Mayer and Brisbin 2008). This species has expanded in range due to its reproductive capability, generalist diet and habitat, and lack of natural predators (Bieber and Ruf 2005, Mayer and Brisbin 2009, Chinn et al. 2022). Humans have contributed to this expansion by moving animals to increase wild pig hunting opportunities (Hernández et al. 2018). These factors have contributed to the current distribution of wild pigs in the United States where abundance is estimated at approximately 6.9 million individuals in 31 states (Ballari and Barrios-Garcia 2014, Bevins et al. 2014, Lewis et al. 2019, USDA 2022).

The extent of wild pig damage is primarily due to their foraging behavior known as rooting. Rooting, the process in which pigs dig their snouts into the soil to find food items, can alter plant community succession and lead to considerable agricultural losses (Arrington et al. 1999, Siemann et al. 2009, Anderson et al. 2016). Row crops are the most affected, although rooting can also negatively impact production of pecans (*Carya illinoinensis*) and recently planted longleaf pine (*Pinus palustris*) seedlings (Hopkins 1947, Boyer et al. 2020, McKee et al. 2020). Given the opportunistic diet of wild pigs, ground nesting birds like eastern wild turkey (*Meleagris gallopavo*) and northern bobwhite (*Colinus virginianus*) are also susceptible to nest depredation by rooting pigs (Rollins and Carrol 2001, Sanders et al. 2020). Another significant wild pig concern is the threat of disease transmission to native wildlife, livestock, and humans. Introduction of nonnative species can lead to the introduction of nonnative diseases and have devastating impacts on industries including commercial pork production (Miller et al. 2017, You et al. 2021).

Wild pig management focuses primarily on protecting valuable resources and reducing damage (Massei et al. 2011). Common methods include corral trapping, night shooting, aerial gunning, and the judas method (West et al. 2009, Campbell and Long 2009). Corral trapping is the most common because of its efficiency in the field despite challenges like limited funding and personnel. This method also increases the chance of eliminating an entire social group, or sounder, which can significantly improve removal programs (Lewis et al. 2020). Identifying pig movement patterns and highlighting predictable behaviors is critical for bait placement during the pre-trapping period. Wild pigs cannot independently regulate their body temperature, thus their movements prioritize dense cover and proximity to water, especially in the southeastern USA (Friebel and Jodice 2009, Clontz et al. 2021). Exploiting these behaviors during trapping ensures that wild pigs encounter the bait and become habituated to the trap site. Ditchkoff and Bodenchuk (2020) recommend placing bait, most commonly whole kernel corn, along movement corridors between bedding cover and foraging areas. Detecting foraging areas used by wild pigs is relatively simple because of the damage left behind from rooting, whereas bedding areas are more difficult to find.

Current knowledge of wild pig bedding habits is incidental in nature and studies have not focused primarily on this behavior. For instance, wild pigs use blown down trees and other structures that harbor dense climbing vegetation for resting/bedding cover (Mayer and Brisbin 2002 and Gaston et al. 2008). Resource selection at the third order, within an animal or group's home range, is valuable for a general understanding of this behavior (Johnson 1980, Clontz et al. 2021). However, finer-scale inferences can assist managers in prioritizing more exact locations for bait placement. Wild pigs might also interact with landscape-level characteristics differently than finer-scale features like the vegetation surrounding a bed, demonstrating a hierarchical relationship (Johnson 1980). We assessed the relationship between wild pig bedding site selection and fourth order habitat features, site-specific resources that are acquired within the home range (Johnson 1980). Detecting these relationships can help prioritize bait placement for trapping and provide justification for altering habitat to reduce invasion risk through forest management practices like prescribed fire and mechanical treatment.

STUDY AREA

Our study was conducted on 8 private properties that focus on northern bobwhite (*Colinus virginianus*) management within Leon and Jefferson counties, Florida, and Thomas County, Georgia USA (Figure 3.1). Known as the Red Hills region, this area falls between Thomasville, Georgia and Tallahassee, Florida and is bordered to the east and west by the Aucilla and Ochlocknee rivers, respectively. The Red Hills region encompasses 176,000 hectares of primarily private lands managed for northern bobwhite hunting and ecosystem management. Most of the Red Hills is comprised of old field loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) regeneration with old growth and second growth longleaf pine (*P. palustris*)-wiregrass (*Aristida sp.*) mixed throughout. Given the topographic gradient the Red Hills is known for, hardwood and bottomland habitat consist of upland oak (*Quercus sp.*) and hickory (*Carya sp.*) forests leading downslope into forested wetlands comprised of cypress (*Taxodium sp.*) and tupelo (*Nyssa sp.*). Agricultural fields, although small (<6 hectares), are scattered throughout most properties. Field plantings varied across our study area depending on management goals, but managers in the region avoided planting corn (*Zea mays*) in recent years due to losses attributable to pigs. Fields are harrowed annually and intermittently left fallow to grow in annual weeds to support northern bobwhite and turkey (*Meleagris gallopavo*) brood habitat. Prescribed fire is regularly applied in the uplands on 2 to 3-year intervals to promote wildlife habitat and reduce hazardous fuels (Sisson et al. 2017).

METHODS

Wild Pig Radio-Collaring and Monitoring

Trapping was conducted by USDA APHIS Wildlife Services between December 2021 and November 2022 in conjunction with intensive removal efforts in the region. Corral-style traps were baited with corn and monitored with cellular cameras (Ditchkoff and Bodenchuk 2020). We physically restrained 1-2 individuals within traps and fitted them with Vectronic-Aerospace Vertex™ Lite GPS collars (Vectronic-Aerospace, Berlin, Germany). For each individual collared, we recorded sex, approximate age (sub-adult or adult), overall condition, and morphological measurements (head length, body length, heart girth). To maintain handling efficiency and reduce cost, we did not anesthetize captured pigs but used only physical restraint. For safety concerns, we collared only individuals that were visually estimated to weigh less than 45 kg. GPS collars recorded location fixes at 2-hour intervals initially and were later increased to 1-hour intervals in March 2022 until April 2023. To reduce location bias, we removed GPS fixes that were not 3D validated (four or more satellites acquired). We also censored location data within the first 3 days of deployment to account for any post-capture behavioral shifts. We conducted all capture and handling in compliance with the Tall Timbers Institutional Animal Care and Use Committee (IACUC # 2023-003).

Resting/Bedding Sites

We used the proprietary software Inventa™ (Vectronic-Aerospace, Berlin, Germany) to visually inspect locations in real time to identify potential bedding areas. Locations (i.e., GPS fixes) were considered potential bed sites when pig movements created clusters of locations that occurred within at least a 6-hour period (3 locations for 2-hour fix rates and 6 for 1-hour fixes). These clusters were then recorded and visited within 4 weeks to observe signs of bedding including flattened vegetation, circular impressions in the ground, and concentrated tracks or scat. We excluded potential sample locations that exhibited no sign of bedding behavior from analysis. We employed a "used-available" design to compare habitat at bedding sites to an available site located 30 m from a bed in a random direction (Johnson et al. 2006). For every collared pig, we sampled 5 confirmed bedding sites and at least another 5 if the collar was deployed for more than 4 months. We did not resample beds that were used repeatedly. At each solitary bed and random site, we measured overstory canopy density (%), groundcover composition (%), basal area (m^2/ha), and vertical obstruction (%). We estimated overstory canopy density using a spherical densiometer at the plot (pig bed) center. Groundcover composition was visually estimated within six 1 m^2 quadrats along a 10 m transect placed in a random direction from the center of the bed. We separately estimated the percent cover of grasses, forbs, leaf litter, bare ground, and woody species to the nearest 5 percent. Basal area of live tree stems was measured at 1.37 m (breast height) using a 10-factor prism. We measured vertical obstruction in 0.25 m increments up a 1.25 m vegetation profile board from 10 m away (Nudds 1977). We classified percent obstruction into 5 cover classes (0-20%, 21-40%...81-100%) and the midpoint of each cover class was used for analysis.

Statistical Analyses

We used a generalized linear model (GLM) with a binary response variable and logit link to predict the probability of a pig bedding in a location relative to available random sites. We used each variable as a covariate in a global logistic regression model after accounting for multicollinearity. We calculated variance inflation factors (VIFs) for all covariates in the model and omitted those with VIFs > 4. Leaf litter composition (VIF = 1360) was removed from the model and remaining covariates were under our VIF cutoff threshold of 4. We fit a single global GLM rather than using model selection because we were interested in evaluating the effect of each variable rather than achieving parsimony. All analyses were conducted using the stats package in the statistical computing software R 4.2.1 (R Core Team 2022).

RESULTS

From December 2021 to November 2022, we collared 13 wild pigs (7 male, 6 female) (Table 3.1). Between 15 December 2021 and 04 April 2023, we identified and sampled 114 beds used by wild pigs and 114 associated random sites across our study area (Table 3.2). Beds were more likely to occur in areas with lower basal area (β = -0.046, 95% CI: -0.092, -0.004, P = 0.0380) and more dense vertical cover from 1 – 1.25 m above the ground (β = 0.024, 95% CI: 0.008, 0.040 P = 0.0031) (Table 3.3). Our model suggests that a 1 m^2/ha increase in basal area decreases the relative probability of using an area for bedding by 4.5%. Furthermore, our model suggests that a 1% increase in vertical cover between 1 and 1.25 m above the ground increases the relative probability of bedding in an area by 2.4%. Ground cover composition, across all plant groups, and overstory canopy cover had no statistically significant effect on the relative probability of bedding in a particular area (Table 3.3).

DISCUSSION

Wild pigs in our study area exhibited no selection for bedding based on percent canopy cover. Pigs lack thermoregulatory mechanisms forcing them to select daytime cover that provides shade from the sun (Kay et al. 2017). Mayer et al. (2002) found solitary beds in South Carolina in which pigs were bedding under a more closed canopy compared to farrowing nests.

The association between this species and a dense canopy has also been identified at a coarser spatial resolution as well (Clontz et al. 2021). Our results suggest that this selection might be scale dependent, due to the lack of significance in our findings at a finer spatial resolution.

Basal area, a measurement more commonly used for timber management, also has its applications for describing wildlife-habitat relationships (Rosche et al. 2019). Basal area has not been used to evaluate pig habitat, but pigs have been documented bedding near large diameter trees (Mayer et al. 2002). Therefore, we predicted that wild pigs would construct beds within higher basal area forests. Our results contradicted our expectations, because pigs in our study were more likely to rest in areas with lower basal area (Figure 3.2). Basal area not only represents tree size, but rather a combination of tree size and tree density within an area. Because we used a basal area prism, we are unable to untie the relationship between tree size and density. However, relatively high estimates of canopy cover (~85%) in used and available sites suggest that cover was primarily comprised of shrubby, shade-tolerant species that were not recorded in basal area measurements.

Vegetative obstruction allows wildlife managers to characterize cover, in this case for bedding, along the ground and often up a vertical gradient (Nudds 1977). We shortened our vegetation profile board to more closely describe the perspective of a wild pig to understand how understory density relates to bedding cover. Our results suggest that understory density above the head of a pig (1 – 1.25 m) is especially important in the decision to bed in a particular area (Figure 3.3). Mayer et al. (2002) also recorded most solitary pig beds located within a denser understory when compared to farrowing nests. Dense vegetation above the ground suggests that wild pigs primarily bed within forests with a later successional understory dominated with shrubs and shade-tolerant species. This vegetation complex is common within bottomland ecotones in the Red Hills that are dominated by mature loblolly pine. These forests are often excluded from prescribed fires that would mitigate the growth of a dense understory.

Living trees and herbaceous plants are not the only structures that provide valuable cover for bedding. Course woody debris (CWD) like fallen snags and blown down trees can also provide similar cover. Gaston et al. (2008) stated that "many" pigs were flushed from under CWD while conducting radiotelemetry in Alabama. We incidentally observed 24 beds (21%) adjacent to these structures. Pursuing dense cover like CWD for bedding might be a relic of ancestral pigs avoiding predators, but the lack of predators in our region could mean that this resting behavior is a response to the local climate. We did not sample beds during the warmest time of the year (July – August), limiting our ability to understand the importance of CWD at a time when it could be used more frequently.

Ground cover composition had little impact on bedding cover selection in our model. Trampled and rooted vegetation is a common symptom of wild pigs on a landscape, which makes it more difficult to evaluate the selection of these features due to damage left behind from wild pigs. While our results might represent the actual relationship, we believe that groundcover composition was altered by pigs in the surrounding area thus skewing results. Because results from our profile board suggest that overhead cover is important for bedding sites, composition among different plant groups might be irrelevant. Ground cover, regardless of species or functional group, may serve the same purpose in the eyes of a wild pig.

Our study was designed to evaluate wild pig bedding site selection from the forest canopy down to the ground. Lower-level attributes including basal area and vertical obstruction are relatively simple to measure in the field and can potentially be used to increase trap success. Understanding drivers of invasive species resource selection can also provide insights into preventative management to mitigate their impacts and expansion. Mechanical and chemical vegetation removal techniques can be used to reduce available refugia for pigs, thus making these areas less desirable for bedding.

MANAGEMENT IMPLICATIONS

This study observed that wild pigs were more likely to construct beds in forest patches with potentially lower basal area and increased vegetative cover from 1 to 1.25 m above ground. This suggests that these characteristics can be used to concentrate monitoring and removal efforts in the field. Our model predicts relative probabilities, which limits our ability to recommend a measurable target threshold for any forest attribute. Therefore, one should use these recommendations in a relative context to what is available within a particular area. We suggest placing bait between identified foraging areas (i.e., rooted patches) and dense thickets of possible bedding cover to increase the probability of bait encounters. Fallen trees, snags, and root balls should also be considered as prospective bedding cover.

LITERATURE CITED

Anderson, A., C. Slootmaker, E. Harper, J. Holderieath, and S. A. Shwiff. 2016. Economic estimates of feral swine damage and control in 11 US states. Crop Protection 89:89–94.

Arrington, D. A., L. A. Toth, and J. W. Koebel. 1999. Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. Wetlands 19:535–544.

Ballari, S. A., and M. N. Barrios-Garcia. 2014. A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges. Mammal Review 44:124–134.

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

Bevins, S. N., K. Pedersen, M. W. Lutman, T. Gidlewski, and T. J. Deliberto. 2014. Consequences associated with the recent range expansion of nonnative feral swine. BioScience 64:291–299.

Bieber, C., and T. Ruf. 2005. Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed food resources. Journal of Applied Ecology 42:1203–1213.

Boyer, K. S., W. S. Fairbanks, C. Rohla, and S. L. Webb. 2020. Surficial soil damage by wild pigs (*Sus scrofa*) decreases pecan harvest efficiency. Crop Protection 128:e104992. https://doi.org/10.1016/j.cropro.2019.104992

Campbell, T. A., and D. B. Long. 2009. Feral swine damage and damage management in forested ecosystems. Forest Ecology and Management 257:2319–2326.

Chinn, S. M., P. E. Schlichting, T. J. Smyser, C. F. Bodwen, and J. C. Beasley. 2022. Factors influencing pregnancy, litter size, and reproductive parameters of invasive wild pigs. Journal of Wildlife Management 86:e22304. https://doi.org/10.1002/jwmg.22304

Clontz, L. M., K. M. Pepin, K. C. VerCauteren, and J. C. Beasley. 2021. Behavioral state resource selection in invasive wild pigs in the Southeastern United States. Scientific Reports 11:e6924. https://doi.org/10.1038/s41598-021-86363-3

Ditchkoff, S. S., and M. J. Bodenchuk. 2020. Management of wild pigs. Pages 175-197 *in* K. C. VerCauteren et al., editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Friebel, B. A., and P. G. R. Jodice. 2009. Home range and habitat use of feral hogs in Congaree National Park, South Carolina. Human-Wildlife Conflicts 31:49–63.

Gaston, W., J. B. Armstrong, W. Arjo, and H. L. Stribling. 2008. Home range and habitat use of feral hogs (*Sus scrofa*) on Lowndes County WMA, Alabama. National Conference on Feral Hogs. Missouri Department of Conservation, 13–15 April 2008, St. Louis, Missouri, USA.

Hernández, F. A., B. M. Parker, C. L. Pylant, T. J. Smyser, A. J. Piaggio, S. L. Lance, M. P. Milleson, J. D. Austin, and S. M. Wisely. 2018. Invasion ecology of wild pigs (Sus scrofa) in Florida, USA: the role of humans in the expansion and colonization of an invasive wild ungulate. Biological Invasions 20:1865–1880.

Hopkins, W. 1947. Hogs or logs? Southern Lumberman 175:151–153.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Kay, S. L., J. W. Fisher, A. J. Monaghan, J. C. Beasley, R. Boughton, T. A. Campbell, S. M. Cooper, S. S. Ditchkoff, S. B. Hartley, J. C. Kilgo, S. M. Wisely, A. C. Wyckoff, K. C. VerCauteren, and K. M. Pepin. 2017. Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Movement Ecology 5:e14. https://doi.org/10.1186/s40462-017-0105-1

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

Lewis, A. A., B. L. Williams, M. D. Smith, and S. S. Ditchkoff. 2020. Shifting to sounders: whole sounder removal eliminates pigs. Wildlife Society Bulletin 46:e1260. https://doi.org/10.1002/wsb.1260

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

Mayer, J. J., and I. L. Brisbin. 2008. Wild pigs in the United States: their history, comparative morphology, and current status. University of Georgia Press, Athens, USA.

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

Mayer, J. J., F. D. Martin, and I. L. Brisbin. 2002. Characteristics of wild pig farrowing nests and beds in the upper Coastal Plain of South Carolina. Applied Animal Behaviour Science 78:1–17.

McKee, S., A. Anderson, K. Carlisle, and S. A. Schwiff. 2020. Economic estimates of invasive wild pig damage to crops in 12 US states. Crop Protection 132:e105105. https://doi.org/10.1016/j.cropro.2020.105105

Miller, R. S., S. J. Sweeney, C. Slootmaker, D. A. Greer, P. A. Di Salvo, D. Kiser, and S. A. Schwiff. 2017. Cross-species transmission potential between wild pigs, livestock, poultry, wildlife, and humans: implications for disease risk management in North America. Scientific Reports 7:e7821. https://doi.org/10.1038/s41598-017-07336-z

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

R Core Team 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rollins, D., and J. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. Wildlife Society Bulletin 29:39–51.

Rosche S. B., C. E. Moorman, k. Pacifici, J. G. Jones, C. S. DePerno. 2019. Northern bobwhite breeding season habitat selection in fire-maintained pine woodland. Journal of Wildlife Management 1226–1236.

Sanders, H. N., D. G. Hewitt, H. L. Perotto-Baldivieso, K. C. VerCauteren, and N. P. Snow. 2020. Invasive wild pigs as primary nest predators for wild turkeys. Scientific Reports 10:e2625. https://doi.org/10.1038/s41598-020-59543-w

Siemann, E., J. A. Carrillo, C. A. Gabler, R. Zipp, and W. E. Rogers. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management 258:546–553.

Sisson, D. C., E. Staller, and W. E. Palmer. 2017. Habitat Management. Pages 33–57 *in* W. E Palmer and D. C. Sisson, editors. Tall Timbers' Bobwhite Quail Management Handbook. Tall Timbers Press, Tallahassee, Florida, USA.

United States Department of Agriculture [USDA]. 2022. History of feral swine in the Americas: distribution maps. <https://www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/operational-activities/feral-swine/sa-fs-history>. Accessed 01 March 2023.

West, B. C., A. L. Cooper, and J. B. Armstrong. 2009. Managing wild pigs: A technical guide. Human-Wildlife Interactions Monograph 1:1–55.

You, S., T. Liu, M. Zhang, X. Zhao, Y. Dong, B. Wu, Y. Wang, J. Li, X. Wei, and B. Shi. 2021. African swine fever outbreaks in China led to gross domestic product and economic losses. Nature Food 2:802-808.

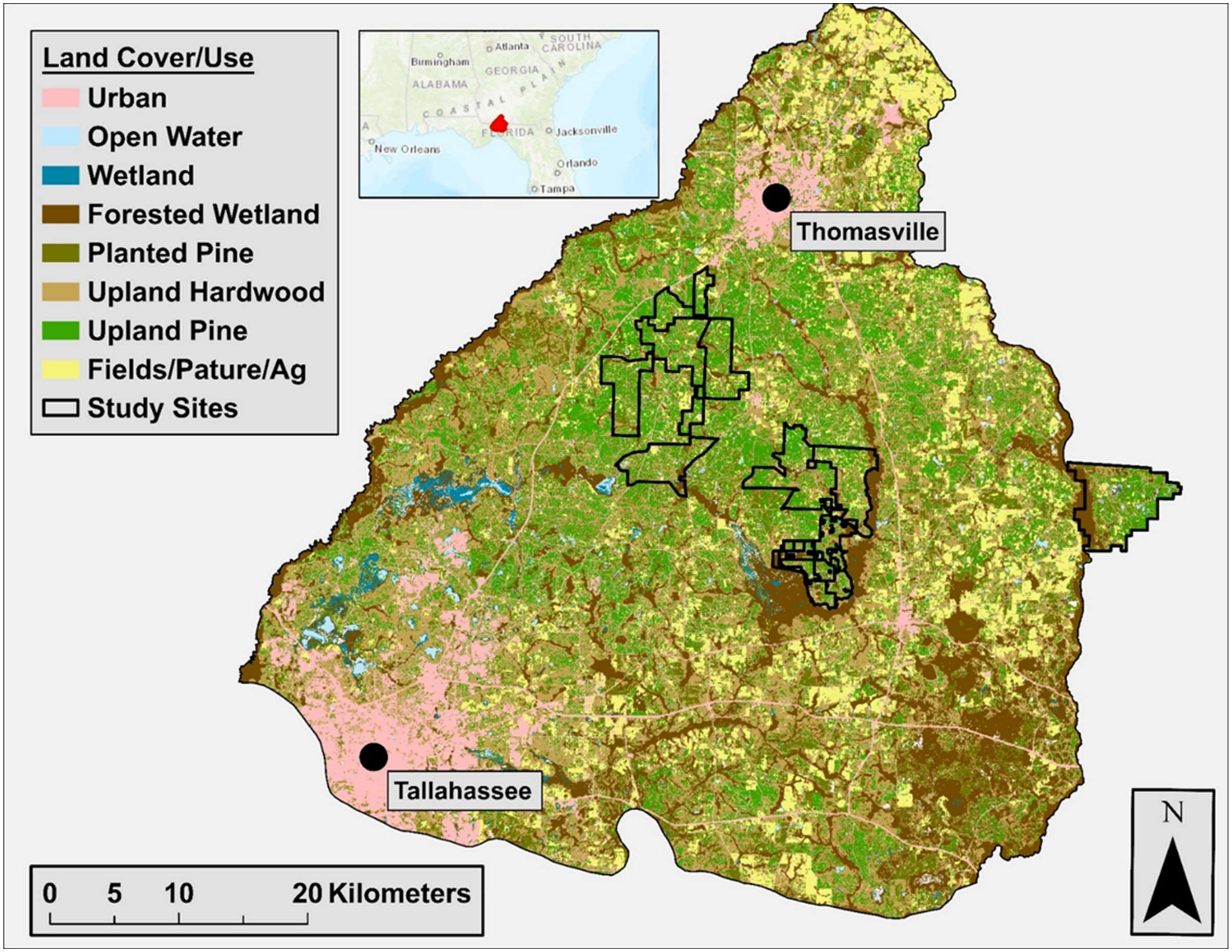

Figure 3.1. Land Cover/Land Use map of the Red Hills region between Thomasville, Georgia and Tallahassee, Florida, USA. Study sites are outlined in black.

Table 3.1. Individual data for GPS collared wild pigs in the Red Hills region of North Florida and South Georgia, USA between December 2021 and April 2023.

ID	Sex	Property	Age	Fix rate (hr)[a]	Length (days)	Number of locations
W1	Male	Dekle	Sub-adult	2	48	576
W2	Male	Livingston Place	Adult	2,1	313	6570
W3	Male	Elsoma	Adult	2,1	109	1990
W4	Male	Meander	Sub-adult	1	260	6197
W5	Male	Mays Pond	Sub-adult	1	163	3941
W6	Male	Mays Pond	Adult	1	246	6037
W8	Male	Warbick Farms	Sub-adult	1	245	5900
Y26	Female	Livingston Place	Adult	2,1	314	6624
Y28	Female	Elsoma	Adult	2,1	215	4602
Y29	Female	Kelly Pond	Sub-adult	1	268	6697
Y30	Female	Warbick Farms	Sub-adult	1	187	4512
Y31	Female	Loveridge	Sub-adult	1	108	2306
Y36	Female	Warbick Farms	Adult	1	130	3021

[a] Fix rates were changed from 2-hour to 1-hour for 4 individuals in March 2022

Table 3.2. Descriptive statistics of data collected for a generalized linear model to evaluate wild pig bedding site selection in the Red Hills region near Tallahassee, Florida, USA between December 2021 and April 2023.

	Used		Available	
Covariate	$\bar{x}$	95% CI	$\bar{x}$	95% CI
Basal area (m^2/ha)	19.03	± 4.43	23.70	± 6.59
Vertical Cover				
0 - 0.25 m (%)[a]	82.59	± 10.43	75.92	± 14.38
0.26 - 0.50 m (%)[a]	78.37	± 11.85	63.07	± 15.46
0.51 - 0.75 m (%)[a]	66.96	± 13.93	44.89	± 16.36
0.76 - 1.00 m (%)[a]	66.41	± 14.89	36.77	± 16.05
1.01 - 1.25 m (%)[a]	58.85	± 16.09	27.39	± 13.98
Canopy cover (%)	85.96	± 9.48	85.05	± 10.43
Bare ground (%)	1.83	± 1.80	1.94	± 1.96
Forb (%)	6.27	± 6.29	7.70	± 8.20
Woody (%)	40.21	± 10.27	32.48	± 9.83
Grass (%)	13.25	± 10.47	16.80	± 10.67

[a] Percent obstruction estimated across a vertical gradient on a modified vegetation profile board.

Table 3.3. Results from a generalized linear model to evaluate wild pig bedding site selection in the Red Hills region near Tallahassee, Florida, USA between December 2021 and April 2023.

		95 % CI			
Covariate	β	Lower	Upper	RSS[a]	$P < 0.05$
Basal area (m^2/ha)	-0.046	-0.092	-0.004	0.955	*
Vertical cover					
0 – 0.25 m (%)[b]	-0.001	-0.023	0.022	0.999	
0.26 - 0.50 m (%)[b]	0.006	-0.017	0.029	1.006	
0.51 - 0.75 m (%)[b]	-0.004	-0.023	0.015	0.996	
0.76 - 1.00 m (%)[b]	0.015	-0.004	0.034	1.015	
1.01 - 1.25 m (%)[b]	0.024	0.008	0.040	1.024	*
Canopy Cover (%)	0.018	-0.005	0.042	1.018	
Bare Ground (%)	-0.006	-0.099	0.087	0.994	
Forb (%)	-0.002	-0.029	0.024	0.998	
Woody (%)	-0.008	-0.032	0.016	0.992	
Grass (%)	0.001	-0.022	0.023	1.001	

[a] Relative selection strength (RSS) is the exponentiated β coefficient estimate. RSS values less than 1 signify that increasing covariate values results in decreasing relative probability of selection.
[b] Percent obstruction across a vertical gradient on a modified vegetation profile board.

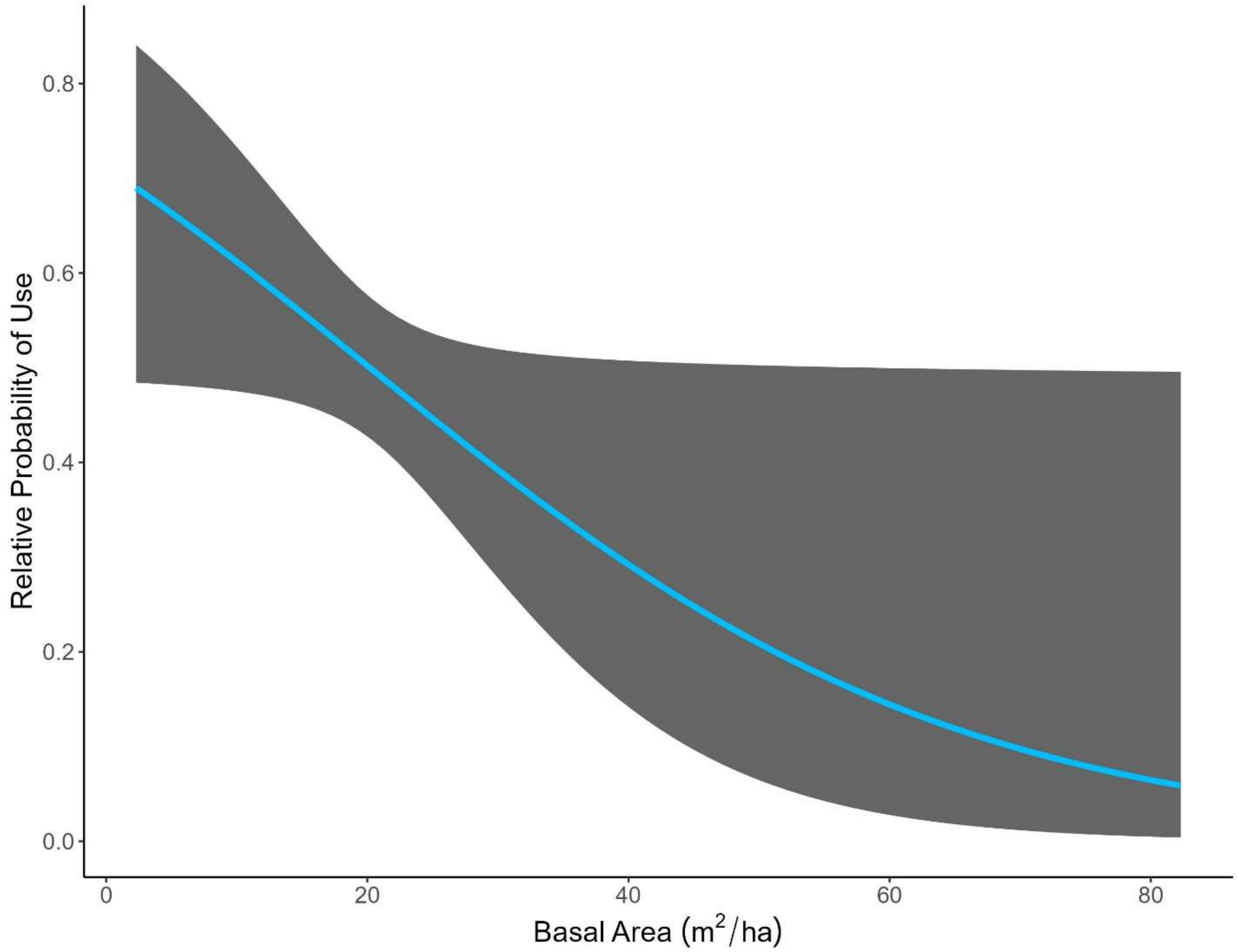

Figure 3.2. Relative probability of use for bedding by wild pigs in the Red Hills region near Tallahassee, Florida, USA plotted against basal area. Error bands represent 95% confidence intervals.

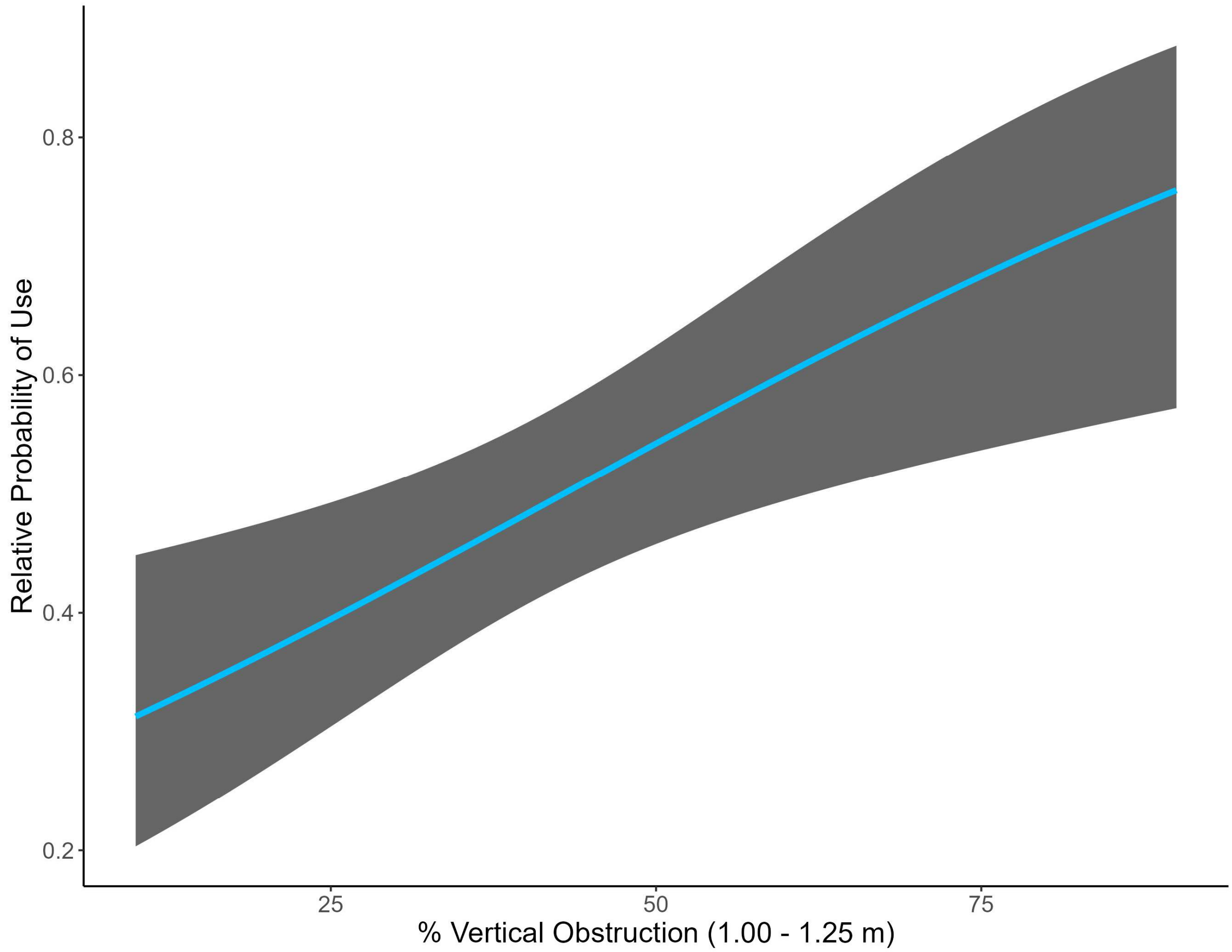

Figure 3.3. Relative probability of use for bedding by wild pigs in the Red Hills region near Tallahassee, Florida, USA plotted against percent vertical obstruction at 1 – 1.25 m (cover). Error bands represent 95% confidence intervals.

CHAPTER 4

CONCLUSION

The management and removal invasive wild pigs (*Sus scrofa*) is a growing concern across the United States given their range expansion and generalist diet and habitat use. Because this species can exploit a variety of new environments, management to prevent further expansion and reduce their distribution relies on region-specific efforts. The Red Hills region is a biodiversity hotspot with high conservation value across its fire-dependent landscape. Although wild pigs have long been established in this region, knowledge of their resource use at any spatial scale is lacking. To bridge this gap, I used GPS data to understand how pigs used the landscape while incorporating factors like land cover, forage availability, and a previously overlooked abiotic factor, fire history. I also investigated wild pig resource use at a finer spatial resolution to understand what forest structural components might contribute to bedding site selection. My results can guide wild pig monitoring and removal efforts by incorporating these species-habitat relationships into an active trapping program. More directly, these relationships can be exploited to proactively monitor and protect areas that are susceptible to wild pig invasion. In an area that has potential for furthering regional habitat management objectives, the Red Hills can also benefit by using my results to alter susceptible habitats and make them less appealing to pigs, thus protecting valuable natural resources.

In Chapter 2, I evaluated wild pig 3rd order resource selection using GPS data from 13 individuals across the region. I found that resource selection was not dependent on forage availability as previously identified southeastern studies. As it relates to the use of agricultural fields, this is likely due to the common wildlife management practices in the region like supplemental feeding and winter-disking; both of which alter forage availability dynamics throughout the year. Wild pigs used areas further from open water in the low forage season (January – April) and selected areas closer to open water in the high forage season (May – December), likely due to increasing temperatures in the summertime. I found that pigs selected for habitats that are commonly associated with the species in both seasons, including forested wetlands, fields, and upland hardwoods. Wild pigs in our study area avoided planted pine and upland pine communities regardless of season. Additionally, time since fire (TSF) interacted significantly with all land cover types except upland hardwood. Increasing TSF increased the relative probability of pigs selecting for forested wetlands, upland and planted pine, and roads. For example, wild pigs avoided planted pine communities that have been more recently been burned and selected for them with increasing TSF.

In Chapter 3, I used the same GPS dataset to identify bedding sites used by pigs throughout the study. After verifying that clusters of locations were actual bedding sites, I evaluated forest structure components at the bed and a random location 30 m away to compare use and availability. I found that the most important factors driving bedding site selection were basal area and vegetative cover from 1 – 1.25 m above the ground. My results indicate that bedding sites were more likely to occur in forests with a later successional understory of shade-tolerant species. High canopy cover at both used and available sites inhibits the growth of most grass and forb (shade intolerant) species, promoting the success of species that provide dense overhead cover above the ground.

The results from my thesis research build upon the growing body of knowledge that has developed in response to the rising wild pig problem across the United States, particularly in the southeast. Although wild pig resource selection has been evaluated across the country, the Red Hills region can now benefit from findings that are more specific to this area. Implications from my study can be used by wildlife managers and future researchers to better understand how pigs are exploiting the landscape. These results can also be used to proactively manage habitat (i.e., restoring natural fire regimes or reducing available cover) to restrict wild pig use, limit the spread of disease, and mitigate further damage to natural resources.