SPATIAL ECOLOGY OF WILD PIGS: EFFECTS OF ENVIRONMENTAL AND DEMOGRAPHIC ATTRIBUTES ON BEHAVIORAL STATE RESOURCE SELECTION AND HOME RANGES

by

LINDSAY MIKAYLA CLONTZ

(Under the Direction of JAMES C. BEASLEY)

ABSTRACT

Wild pigs (*Sus scrofa*) are one of the most widespread and successful species in the world. Understanding how wild pigs move throughout the landscape and interact with or react to abiotic and biotic factors is important for advising management. Using movement characteristics from GPS data to define behaviors, I explored the connection between behavior and resource selection for both sexes between two distinct seasons based on forage availability. I also constructed weekly 50% and 95% home ranges to quantify the effects of biotic and abiotic factors on home range size and shape. Wild pigs selected for bottomland hardwoods and dense canopy cover in all behavioral states in both seasons. Proportion of bottomland hardwoods, meteorological conditions, and sex impacted wild pig weekly home range size. In addition, proportion of upland pines and distance to streams influenced home range shape. This research may be useful for allowing more effective and efficient management planning.

INDEX WORDS: Behavioral analysis, habitat selection, hidden Markov models, resource selection function, wild pig movement, home range, core area, invasive species

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DEDICATION

Dedicated to my mom, Karen Clontz, who has been my role model, my rock, and my inspiration. Also, dedicated to my dog, Levi, who has been by my side night and day through all the analytics and writing that went into this thesis. He has been the light in every moment.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Over the past several centuries, domestic pigs and wild boar (*Sus scrofa*) have been introduced from native populations in Europe and Asia and allowed to expand their range throughout numerous countries (Barrios-Garcia and Ballari 2012). Within the United States, wild pigs originated through introduction of domestic pigs in the 1500s by Spanish explorers as a source of meat (Seward et al. 2004), which later hybridized with introduced Eurasian wild boar (Seward et al. 2004, Goedbloed et al. 2013, Keiter et al. 2016, VerCauteren et al. 2020). Wild pig populations have continued to increase due to both intentional and accidental methods of introduction such as translocation for hunting, escapees from confinement operations, and dispersal from other established populations (VerCauteren et al. 2020). Over the past 30 years, the expansion of the geographic range and population of wild pigs in the United States has increased dramatically with a total of 38 states reporting wild pigs in 2011 compared to only 17 states in 1988 (Bevins et al. 2014).

Wild pigs pose a complicated division in their invasive range among wildlife managers, veterinarians, and farmers who all deal with the negative impacts of wild pigs, and hunters who value wild pigs as an important game species (Massei et al. 2011). Therefore, they have become somewhat of a paradox in that they cause substantive damage to natural and agricultural landscapes through rooting, wallowing, and other behaviors (Seward et al. 2004), but they are also a popular big-game species and desirable to some hunters (Zivin et al. 2000). For example, in the United States it has been estimated that wild pigs cause approximately $800 million in agricultural damage per year, and due to the difficulty of placing a monetary value on environmental damage and potential for animal and zoonotic disease transmission, the broader economic impacts of invasive wild pigs are considerably higher (Pimental 2007). Given the continued growth in abundance and geographic spread of wild pigs and resulting impacts on humans, plants, and animals (i.e., environmental damage, agricultural damage, reservoir for disease, etc.) (Barrios-Garcia and Ballari 2012), it is evident that current management strategies are insufficient.

To address the rapidly expanding wild pig population in the United States, there is a critical need for increasing the efficiency and efficacy of management strategies that are currently employed for controlling wild pig populations. However, there are numerous critical data gaps that need to be addressed to better understand the general ecology of wild pigs (Beasley et al. 2018). For example, there has been limited research on wild pig movement ecology compared to other ungulates. In fact, there are seven times fewer publications on movement ecology of wild pigs than there are on elk (*Cervus elaphus*) (Morelle et al. 2014). A significant portion of the research conducted on wild pig movement ecology has focused on the habitat types wild pigs prefer and how they use these habitat types (Cahill et al. 2003, Hayes et al. 2009). However, behavioral states have not been directly correlated with resource selection in terms of movement, nor has it been documented how wild pigs move between and within certain habitats (Morelle et al. 2014). Also, exploring underlying attributes that drive wild pig home range shape and size at a fine temporal scale has not been attempted in the literature. According to

Morelle et al. (2015), aspects of the movement ecology of wild pigs such as their advanced complex spatial memory combined with their generalist characteristics (i.e., high reproduction rate, plastic diet, etc.) are some of the most important and recognized causes of the rapid spread of wild pigs around the world, and therefore, should be explored further.

Understanding how animals move on the landscape and interact with resources in various habitat types is important for informing management; therefore, it is one of the central goals of ecological research (Wiens et al. 1993, Ellner et al. 2001). The landscape patterns observed that make up an animal's home range are determined by single movement steps, which in turn provide information on the interactions among the individual's external environment and individual state (Moorcroft et al. 2006, Boerger et al. 2008). These movement patterns which essentially depend on the behavioral state of an animal, assuming they are not random, represent that animal's response to the environment (Forester et al. 2007). In the case of an adaptable generalist like the wild pig (Senior et al. 2016), the correlation between behavior and landscape patterns can depict how unexpected populations emerge in new places, which is a concern for wildlife managers since wild pigs have the potential to alter ecosystems across broad spatial scales (Forester et al. 2007). The way in which wild pigs move is largely driven by resources distributed throughout the surrounding landscape. Wild pigs move in a deliberate manner choosing different resource patches depending on what they need (rest, forage, mating, etc.) in reference to what is available and whether or not the tradeoff for accessing these resources is biologically reasonable or not (Fortin et al. 2005, Forester et al. 2009). When targeting resources for specific behaviors or needs, wild pig movements tend to be methodical, and they tend to consistently use the same trails and interact with the same areas on the landscape habitually (Hanson and Karstad 1959, Oliveira-Santos et al. 2016). Research regarding how specific behaviors (e.g., resting, foraging, traveling) and movement patterns are associated with resources could provide background knowledge necessary to inform site-specific management techniques. Thus, in this thesis I used the above characteristics of wild pigs to distinguish and define movement patterns and associated behavioral states (e.g., resting, foraging, traveling), and explore the connection between these behavioral states and resource selection.

Knowledge of home range size is also critical for making management decisions, especially when considering wild pigs can efficiently exploit a variety of habitats. Key habitat requirements for wild pigs include water, food resources, and protection from thermal stress (Froese et al. 2015, Gray et al. 2020). Understanding how environmental variation, sex, habitat type, landscape characteristics, and other variables affect home range size and shape of wild pigs at a fine scale (i.e., weekly) is important for efficiently advising methods of management such as trapping, aerial gunning, etc. (Schlichting et al. 2016, Kay et al. 2017). To date, most studies that have quantified the influence of environmental attributes on wild pig movements have done so at a relatively coarse scale (e.g., annual, bimonthly, monthly) (Morelle et al. 2014, Schlichting et al. 2016, Kay et al. 2017). However, most management activities and decisions geared toward wild pigs must be adaptive, and therefore occur on a fine temporal scale (i.e., daily or weekly).

Sex, weather, season, geographic region, and distance to water sources have all been found to affect movement rates, which ultimately affects home range size (Kay et al. 2017). Also, the impact of habitat and landscape characteristics on the shape of home ranges of wild pigs in the southeastern United States has not been studied at a fine scale. The shape of wild pig home ranges can be variable ranging from circular to elongate depending on resource distribution, terrain, and general biological requirements (Singer et al. 1981). Wild pigs tend to seek out river systems and riverine woodlands in hot and humid environments like the southeastern United States in order to thermoregulate when heat loads are high (Dexter 1998). This biological restriction confines wild pigs to areas close to riparian areas; therefore, the composition of the landscape and distribution of riparian areas may have a substantial influence on the shape and distribution of wild pig home ranges. These requirements ultimately depict the level of habitat suitability (Froese et al. 2015) and can help describe and explain the variability in home range shape and size in different habitat types in a defined region. Therefore, this study will use these requirements along with other environmental variables to look at both home range shape and size at a fine spatial and temporal scale.

The overarching objective of this study is to better understand wild pig movement ecology to inform and improve management practices for reducing economic loss, environmental degradation, and chances of disease transmission from wild pigs to other animals and people. Specifically, my objectives are to: (1) use movement characteristics of wild pigs to distinguish and define behavioral states and explore the connection between these behavioral states and resource selection, and (2) quantify wild pig home ranges at the weekly scale to provide a better understanding of how landscape composition, meteorological conditions, and individual-level attributes affect movements, and ultimately, home range size and shape.

LITERATURE CITED

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

Beasley, J. C., S. S. Ditchkoff, J. J. Mayer, M. D. Smith, and K. C. VerCauteren. 2018. Research priorities for managing invasive wild pigs in North America. Journal of Wildlife Management 82:674–681.

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.

Boerger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650.

Cahill, S., F. Llimona, and J. Gràcia. 2003. Spacing and nocturnal activity of wild boar Sus scrofa in a Mediterranean metropolitan park. Wildlife Biology 9:3–13.

Dexter, N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. Wildlife Research 25:547–559.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State–space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Froese, J., C. Smith, C. Mcalpine, P. Durr, and R. Van Klinken. 2015. Moving window analysis links landscape-scale resource utilization to habitat suitability models of feral pigs in northern Australia. Pages 1352–1358 in Gold Coast, Australia.

Goedbloed, D. J., H. J. Megens, P. V. Hooft, J. M. Herrero-Medrano, W. Lutz, P. Alexandri, R. P. M. A. Crooijmans, M. Groenen, S. E. V. Wieren, R. C. Ydenberg, and H. H. T. Prins. 2013. Genome-wide single nucleotide polymorphism analysis reveals recent genetic introgression from domestic pigs into northwest European wild boar populations. Molecular Ecology 22:856–866.

Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia 87:343–348.

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*. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Hanson, R. P., and L. Karstad. 1959. Feral swine in the southeastern United States. Journal of Wildlife Management 23:64.

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

Kay, S. L., J. W. Fischer, 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. <http://proxy-remote.galib.uga.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edswsc&AN=000403549100001&site=eds-live>.

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 40:384–387.

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.

Moorcroft, P. R., P. Moorcroft, and M. A. Lewis. 2006. Mechanistic home range analysis. Princeton University Press, Princeton, NJ, USA.

Morelle, K., F. Lehaire, and P. Lejeune. 2014. Is wild boar heading towards movement ecology? A review of trends and gaps. Wildlife Biology 20:196–205.

Oliveira-Santos, L. G. R., J. D. Forester, U. Piovezan, W. M. Tomas, and F. A. S. Fernandez. 2016. Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology 85:516–524.

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

Senior, A. M., C. E. Grueber, G. Machovsky-Capuska, S. J. Simpson, and D. Raubenheimer. 2016. Macronutritional consequences of food generalism in an invasive mammal, the wild boar. Mammalian Biology 81:523–526.

Seward, N. W., K. C. VerCauteren, G. W. Witmer, and R. M. Engeman. 2004. Feral swine impacts on agriculture and the environment. Sheep & Goat Research Journal 19:34–40.

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.

VerCauteren, K. C., J. J. Mayer, J. C. Beasley, S. S. Ditchkoff, G. J. Roloff, and B. K. Strickland. 2020. Introduction. Pages 1–5 *in* Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Zivin, J., B. M. Hueth, and D. Zilberman. 2000. Managing a multiple-use resource: the case of feral pig management in California rangeland. Journal of Environmental Economics and Management 39:189–204.

CHAPTER 2

CONNECTING THE DOTS: BEHAVIORAL STATE RESOURCE SELECTION IN WILD PIGS IN THE SOUTHEAST UNITED STATES

Clontz, L. M., K. M. Pepin, K. C. VerCauteren, and J. C. Beasley. 2020. To be submitted to *Scientific Reports.*

ABSTRACT

Elucidating correlations between wild pig (*Sus scrofa*) behavior and landscape attributes can aid in the advancement of management strategies for controlling populations. Using GPS data from 49 wild pigs in the southeastern U.S., we used movement characteristics to define behaviors and explore the connection between these behaviors and resource selection for both sexes between two distinct seasons based on forage availability. Females demonstrated a crepuscular activity pattern in the high-forage season and a variable pattern in the low-forage season, while males exhibited nocturnal activity patterns across both seasons. At the population scale, wild pigs selected for areas near streams in both seasons. At the home-range scale, wild pigs selected for bottomland hardwoods and dense canopy cover in all behavioral states in both seasons. Males selected for diversity in vegetation types while foraging in the low-forage season compared to the high-forage season and demonstrated an increased use of linear anthropogenic features across seasons while traveling. Wild pigs can establish populations and home ranges in an array of landscapes, and our results demonstrate male and female pigs exhibit clear differences in movement behavior and there are key resources associated with common behaviors that can be targeted to improve the efficiency of management programs.

KEYWORDS

Behavioral analysis, habitat selection, hidden Markov models, resource selection function, wild pig movement

INTRODUCTION

Understanding how animals move throughout landscapes and interact with heterogeneously distributed resources is critical for management of invasive species because this knowledge provides insight regarding how populations persist and expand, and is thus one of the central goals of ecological research (Wiens et al. 1993, Ellner et al. 2001). Habitat characteristics that meet specific needs for different behavioral states (e.g., resting vs. foraging) of an animal are usually spatially segregated; therefore, investigation of movement patterns and habitat selection at a fine spatial scale can be used to illustrate the asynchrony of the behavioral strategies employed over time (Roever et al. 2014). The observed movement patterns that make up an animal's home range are determined by single movement steps that provide information on the interactions between the individual's external environment and behavioral state (Moorcroft et al. 2006, Boerger et al. 2008). Therefore, this interaction represents an animal's response to the environment (Forester et al. 2007). For example, in heterogeneous landscapes an animal can respond to variable stimuli such as food availability, cover, and water that can change the trajectory of their movement path (Forester et al. 2007). These responses are ultimately the result of a continual decision-making trade-offs every animal has to make about the wide range of competing demands to survive and reproduce (Roever et al. 2014). Understanding these underlying fine-scale interactions (e.g., behavioral) with resources allows managers to predict movements of animals in different landscapes to optimize management planning.

Despite the relevance of these fine-scale behavioral questions to conservation and management goals, behavior-specific resource selection is understudied in most species due to the lack of behavioral context associated with animal location data (Beyer et al. 2010). Animal behaviors, and the driving factors behind these behaviors, are difficult to quantify in the absence of proper data resolution and analytical tools (Patterson et al. 2009). However, continued advancements in global positioning system (GPS) tracking technologies and behavioral analysis techniques provide the ability to estimate behavioral states using movement path characteristics such as turning angles and step-lengths (Franke et al. 2004, Michelot et al. 2016, Leos-Barajas et al. 2017). In particular, hidden Markov models (HMM) allow for the exploration of patterns in movement path characteristics created by underlying behavioral states and estimation of the probabilities of transitioning among the identifiable states (Schick et al. 2008, Patterson et al. 2009, Zucchini et al. 2016). Thus, the application of HMMs to animal relocation data can uncover physiological or behavioral states of tracked individuals, which in turn can be used in a resource selection analysis to infer resource selection associated with identified behaviors.

In the case of an adaptable generalist like invasive wild pigs (*Sus scrofa*), innovative management is critical given the rapid increase in size and distribution of populations throughout their introduced range. In addition, management is important to mitigate the extensive impacts of this species on anthropogenic and natural systems (Beasley et al. 2018, VerCauteren et al. 2020). The correlation between behavior and landscape patterns can inform how unexpected populations emerge in new places and continue to expand their range, as well as help identify areas that may act as hotspots for disease transmission. These are major concerns for wildlife managers since wild pigs have the potential to alter ecosystems across broad spatial scales and have extreme economic impacts (Forester et al. 2007, Barrios-Garcia and Ballari 2012, Beasley et al. 2018, VerCauteren et al. 2020). Like most wild animals, the movement behavior of wild pigs is largely driven by spatio-temporal variation in the distribution of resources throughout the landscape. Wild pigs move deliberately, choosing different resource patches depending on their current needs (rest, forage, mates, etc.) relative to what is available. Their movements also depend on whether or not the tradeoff for accessing these resources is energetically reasonable (Fortin et al. 2005, Forester et al. 2009, Wilber et al. 2020). When targeting these resources for specific behaviors or needs, wild pig movements tend to be methodical, as they often consistently use the same trails and interact with the same areas on the landscape (Hanson and Karstad 1959, Oliveira-Santos et al. 2016). These patterns tend to change at a broad scale with food availability and dietary shifts throughout the year (Mayer 2009); however, there is little to no information regarding how wild pigs change fine-scale resource selection and activity patterns associated with specific behaviors as a result of changing landscape characteristics or food availability. Identifying fine-scale behavioral resource selection and activity patterns of wild pigs can inform more effective and efficient selection and development of site-specific management techniques.

In this study, we estimated population-level resource selection patterns (Second Order; Johnson 1980) of wild pigs across two distinct periods (hereafter ‘seasons’) based on food availability (high- and low-forage availability) in the Southeast U.S. We then used HMM’s to distinguish and define movement patterns into associated behavioral states (e.g., resting, foraging, traveling) of wild pigs. Lastly, we evaluated the relationship between behavioral states and resource selection. We tested the hypothesis that wild pigs exhibit differential resource selection patterns depending on their behavioral state (Third Order; Johnson 1980) and availability of forage resources. We expected females and males to demonstrate different movement patterns throughout the day (i.e., diel patterns) due to differences in reproductive strategies. In addition, we expected these patterns to shift throughout the year based on food availability. Overall, given their association with riparian areas (Singer et al. 1981, Gaston et al. 2008, Gray et al. 2020), we expected behavioral states that aligned with restricted movements (i.e., resting and foraging) to be associated with forested areas proximal to water (i.e., bottomland hardwoods) and areas with greater canopy cover, especially in the warmer and mast- (e.g., acorns) producing months. In contrast, given the heterogeneous distribution of riparian areas throughout our study site, we expected wild pigs would more extensively use upland pines and linear features such as roads while traveling. During low-forage months, we expected wild pigs to be more opportunistic foragers leading to more variable patterns of resource selection while foraging.

METHODS

Study area

Our work was conducted on the Savannah River Site (SRS), a ~800-km^2 site managed by the U.S. Department of Energy (DOE) on the Georgia-South Carolina border (Fig. 2.1). Although established for industrial activities, facilities and infrastructure comprise a small proportion of the landscape, with most of the landscape being managed by the United States Forest Service (USFS) for timber production and wildlife conservation. The SRS was comprised of approximately 50% upland pine including loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), and slash pine (*Pinus* *elliottii*), 25% was bottomland hardwood forest, 10% shrub/herbaceous-dominated areas, 8% upland hardwoods, and the rest was mixed forest, developed, and barren land. Wild pigs have been managed on the SRS since the early 1950s, when an active live-trap-and-removal program was initiated to mitigate damages caused by wild pigs (Mayer et al. 2020*a*). This program is managed by USFS and currently removes ~1,300-1,800 pigs annually (Beasley et al. 2014). Despite this control, there are several thousand wild pigs inhabiting the SRS that are distributed throughout the site (Keiter et al. 2017). Since the SRS was previously used to manufacture nuclear materials and manage nuclear waste (White and Gaines 2000), there is limited public access across the site. The diversity of habitat types of the SRS combined with the limited public access, diversity of other wildlife species present, and high wild pig densities make the site an ideal location to study movement patterns and resource selection of this species.

Field methods

We captured wild pigs throughout the SRS from January 2014 – December 2019 using baited-corral traps equipped with a combination of remote-operated and trip-wire mechanisms. We monitored traps using remote cameras (Reconyx PC900, Holmen, WI, USA) to identify dominant sows to receive GPS collars, as well as all breeding-aged males. We used a dart rifle (X-Caliber, Pneu-Dart Inc., Pennsylvania, USA) to anesthetize captured pigs using a combination of butorphanol [0.077 mg/kg], azaperone [0.026 mg/kg], medetomidine [0.031 mg/kg] (BAM; 0.031 ml/kg; Wildlife Pharmaceuticals Inc., Colorado, USA; Ellis et al. 2019) and Ketamine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., Colorado, USA) or Xylazine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., Colorado, USA) and Telazol (4.4 mg/kg; MWI Veterinary Supply, Idaho, USA). While under anesthesia, we recorded sex and assessed age through examination of tooth eruption (Mayer et al. 2020*b*). We placed uniquely identifiable ear tags in both ears of all captured wild pigs and fit the largest adult female in each sounder (i.e., social unit) and breeding-aged males with an iridium GPS collar (Telonics Gen4 GPS/Iridium System, Telonics, Inc., Mesa, Arizona or VECTRONIC GPS PLUS Globalstar-3, VECTRONIC Aerospace, Coralville, Iowa). Anesthetized wild pigs were allowed to recover at the capture site after being reversed with a combination of Atipamezole (25mg/ml; Wildlife Pharmaceuticals Inc.) and Naltrexone (50 mg/ml; Wildlife Pharmaceuticals Inc., Colorado, USA). Collars were programmed to record GPS locations at 30-minute or one-hour intervals and equipped with a mortality sensor that became activated after 12 hours with no movement by the animal. All capture, handling, and procedures was conducted in compliance with the University of Georgia's Animal Care and Use Committee (Protocols: A2012 08-004, A2015 05-004, and A2018 08-013).

To estimate location error of GPS transmitters, we left a subset of three collars out for 10 days in fixed locations, five days in open vegetation and five days in forest vegetation. We used these data to calculate the average error among fixes for each habitat type.

Identification of movement states

We used HMMs to model the movement characteristics and associated behavioral states of wild pigs for two distinct seasons based on food availability. We considered January through April to represent a low-food availability time period based on dietary preferences of wild pigs (Gray et al. 2020), which also generally represents the peak trapping season in the Southeastern U.S. May through December was considered a high-food availability time period when ample amounts of fruits and plants are available throughout the Spring and Summer months, followed by acorns and other mast in Fall and early Winter. Prior to HMM modeling, we subset data for wild pigs with a 30-minute GPS fix rate to one-hour intervals to maintain an equivalent temporal resolution within our dataset. We also removed any duplicate locations (e.g., same date-time stamp) and locations associated with non-pig movements (e.g., locations after mortality). From collars we were able to retrieve and download, less than 0.01% of locations were 2-Dimensional fixes (i.e., locations collected with three satellites). Therefore, we included all locations regardless of dimensional fix within our dataset to be consistent across all individuals. We also removed the first 48 hours of GPS fixes to account for any potential bias associated with residual anesthetic effects.

We used step-lengths and turning angles as our observational input data in HMMs to differentiate among behaviors. We compared HMM results from 25 different sets of randomly chosen starting values for step-lengths and turning angle distribution parameters for each behavioral state to ensure we were capturing global maximums of the likelihood function (Michelot et al. 2016). In addition, using an array of starting values from parameter distributions ensures that models were numerically stable (Michelot et al. 2016). We tested HMMs with two and three movement states based on model parsimony (Leos-Barajas et al. 2017), but also took into consideration the biological relevance of identified states because model selection criteria sometimes tend to favor models with a greater number of states than makes biological sense (Pohle et al. 2017).

Sex has been found to be an important predictor of wild pig home range size, with males typically having a larger home range and greater movement rates than females

(Kay et al. 2017). Also, wild pigs have demonstrated seasonal differences in home range size and habitat selection based on resource availability (Keuling et al. 2009, Gray et al. 2020, Wilber et al. 2020). Therefore, we expected sex-specific and seasonal-specific differences in the movement parameters (e.g., step-lengths and turning angles) associated with each behavioral state. We also expected differences in transition probabilities among states throughout the diel period, which ultimately adds to the insight of the model when using it to decode states. We ran two and three movement state HMMs separately for males and females in both the low- and high-forage seasons and tested for an additive effect of time of day on the probability of transitioning among states. Therefore, we ran a total of eight HMMs (Table 2.1). We selected the most parsimonious model for both seasons for females and males separately using Akaike Information Criterion (AIC; (Burnham and Anderson 2002)). Next, we decoded the most likely sequence of states to have produced each location in the movement path of each wild pig given the most parsimonious model using the Viterbi algorithm (Zucchini et al. 2016). All computations were done using the moveHMM package (Michelot et al. 2016) in the statistical computing software R 3.6.1 (R Core Team 2019). We partitioned GPS locations into appropriate behavioral states and quantified resource selection for both sexes in each season and behavioral state at the third-order (i.e., home range) spatial scale (Johnson 1980).

Resource selection analyses

Habitat covariates

We generated individual raster layers for four types of vegetative cover from the 2016 National Land Cover Database (NLCD) raster layer (30 x 30 m-resolution; (Jin et al. 2019)) for resource selection analyses: (1) upland pines, (2) bottomland hardwoods, (3) shrub and herbaceous, and (4) upland hardwoods. We also characterized the distribution of streams and roads within our study area from existing SRS geospatial layers. We classified primary roads as those that were paved and routinely used for travel by SRS employees, whereas secondary roads were unpaved gravel and/or logging roads. We used the Euclidean distance tool in ArcGIS 10.7.1 (Environmental System Research Institute, Inc., Redlands, CA, USA) to calculate the distance to each of the habitat covariates for used and available locations to provide a less ambiguous approach compared to a classification or categorical-approach (Conner et al. 2003) (i.e., a location would receive a “0” for the vegetation type it was observed in). Lastly, we used the NLCD 2016 USFS tree canopy cover raster (30 x 30 m-resolution) to estimate the percent canopy cover.

Second order

We selected a 481-km^2 area within the SRS to represent the study area for this analysis. We generated a minimum convex polygon (MCP) around all GPS locations and buffered it by 1.2 km to account for any long distance movements (Fig. 2.2; Kay et al. 2017, Gray et al. 2020). We quantified habitat availability for the population at the second order by systematically sampling the study area (every 3rd pixel, i.e., 90m; available locations). We compared these locations to locations classified as ‘used’ generated by systematically sampling (every 3rd pixel, i.e., 90m; used locations) within a 95% fixed kernel home range for each individual. Uniformly sampling locations across home ranges allows a comprehensive representation of the resources within a home range to compare to the available locations within the study area. We used the adehabitat package with the reference bandwidth (href) smoothing parameter (Calenge 2006) in the statistical computing software R 3.6.1 (R Core Team 2019) to generate and sample all home ranges. We created individual home ranges for both seasons to compare seasonal shifts in home range distribution. We evaluated used locations specific to each individual home range against the same set of available locations throughout the study area for all individuals. We calculated Pearson's correlation coefficients to test for collinearity between each of our habitat covariates (Roever et al. 2014). We then fit a global (i.e., including all habitat covariates) generalized linear model (GLM) with binomial response distribution (logistic regression) and logit link to the used-available data individually for both sexes in both the low-forage and high-forage seasons (Manly et al. 2002, Johnson et al. 2006). This resulted in four comprehensive models representative of second-order resource selection for females and males in the low-forage season and high-forage seasons (Table 2.1). We standardized all variables prior to model development $[(x_i - \bar{x})/s]$ (Table 2.2). We then back-transformed, exponentiated, and raised all distance variable coefficients to the one-hundredth power to represent 100 m increments and canopy cover to the tenth power to represent 10 percent increments for interpretation using predictive odds ratios. We did not use a model selection technique to rank candidate models because a global model included the full set of covariates that were of interest for hypothesis testing and, therefore, allowed a direct comparison between coefficient estimates across sexes and seasons (Kohl et al. 2013). All GLM models were computed using the glm function in R version 3.6.1 (Bates et al. 2014, R Core Team 2019). We assessed how well the second-order model explained the data using area under the receiver-operating characteristic curve (AUC; (Fielding and Bell 1997, Zipkin et al. 2012, Latif et al. 2020)), which we computed using the pROC package in R version 3.6.1 (Robin et al. 2011, R Core Team 2019). A value of 0.5 indicates the model provides predictions that are no better than random predictions, but values greater than 0.7 indicate a better model fit with more accurate predictions (Zipkin et al. 2012).

Third order

To assess fine-scale resource selection of wild pigs, we used a resource selection function (RSF) framework (Manly et al. 2002) to compare resource selection of wild pigs across the three behavioral states associated with the movement path characteristics identified from the HMM (i.e., resting, foraging, and traveling). We quantified habitat availability for individuals at the third order by comparing GPS locations (i.e., used locations) to systematically sampled locations (every 3rd pixel, i.e., 90m; available locations) within home ranges across each of the aforementioned covariates (see above). The sampling framework provided inference on the similarities and differences of wild pig resource selection in three prominent behavioral states that can be extracted to the population level. We used a generalized linear mixed model (GLMM) with binomial response distribution (i.e., used vs. available, logistic regression; Johnson et al. 2006), logit link, and a random intercept to account for variation among individuals (Gillies et al. 2006). We standardized all variables prior to model development $[(x_i - \bar{x})/s]$. We then back-transformed, exponentiated, and raised all distance variable coefficients to the one-hundredth power to represent 100 m increments and canopy cover to the tenth power to represent 10 percent increments for interpretation using predictive odds ratios. All GLMM models were computed using the lme4 package in R version 3.6.1 (Bates et al. 2014, R Core Team 2019).

We calculated Pearson's correlation coefficients to test for collinearity between each of our habitat covariates (Roever et al. 2014). We created a global model including all covariates for each sex in each behavioral state in each season (i.e., 2 sexes*3 behavioral states*2 seasons = 12 RSFs) (Table 2.1). As with our second-order analyses, we did not use a model selection technique, and used AUC to assess how well the model explained the data (Fielding and Bell 1997, Zipkin et al. 2012, Latif et al. 2020).

RESULTS

Identification of movement states

We used a sample of 49 wild pigs tracked between January 2014 and December 2019, resulting in 117,150 validated and cleaned GPS locations (Table 2.3). In the low-forage season (January-April), we tracked 37 wild pigs (21 females, 16 males), resulting in 47,983 GPS locations, and in the high-forage season (May – December) we tracked 41 wild pigs (20 females, 21 males), resulting in 69,177 GPS locations (Table 2.3). From these data, we estimated movement path characteristics (e.g., behavioral states) for 29,433 and 42,277 locations for females during the low- and high-forage seasons, respectively. For males, we had 18,550 locations during the low-forage season and 26,900 during the high-forage season to inform our analyses (Table 2.3). We determined average collar error in forested vegetation to be 22.3 m and in open vegetation to be 11.9 m.

We concluded a three-state HMM with a Gamma distribution for step-length, a wrapped Cauchy distribution for turning angle, and an added covariate of hour in the diel period fit the data of both sexes in both seasons best and provided the most reasonable biological interpretation (Table 2.4). From the three-state HMMs, we identified three general types of movements associated with common behavioral states: (1) a state with short step-lengths and high degrees of turning concentrated around π radians; (2) a state with short to intermediate step-lengths and high degrees of turning concentrated around π radians; and (3) a state with long step-lengths and more straightforward movements with turning concentrated around 0 radians, which likely represents resting, foraging, and traveling behaviors, respectively (Table 2.5; Fig. 2.3, Fig. 2.4).

Male and female wild pigs exhibited clear differences in movement behavior. Specifically, average step-lengths differed between sexes, and males and females exhibited differences in partitioning of behavioral states across the diel period (Fig. 2.5). Males typically traveled farther than females in hour segments (Table 2.3) and demonstrated evident nocturnal activity by traveling mainly throughout the nighttime hours and resting during most of the day (Fig. 2.5). Males also maintained a consistent movement pattern across seasons. In contrast, females exhibited their longest step-lengths in the evening hours around dusk in the low-forage season and had a variable behavioral pattern throughout the remainder of the day. However, in high-forage months females had a crepuscular activity pattern with peak traveling and foraging movements around dawn and dusk (Fig. 2.5). Step-lengths for both sexes were longer during the resting and foraging behaviors in the high-forage season compared to the low-forage season (Table 2.5).

Resource selection

Second Order

Female wild pigs selected all vegetation types (i.e., upland pines, upland hardwoods, bottomland hardwoods, shrub/herbaceous) across our study area in their home-range placement at the second order in both the low and high-forage seasons (Fig. 2.6, Table 2.6), likely reflecting the ubiquitous establishment of wild pigs across the Savannah River Site (Keiter et al. 2017). Females also selected locations closer to streams and avoided areas near roads. In contrast, males in the low-forage season selected home ranges in or near upland pines, shrub/herbaceous vegetation, and bottomland hardwoods (Fig. 2.6). In addition, males selected areas close to streams and primary roads. During the high-forage season, males selected resources similarly to the low-forage season, with the main difference of primary roads no longer being an important driver of home range placement (Fig. 2.6). AUC values in the low-forage season models for females and males were 0.62, 0.66 and in the high-forage season as 0.64, 0.59, respectively.

Third order

During the resting state, female wild pigs in the low-forage season strongly selected areas in or close to bottomland hardwoods and shrub/herbaceous habitats (Fig. 2.7, Table 2.7). For example, there was a 23% decrease in use for every 100 m farther away from bottomland hardwoods, and a there was a 10% decrease in use for every 100 m farther away from shrub and herbaceous habitats. During the high-forage season, female wild pigs selected resting areas similarly to the low-forage season with the addition of a strong selection for upland hardwoods (Table 2.7). Also, the resting model for females in both seasons indicated they avoided areas near secondary roads and streams (Fig. 2.7). Similarly, males selected resting areas in or close to bottomland hardwoods, upland hardwoods, and shrub/herbaceous communities in both seasons. However, males differed between seasons in selecting to rest near streams during the low-forage season but not during the high-forage season. For example, males demonstrated a 5.4% decrease in use for every 100 m farther away from a stream during the low-forage season (Fig. 2.7).

Throughout the foraging state, females differed in relative probability of selection for specific vegetation types and landscape characteristics between the low- and high-forage seasons (Fig. 2.7). For example, females selected areas near primary roads and bottomland hardwoods during the low-forage season, yet during the high-forage season they selected areas near upland hardwoods, upland pines, bottomland hardwoods, and areas near primary roads. Males demonstrated more diversity in selection while foraging in the low-forage season including shrub/herbaceous, bottomland hardwoods, and both secondary and primary roads; however, during the high-forage season, males concentrated foraging in areas near or in bottomland hardwood vegetation (Fig. 2.7). During the high-forage season, males exhibited a 23% decrease in use for every 100 m farther from bottomland hardwoods. In addition, the selection for areas with a high percentage of canopy cover was consistent between sexes and seasons within the foraging behavioral state (Fig. 2.7).

When traveling, resource selection was similar between seasons for females and males. Females selected primary roads and bottomland hardwoods when traveling in both seasons, with the addition of upland hardwoods in the high-forage season (Fig. 2.7). Males selected shrub/herbaceous vegetation, primary and secondary roads, and bottomland hardwoods while traveling in both seasons (Fig. 2.7). For example, in the high-forage season, males displayed a 16% decrease in use for every 100 m farther from secondary roads while traveling (Fig. 2.7).

The AUC values (overall fit for resting, foraging, and traveling behavioral states in low- and high-forage seasons) were 0.81, 0.79, 0.76 and 0.73, 0.75, 0.73 for females and 0.77, 0.80, 0.70 and 0.77, 0.80, 0.74 for males, respectively.

DISCUSSION

Wild pigs are a major agricultural and environmental pest in their invasive range, and managing impacts is often expensive and difficult to implement (VerCauteren et al. 2020). Therefore, acquiring and analyzing movement data at a fine scale provides important insight on when and where damage or disease transmission is likely to occur. This information provides the ability to improve the efficiency and effectiveness of current management strategies. Therefore, using an extensive dataset of wild pig GPS data across a heterogeneous landscape in the Southeastern U.S., here we demonstrate the differential resource selection tactics employed by wild pigs at both broad (i.e., home range placement) and fine (i.e., within-home-range, behavior-specific) spatial scales for males and females across two distinct seasons. Movement path characteristics of wild pigs in our study were influenced by a combination of local and landscape-level habitat attributes such as bottomland and upland hardwoods, streams, secondary roads, and shrub/herbaceous vegetation communities. While males and females tended to select areas to establish home ranges (population scale) similarly, we found notable differences in the fine-scale use of habitats within home ranges between sexes and seasons. However, both males and females selected bottomland hardwood habitats and areas with extensive canopy cover extensively. Further, through the use of step-lengths and turn angles to define behavioral-based resource selection patterns, we found that females and males differed in daily movement patterns. In addition, we found that wild pigs exhibited differential selection of landscape attributes among behavioral states.

Based on the results of our HMM analyses, we distinguished three biologically relevant behavioral states generally based on patterns in the movement characteristics of wild pigs (i.e., resting, foraging, traveling). Previous studies have identified similar patterns for other species (Franke et al. 2004, Pohle et al. 2017, Karelus et al. 2019); however, behavioral states associated with movement characteristics may be assigned differently depending on prior knowledge of different animal species and fix rate at which GPS data were collected. Although wild pigs exhibit several behaviors that correspond to short and intermediate step-lengths and tight turn angles (e.g., resting, wallowing, rubbing, tusking, foraging, etc.), for management purposes of wild pigs classifying behaviors into resting, foraging, and traveling encapsulated the most common and consistent motivations of space use (e.g., forage, cover, thermoregulation; Gray et al. 2020). For example, classifying these dominant behaviors, and understanding that other similar movement-type behaviors are encompassed as well, allows the development of knowledge about where to target certain management strategies or further research.

Both females and males decreased movements or traveling behavior in the mid-day, most likely due to the association with high temperatures in the southeast during the high-forage season (Kay et al. 2017, Gray et al. 2020), and males maintained a consistent nocturnal activity pattern between seasons. However, females exhibited seasonal differences in movement patterns that were likely related to stages of the reproductive cycle throughout the year, as the timing of farrowing is related to the seasonal availability of forage (Comer and Mayer 2009, Snow et al. 2020). In the low-forage season, which corresponded with peak farrowing in our study area (Comer and Mayer 2009; Chinn, unpublished data), females demonstrated a sharp increase in traveling at dusk, an increase in foraging throughout daytime hours, a slight increase in resting mid-day, and a distinct increase in resting throughout nighttime hours. However, during the high-forage season when farrowing rates are lower and juvenile pigs are more mobile, females demonstrated a more crepuscular activity pattern compared to the low-forage season. Pre-parturition and parturition-associated behaviors in some wildlife species, such as wild pigs, are associated with reduced movements and home range sizes (Mayer 2009, Kay et al. 2017). Irregular and/or reduced movements can continue after parturition causing an unusual activity pattern in females (Snow et al. 2020), as we found throughout the low-forage season. While reproduction can make it more difficult to assign behaviors and demonstrate consistent patterns in movements for females, this demonstration of a change in activity patterns across seasons is consistent with previous literature and reveals the rigor of the methods used in this study. Males and females have different reproductive tendencies and responsibilities as a polygamous species (Matiuti et al. 2010) in which males breed multiple females and provide no parental care. Therefore, behavioral differences between sexes likely reflect different reproductive obligations (Snow et al. 2020) and should be a focus for further research, as well as a consideration when designing management plans.

Although wild pigs are an invasive habitat generalist, our approach of evaluating population-scale resource selection in contrast to fine-scale behavioral resource selection revealed wild pigs exhibit differential selection of habitats relative to spatial scale. In areas where wild pigs are abundant, they often occur throughout the landscape, which was reflected in our second-order (i.e., home range placement) analysis as wild pigs established home ranges in areas proximal to streams containing broad availability of most vegetation types present on the landscape. However, although wild pigs are well documented to select for areas near streams (Dexter 1998, Beasley et al. 2014, Gray et al. 2020), here we demonstrate this selection is scale dependent, as neither males or females exhibited focused activity within their home ranges around streams across behavioral states. This difference in selection between spatial scales should be considered when targeting an invasive species for management purposes. The second-order models for males and females did not demonstrate much strength in the AUC evaluation (<0.7); therefore, indicating these models do not fit the data exceptionally well. However, we believe this is due to extensive variation in habitat selection among individuals stemming from the fact that wild pigs are a habitat generalist at the population scale.

Wild pigs can demonstrate multiple behaviors in similar vegetation types (Abrahms et al. 2016), but there are certain habitat characteristics and vegetation types that facilitate specific behaviors (e.g., relocation using roads; Forester et al. 2007). Although wild pigs are ecological generalists, they exhibit spatio-temporal differences in resource selection that reflect underlying biological needs (e.g., thermoregulation; Keuling et al. 2009, Gray et al. 2020). Dense cover and areas proximal to water (i.e., bottomland hardwoods) are two key vegetation characteristics that provide resources that pigs require (Gray et al. 2020), and we found that females and males selected for bottomland hardwoods and areas with high percentages of canopy cover in every behavioral state during the low-forage season. In addition, wild pigs forage on subterranean foods such as roots and tubers when other sources are scarce (Ditchkoff and

Mayer 2009, Ballari and Barrios-García 2014, Gray et al. 2020); therefore, selecting bottomland hardwoods and areas with extensive canopy cover typically coincide with these forage types and provide access to water and cover.

While foraging, males selected for a variety of vegetation types and structures throughout the low-forage season. For example, at the home-range scale males demonstrated a change in selection for primary roads between seasons. In the low-forage season, males selected for areas closer to primary roads in all three behavioral states. Also, males selected for secondary roads in the foraging and traveling states at the home-range scale. The selection for areas near or along both primary and secondary roads while foraging is likely due to the decrease in resources in adjacent natural areas and the consistent availability of grasses along open roadsides during the low-forage season (Ballari and Barrios-García 2014, Lewis et al. 2020). These results coincide with the increase in use of urbanized and anthropogenic areas when natural forage is scarce (Podgórski et al. 2013, Castillo-Contreras et al. 2018). However, the result of wild pigs utilizing roads could shift in other areas that are associated with hunting or shooting pigs on roads. Wild pigs on the SRS are rarely persecuted (i.e., dog hunting, etc.) on roads; therefore, we expect roads are not associated with negative interactions with humans. Lastly, during the resting state females demonstrated selection for shrub and herbaceous vegetation, which was characterized by a mixture of areas in early successional stages and grasslands that both typically occurred together near linear features such as secondary roads, power lines, and streams, while males selected for this vegetation type in every behavioral state. Areas dominated by this vegetation type most likely provided forage, cover, and easy access to linear features when transitioning to traveling in the low-forage season. Therefore, interactions between wild pig behavior and the attributes of vegetation demonstrated in shrub and herbaceous communities in this study allows for the design of a more informed management plan.

During the high-forage season, at the home-range scale males selected for areas closer to secondary roads while traveling but avoided these areas when foraging and resting. Selecting for anthropogenic and natural linear features can help increase an animal’s pace (step-length) and directional movement, which can assist in traversing the landscape quickly when dispersing, searching for a mate, or transitioning between resting and foraging behaviors (Brown et al. 2006, Thurfjell et al. 2009, Gray et al. 2020). Also, males selected primarily for bottomland hardwoods while foraging in the high-forage season, and females selected for upland and bottomland hardwoods during all behavioral states, likely reflecting the availability of food, water, and cover in these habitats (Gray et al. 2020). Selection for bottomland hardwoods is most likely associated with mast producing hardwoods (e.g., oak acorns) and productive plants in the understory throughout summer months, as well as dense cover and proximity to water. Lastly, throughout the high-forage season, males and females avoided streams at the home-range scale, which is likely due to the extensive stream system throughout the SRS and the ability to access dense cover away from streams during times of extreme temperatures. Other studies have demonstrated the insignificance of streams at the home-range scale throughout certain times of the year when water is generally present throughout the landscape (Thurfjell et al. 2009). Unlike the second-order models, the AUC values of all third-order resource selection models were greater than 0.7 indicating good model fits with meaningful predictions.

Wild pigs exhibit substantive behavioral plasticity making them the perfect invasive species (VerCauteren et al. 2020). They can adjust their life history strategies such as daily activity patterns to decrease interaction with humans in populated areas. In addition, wild pigs can adjust their diet throughout the year and in a variety of climatic conditions to benefit their long-term survival depending on local environmental conditions (Podgórski et al. 2013, Senior et al. 2016, Gray et al. 2020, Lyons et al. 2020). Although our study was limited to the SRS in the Southeastern U.S., wild pigs demonstrate consistent selection patterns for vegetation types associated with certain resources (i.e., water, mast, etc.; Graves 1984, Dardaillon 1986, Meriggi and Sacchi 2001, Mayer 2009, Gray et al. 2020). Therefore, our findings are likely applicable in similar areas throughout this species' native and introduced range. Further research, though, should focus on wild pig behavioral state resource selection in other geographic regions to elucidate spatio-temporal differences in wild pig behavior across areas of differing climate and resource base. In addition, due to rapid growth in body weights and associated limitations of collecting long-term GPS data on free-ranging wild pigs, not all individuals within our dataset were represented across both seasons. We recognize comparing different individuals across seasons could influence the overall results but given our robust sample size, any differences due to individual variation likely would be minor and not alter the ultimate management implications of this work.

While our general findings are consistent with previous literature on wild pig habitat selection, through the investigation of fine-scale movement patterns coupled with behavioral-based resource selection we were able to demonstrate pigs exhibit clear differences in temporal patterns of activity and selection of habitats among behavioral states. Thus, delineating GPS observational data into unique behavioral states provides unique insights into the relative importance of environmental attributes critical to the invasion of an ecosystem or management of a species that may otherwise be obscured through more coarse-scale resource selection approaches (Roever et al. 2014).

MANAGEMENT IMPLICATIONS

Accounting for behavior when studying habitat selection can provide more useful and accurate information for managers dealing with an invasive species. Specifically, for wild pigs, understanding the driving forces of resource selection at a fine scale can inform when, where, and how to deploy traps, toxicants, attractants, etc. to ensure visitations occur quickly and consistently (Gray et al. 2020, Pepin et al. 2020), as well as areas to focus mitigation efforts from wild pig damage. In addition, understanding how wild pigs use the landscape can provide an advantage for managers and/or disease biologists when trying to predict areas of high risk for disease transmission. Our results indicated vegetation class and other landscape features all determined habitat use by wild pigs when resting, foraging, and traveling. Therefore, targeting specific vegetation types, features, and times throughout the diel period could provide an advantage for managers when strategically employing specific management techniques in areas where wild pigs would be most vulnerable. For example, to increase efficiency and effectiveness of management techniques such as trapping and toxicant deployment, targeting wild pigs in habitat types they select for during the foraging and/or traveling behavioral states could greatly increase the number of pigs removed during these management processes (Pepin et al. 2020).

LITERATURE CITED

Abrahms, B., N. R. Jordan, K. A. Golabek, J. W. McNutt, A. M. Wilson, and J. S. Brashares. 2016. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. Animal Conservation 19:247–255.

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

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* <http://arxiv.org/abs/1406.5823>. Accessed 6 Jan 2020.

Beasley, J. C., S. S. Ditchkoff, J. J. Mayer, M. D. Smith, and K. C. Vercauteren. 2018. Research priorities for managing invasive wild pigs in North America. The Journal of Wildlife Management 82:674–681.

Beasley, J. C., T. E. Grazia, P. E. Johns, and J. J. Mayer. 2014. Habitats associated with vehicle collisions with wild pigs. Wildlife Research 40:654–660.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use–availability designs. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2245–2254.

Boerger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650.

Brown, G. P., B. L. Phillips, J. K. Webb, and R. Shine. 2006. Toad on the road: use of roads as dispersal corridors by cane toads (Bufo marinus) at an invasion front in tropical Australia. Biological Conservation 133:88–94.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Sociological Methods & Research 33:261–304.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Castillo-Contreras, R., J. Carvalho, E. Serrano, G. Mentaberre, X. Fernández-Aguilar, A. Colom, C. González-Crespo, S. Lavín, and J. R. López-Olvera. 2018. Urban wild boars prefer fragmented areas with food resources near natural corridors. Science of The Total Environment 615:282–288.

Comer, C. E., and J. J. Mayer. 2009. Wild pigs: biology, damage, control techniques and management. 1–408.

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

Dardaillon, M. 1986. Seasonal variations in habitat selection and spatial distribution of wild boar (Sus Scrofa) in the Camargue, Southern France. Behavioural Processes 13:251–268.

Dexter, N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. Wildlife Research 25:547–559.

Ditchkoff, S. S., and J. J. Mayer. 2009. Wild pig food habits. Pages 105–143 *in*. Wild pigs: biology, damage, control techniques and management. Savannah River Nuclear Solutions LLC, Savannah River Site Aiken, SC, USA.

Ellis, C. K., M. E. Wehtje, L. L. Wolfe, P. L. Wolff, C. D. Hilton, M. C. Fisher, S. Green, M. P. Glow, J. M. Halseth, M. J. Lavelle, N. P. Snow, E. H. VanNatta, J. C. Rhyan, K. C. VerCauteren, W. R. Lance, and P. Nol. 2019. Comparison of the efficacy of four drug combinations for immobilization of wild pigs. European Journal of Wildlife Research 65:78.

Ellner, S. P., E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, and W. W. Murdoch. 2001. Habitat structure and population persistence in an experimental community. Nature 412:538–543.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State–space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Franke, A., T. Caelli, and R. J. Hudson. 2004. Analysis of movements and behavior of caribou (Rangifer tarandus) using hidden Markov models. Ecological Modelling 173:259–270.

Gaston, W., J. 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. <https://digitalcommons.unl.edu/feralhog/6>.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

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

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*. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Hanson, R. P., and L. Karstad. 1959. Feral swine in the southeastern United States. The Journal of Wildlife Management 23:64.

Jin, S., C. Homer, L. Yang, P. Danielson, J. Dewitz, C. Li, Z. Zhu, G. Xian, and D. Howard. 2019. Overall methodology design for the United States national land cover database 2016 products. Remote Sensing 11:2–32.

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. The Journal of Wildlife Management 70:347–357.

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

Karelus, D. L., J. W. McCown, B. K. Scheick, M. van de Kerk, B. M. Bolker, and M. K. Oli. 2019. Incorporating movement patterns to discern habitat selection: black bears as a case study. Wildlife Research 46:76–88.

Kay, S. L., J. W. Fischer, 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. <http://proxy-remote.galib.uga.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edswsc&AN=000403549100001&site=eds-live>.

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

Keuling, O., N. Stier, and M. Roth. 2009. Annual and seasonal space use of different age classes of female wild boar Sus scrofa L. European Journal of Wildlife Research 54:403–412.

Kohl, M. T., P. R. Krausman, K. Kunkel, and D. M. Williams. 2013. Bison versus cattle: are they ecologically synonymous? Rangeland Ecology & Management 66:721–731.

Latif, Q. S., V. A. Saab, J. G. Dudley, A. Markus, and K. Mellen-McLean. 2020. Development and evaluation of habitat suitability models for nesting white-headed woodpecker (Dryobates albolarvatus) in burned forest. PLoS One; San Francisco 15:e0233043.

Leos-Barajas, V., E. J. Gangloff, T. Adam, R. Langrock, F. M. van Beest, J. Nabe-Nielsen, and J. M. Morales. 2017. Multi-scale modeling of animal movement and general behavior data using hidden markov models with hierarchical structures. Journal of Agricultural, Biological and Environmental Statistics 22:232–248.

Lewis, J. S., K. C. VerCauteren, R. M. Denkhaus, and J. J. Mayer. 2020. Wild pig populations along the urban gradient. Pages 439–464 *in*. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Lyons, P. C., K. Okuda, M. T. Hamilton, T. G. Hinton, and J. C. Beasley. 2020. Rewilding of Fukushima’s human evacuation zone. Frontiers in Ecology and the Environment 18:127–134.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection functions from logistic regression. Pages 83–110 *in*.

Resource selection by animals: statistical analysis and design for field studies. Kluwer Academic Publishers, Nordrecht, The Netherlands.

Matiuti, M., A. T. Bogdan, E. Crainiceanu, and C. Matiuti. 2010. Research regarding the hybrids resulted from the domestic pig and the wild boar. Scientific Papers: Animal Science and Biotechnologies 43:188-191.

Mayer, J. J. 2009. Wild pig behavior. Page 408 *in*. Wild pigs: biology, damage, control techniques and management.

Mayer, J. J., J. C. Beasley, R. Boughton, and S. S. Ditchkoff. 2020a. Wild Pigs in the southeastern North America. Pages 369–402 *in.* Invasive Wild Pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA.

Mayer, J. J., T. J. Smyser, A. J. Piaggio, and S. M. Zervanos. 2020b. Wild pig taxonomy, morphology, genetics, and physiology. Pages 7–32 *in.* Invasive Wild Pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA.

Meriggi, A., and O. Sacchi. 2001. Habitat requirements of wild boars in the northern Apennines (N Italy): A multi-level approach. Italian Journal of Zoology 68:47–55.

Michelot, T., R. Langrock, and T. Patterson. 2016. moveHMM: An R package for the analysis of animal movement data. 7:20.

Moorcroft, P. R., P. Moorcroft, and M. A. Lewis. 2006. Mechanistic home range analysis. Princeton University Press.

Oliveira-Santos, L. G. R., J. D. Forester, U. Piovezan, W. M. Tomas, and F. A. S. Fernandez. 2016. Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology 85:516–524.

Patterson, T. A., M. Basson, M. V. Bravington, and J. S. Gunn. 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. Journal of Animal Ecology 78:1113–1123.

Pepin, K. M., N. P. Snow, and K. C. VerCauteren. 2020. Optimal bait density for delivery of acute toxicants to vertebrate pests. Journal of Pest Science 93:723–735.

Podgórski, T., G. Baś, B. Jędrzejewska, L. Sönnichsen, S. Śnieżko, W. Jędrzejewski, and H. Okarma. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. Journal of Mammalogy 94:109–119.

Pohle, J., R. Langrock, F. M. van Beest, and N. M. Schmidt. 2017. Selecting the number of states in hidden markov models: pragmatic solutions illustrated using animal movement. Journal of Agricultural, Biological and Environmental Statistics 22:270–293.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J.-C. Sanchez, and M. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77.

Roever, C. L., H. L. Beyer, M. J. Chase, and R. J. van Aarde. 2014. The pitfalls of ignoring behaviour when quantifying habitat selection. Diversity and Distributions 20:322–333.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338–1350.

Senior, A. M., C. E. Grueber, G. Machovsky-Capuska, S. J. Simpson, and D. Raubenheimer. 2016. Macronutritional consequences of food generalism in an invasive mammal, the wild boar. Mammalian Biology 81:523–526.

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.

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

Thurfjell, H., J. P. Ball, P.-A. Åhlén, P. Kornacher, H. Dettki, and K. Sjöberg. 2009. Habitat use and spatial patterns of wild boar Sus scrofa (L.): agricultural fields and edges. European Journal of Wildlife Research 55:517–523.

VerCauteren, K. C., J. J. Mayer, J. C. Beasley, S. S. Ditchkoff, G. J. Roloff, and B. K. Strickland. 2020. Introduction. Pages 1–5 *in*. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

White, D. L., and K. F. Gaines. 2000. The savannah river site: site description, land use and management history. 8–17.

Wiens, J. A., N. Chr. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological Mechanisms and Landscape Ecology. Oikos 66:369–380.

Wilber, M. Q., S. M. Chinn, J. C. Beasley, R. K. Boughton, R. K. Brook, S. S. Ditchkoff, J. W. Fischer, S. B. Hartley, L. K. Holmstrom, J. C. Kilgo, J. S. Lewis, R. S. Miller, N. P. Snow, K. C. VerCauteren, S. M. Wisely, C. T. Webb, and K. M. Pepin. 2020. Predicting functional responses in agro-ecosystems from animal movement data to improve management of invasive pests. Ecological Applications 30:e02015.

Zipkin, E. F., E. H. C. Grant, and W. F. Fagan. 2012. Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. Ecological Applications 22:1962–1972.

Zucchini, W., I. L. MacDonald, R. Langrock, I. L. MacDonald, and R. Langrock. 2016. Hidden markov models for time series : an introduction using R, second edition. Chapman and Hall/CRC. <http://www.taylorfrancis.com/books/9781315372488>. Accessed 18 Feb 2020.

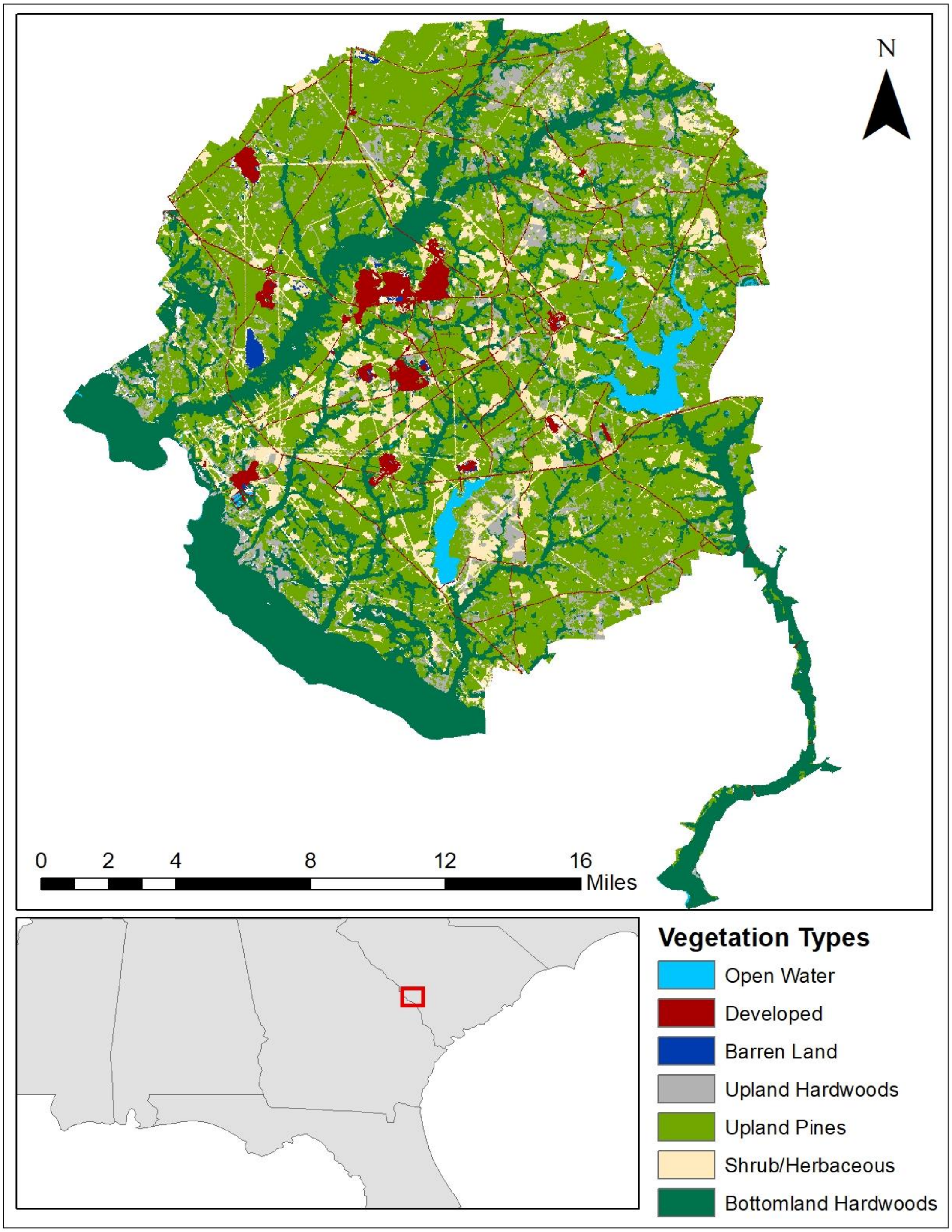

Figure 2.1. Study area with distinct vegetative communities used to develop hidden Markov models and third-order resource selection functions of male and female wild pigs (*Sus scrofa*) during two distinct seasons (i.e., low-forage and high forage) between Janurary 2014 – December 2019 in South Carolina, USA.

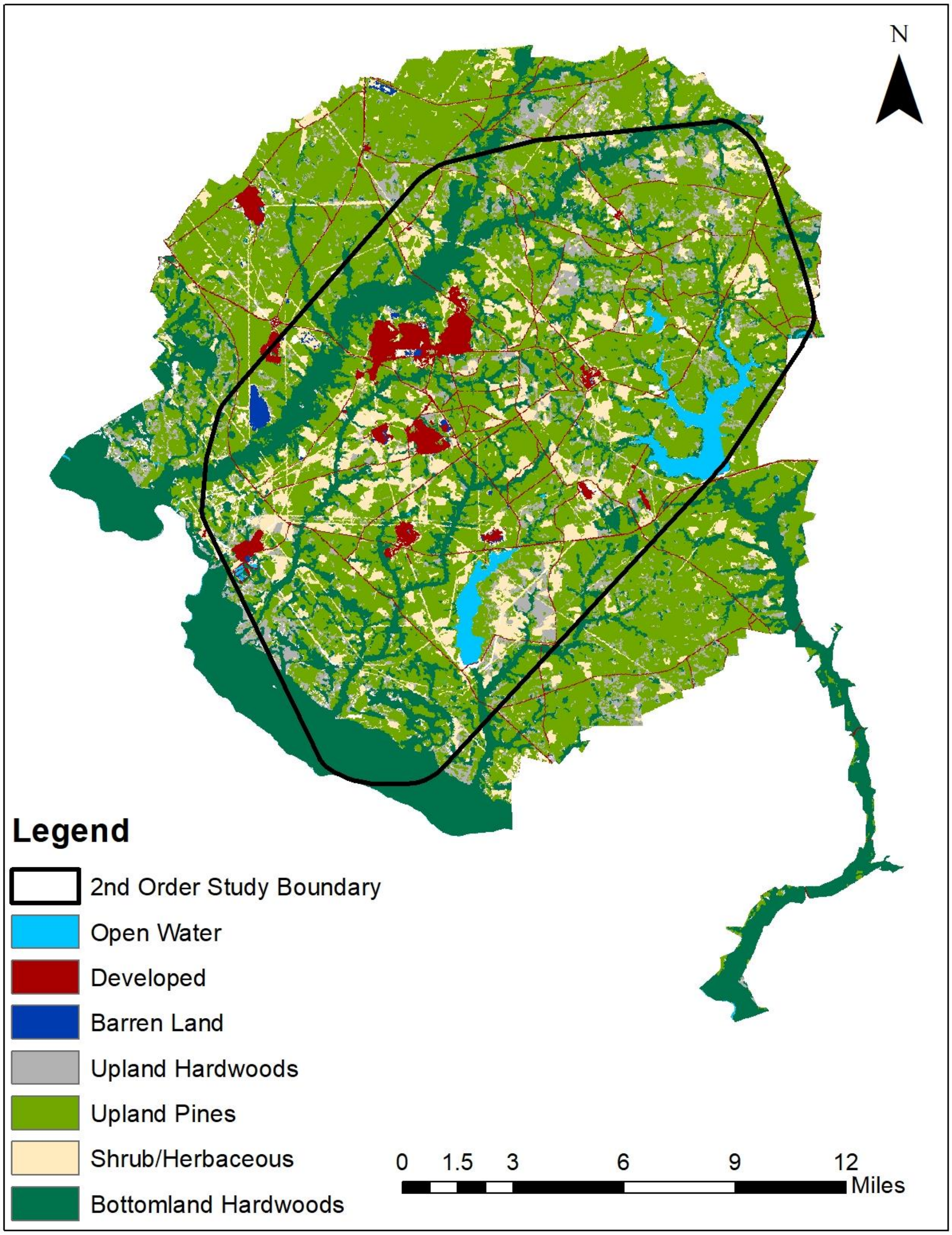

Figure 2.2. Overall study area with distinct vegetative communities and the 1.2 km^2 polygon representing the specified area used to develop available locations for second-order resource selection functions of male and female wild pigs (*Sus scrofa*) during two distinct seasons (i.e., low-forage and high forage) between Janurary 2014 – December 2019 in South Carolina, USA.

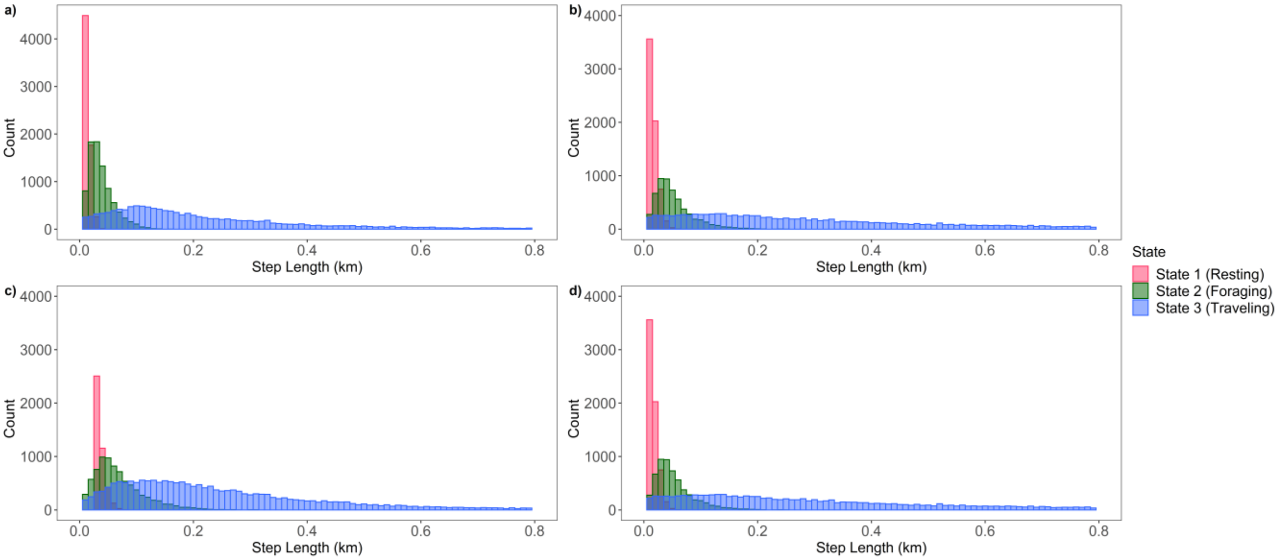

Figure 2.3. Step-length parameter distributions from three-state hidden Markov models (HMMs) for wild pigs (*Sus scrofa*) in the Southeast USA by sex and season: (a) females in low-forage months (January – April); (b) males in low-forage months; (c) females in high-forage months (May – December); (d) males in high-forage months.

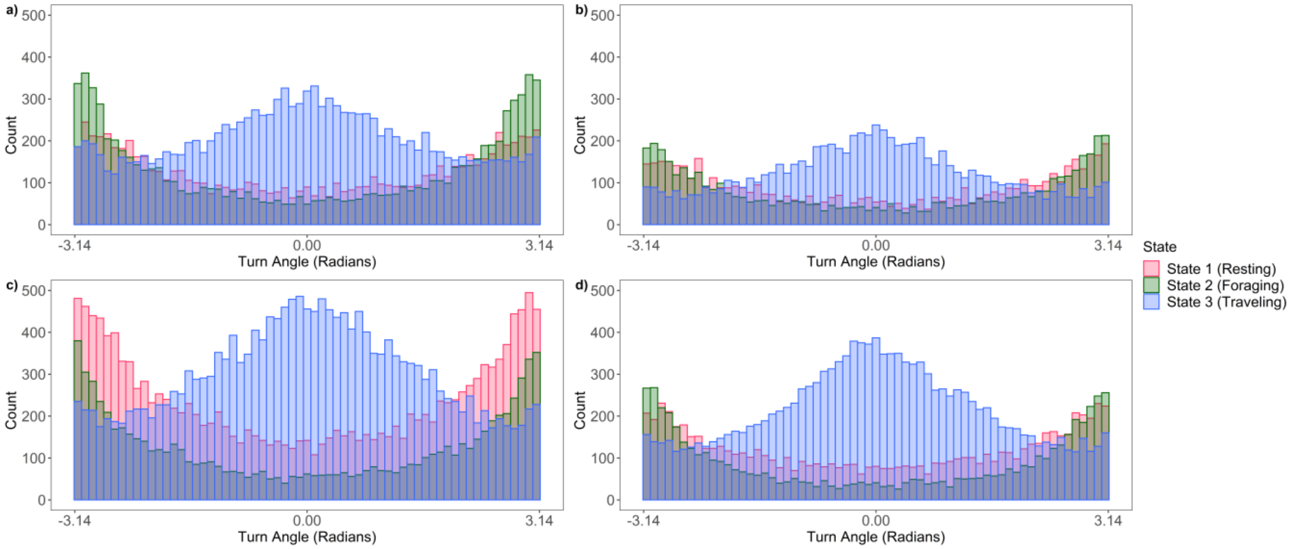

Figure 2.4. Turn angle parameter distributions from three-state hidden Markov models (HMMs) for wild pigs (*Sus scrofa*) in the Southeast USA by sex and season: (a) females in low-forage months (January – April); (b) males in low-forage months; (c) females in high-forage months (May – December); (d) males in high-forage months.

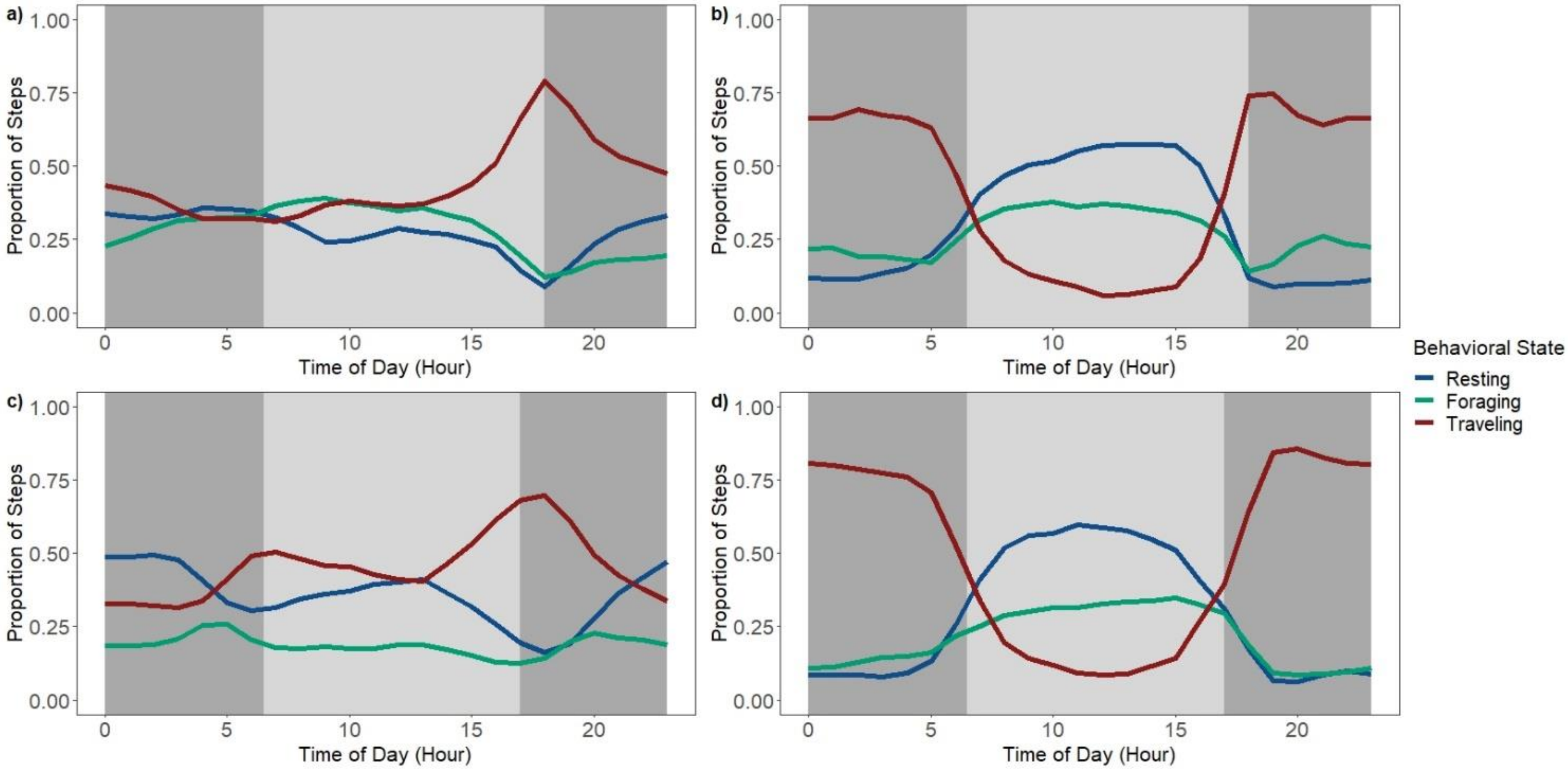

Figure 2.5. Proportion of steps per hour for each behavioral state of wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina by sex and season: (a) females in low-forage months (January – April); (b) males in low-forage months; (c) females in high-forage months (May – December); (d) males in high-forage months. The dark gray bars represent average nighttime hours while the light gray bar represents the average daytime hours.

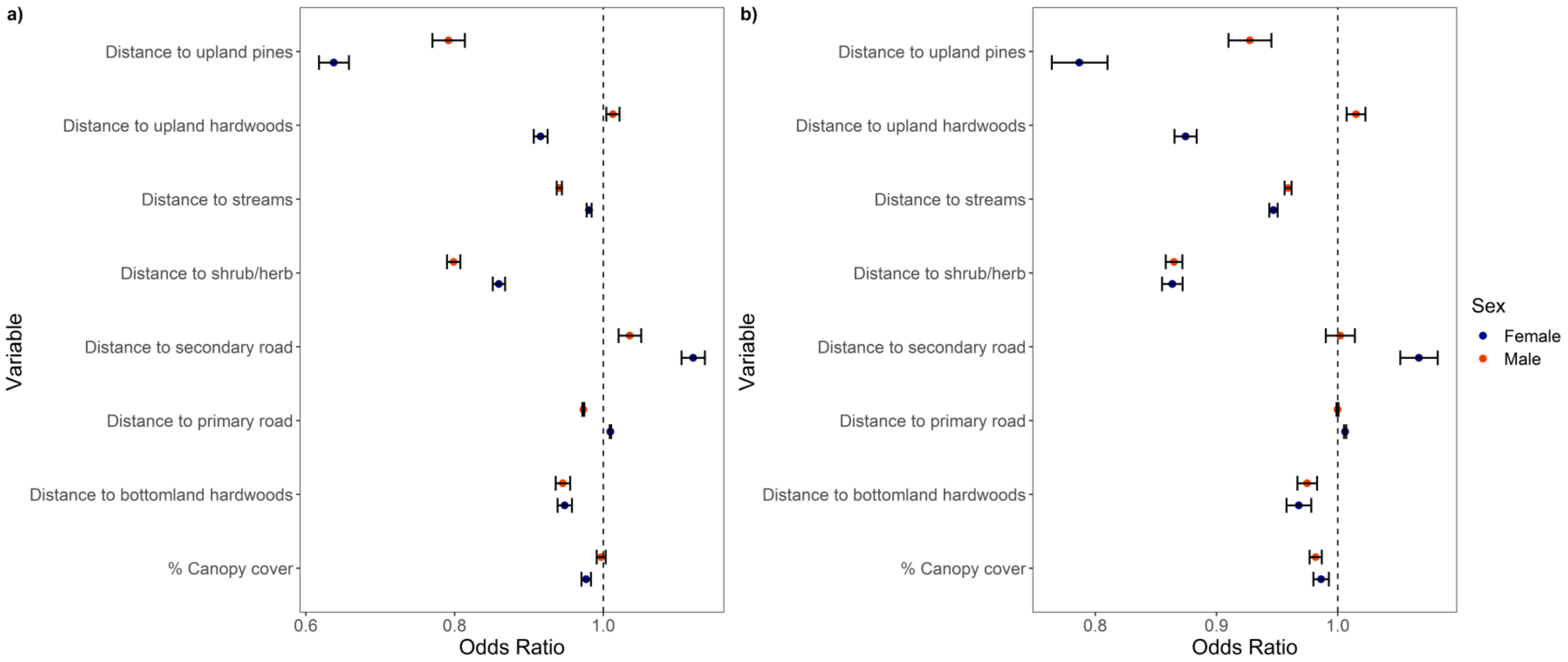

Figure 2.6. Predictive odds with 95% confidence intervals for second-order selection (Johnson 1980) of female and male wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability, (a) low-forage availability (January – April) and (b) high-forage availability (May – December), for every 100 m increase for distance variables and every 10% increase for canopy cover. In cases where the confidence interval crosses 1, the variable is considered not significant.

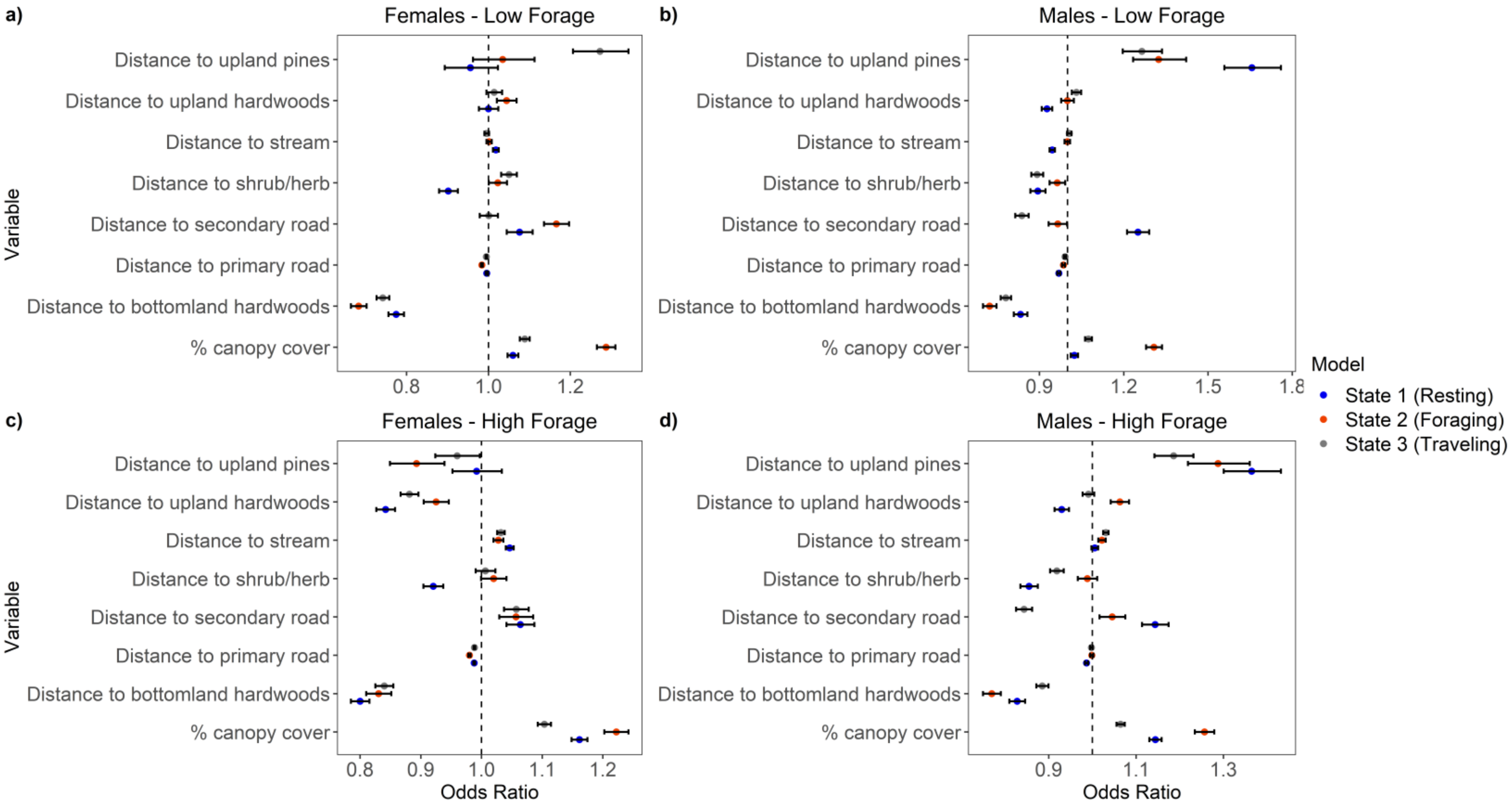

Figure 2.7. Predictive odds with 95% confidence intervals of third-order selection of male and female wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability (i.e., low-forage season (January – April) and the high-forage season (May – December)). It demonstrates selection or avoidance of vegetation types, streams, and characteristics of development (e.g., roads) for every 100 m increase and canopy cover for every 10% increase by state where states represent resting, foraging, and traveling behaviors, respectively: (a) Females in low-forage months (January – April); (b) males in low-forage months; (c) females in high-forage months (May – December); (d) males in high-forage months. In cases where the confidence interval crosses 1, the variable is considered not significant.

Table 2.1. A demonstration of all models ran for female and male wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability, low-forage availability (January – April) and high-forage availability (May – December) separated by type including: (a) hidden Markov models, (b) second-order resource selection functions, and (c) third-order resource selection functions.

(a)

Model	Sex	Season	Covariates
2-State	Female	Low-Forage	Time of Day (Hour)
2-State	Male	Low-Forage	Time of Day (Hour)
3-State	Female	Low-Forage	Time of Day (Hour)
3-State	Male	Low-Forage	Time of Day (Hour)
2-State	Female	High-Forage	Time of Day (Hour)
2-State	Male	High-Forage	Time of Day (Hour)
3-State	Female	High-Forage	Time of Day (Hour)
3-State	Male	High-Forage	Time of Day (Hour)

(b)

Model	Sex	Season	Covariates
2nd Order RSF	Female	Low-Forage	All[a]
2nd Order RSF	Male	Low-Forage	All[a]
2nd Order RSF	Female	High-Forage	All[a]
2nd Order RSF	Male	High-Forage	All[a]

(c)

Model	Sex	Season	Covariates
Resting	Female	Low-Forage	All[a]
Foraging	Female	Low-Forage	All[a]
Traveling	Female	Low-Forage	All[a]
Resting	Male	Low-Forage	All[a]
Foraging	Male	Low-Forage	All[a]
Traveling	Male	Low-Forage	All[a]
Resting	Female	High-Forage	All[a]
Foraging	Female	High-Forage	All[a]
Traveling	Female	High-Forage	All[a]
Resting	Male	High-Forage	All[a]
Foraging	Male	High-Forage	All[a]
Traveling	Male	High-Forage	All[a]

[a] All covariates includes distance to upland pines, distance to upland hardwoods, distance to streams, distance to shrub/herb, distance to secondary road, distance to primary road, distance to bottomland hardwoods, and percent canopy cover.

Table 2.2. Standardized metrics for all covariates in both second and third-order resource selection analyses of male and female wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability (i.e., low-forage availability (January – April) and high-forage availability (May – December)).

Analysis	Season	Variable	mean	sd	min	max
2nd Order RSF	Low-Forage	Distance to Stream	643.36	472.07	0.00	2670.67
		Distance to Primary Road	1573.54	1654.22	0.00	8669.38
		Distance to Secondary Road	146.82	164.75	0.00	2373.60
		Distance to Upland Hardwoods	206.16	198.73	0.00	2315.25
		Distance to Upland Pines	53.18	139.72	0.00	2296.52
		Distance to Shrub/Herb	207.11	266.24	0.00	2991.74
		Distance to Bottomland Hardwood	173.35	168.13	0.00	1259.29
		% Canopy Cover	69.95	29.54	0.00	100.00
2nd Order RSF	High-Forage	Distance to Stream	631.18	467.46	0.00	2618.43
		Distance to Primary Road	1634.48	1732.57	0.00	8668.29
		Distance to Secondary Road	145.60	161.55	0.00	2363.15
		Distance to Upland Hardwoods	204.78	197.48	0.00	2310.00
		Distance to Upland Pines	55.09	137.03	0.00	2303.76
		Distance to Shrub/Herb	207.49	262.16	0.00	2978.93
		Distance to Bottomland Hardwood	174.69	170.90	0.00	1288.60
		% Canopy Cover	69.33	30.05	0.00	100.00
3rd Order RSF	Low-Forage	Distance to Stream	576.04	482.41	0.00	2241.99
		Distance to Primary Road	1311.39	1414.48	0.00	7956.11
		Distance to Secondary Road	136.29	110.36	0.00	778.27
		Distance to Upland Hardwoods	187.87	159.81	0.00	1209.34
		Distance to Upland Pines	37.99	53.27	0.00	536.66
		Distance to Shrub/Herb	157.64	141.89	0.00	800.50
		Distance to Bottomland Hardwood	140.55	149.17	0.00	953.41
		% Canopy Cover	72.27	29.18	0.00	100.00
3rd Order RSF	High-Forage	Distance to Stream	596.38	484.95	0.00	2278.82
		Distance to Primary Road	1480.70	1615.76	0.00	7865.55
		Distance to Secondary Road	136.41	116.31	0.00	1140.39

	Distance to Upland Hardwoods	177.18	158.12	0.00	1273.50
	Distance to Upland Pines	40.01	66.07	0.00	1087.06
	Distance to Shrub/Herb	172.38	160.00	0.00	1766.95
	Distance to Bottomland Hardwood	146.99	155.12	0.00	1005.78
	% Canopy Cover	72.78	28.06	0.00	100.00

Table 2.3 Summary of global positioning system (GPS) information, average step-lengths (± SE of the mean parameter) and turning angles of female and male wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina based on GPS locations from January 2014 – December 2019.

Sex	**Months (Season)**	**Number of Pigs**	**Number of Locations**	**Mean Number ± SE of Locations**	**Range of Locations per Individual**	**Avg. Step-length ± SE (m)**	**Avg. Turning Angle (radians)**
Females	January - April	21	29433	1401.57 ± 137.97	240 - 2987	124.32 ± 1.23	1.72 ± 0.006
	May - December	20	42277	2113.85 ± 360.46	432 - 5843	144.97 ± 1.06	1.68 ± 0.005
Males	January - April	16	18550	1159.38 ± 174.59	328 - 2232	186.01 ± 2.36	1.67 ± 0.007
	May - December	21	26900	1280.95 ± 276.67	239 - 4263	229.18 ± 2.31	1.62 ± 0.006

Table 2.4. Model selection results for (a) female wild pigs in the low-forage season, (b) female wild pigs in the high-forage season, (c) male wild pigs in the low-forage season, and (d) male wild pigs in the high-forage season from hidden Markov models (HMMs) testing for the number of movement states and additive effect of time of day on the transition probabilities among movement states. Only two and three states were tested because we did not see a biologically significant benefit to discern a fourth behavioral state for the purpose of this paper.

(a)

Rank	**Model**	**ΔLogLik**	**ΔAIC**	**Weight**
1	3 State: Hour	0.00	0.00	1.00
2	3 State: Null	202.31	380.61	0.00
3	2 State: Hour	1333.04	2632.08	0.00
4	2 State: Null	1501.39	2960.77	0.00

(b)

Rank	**Model**	**ΔLogLik**	**ΔAIC**	**Weight**
1	3 State: Hour	0.00	0.00	1.00
2	3 State: Null	211.36	398.72	0.00
3	2 State: Hour	1642.37	3250.73	0.00
4	2 State: Null	1747.69	3453.38	0.00

(c)

Rank	**Model**	**ΔLogLik**	**ΔAIC**	**Weight**
1	3 State: Hour	0.00	0.00	1.00
2	3 State: Null	827.61	1631.22	0.00
3	2 State: Hour	1823.26	3608.52	0.00
4	2 State: Null	1875.66	3709.33	0.00

(d)

Rank	**Model**	**ΔLogLik**	**ΔAIC**	**Weight**
1	3 State: Hour	0.00	0.00	1.00
2	3 State: Null	1400.02	2776.03	0.00
3	2 State: Hour	2442.18	4846.36	0.00
4	2 State: Null	2582.5	5122.99	0.00

Table 2.5. Average step-lengths (± SE) and turning angles for each designated behavioral state by sex in the 3-state HMMs with the additive effect of hour of day of wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina based on GPS locations from two distinct seasons based on forage availability (i.e., low-forage availability (January – April) and high-forage availability (May – December)).

	January - April			**May - December**		
Mean Parameters - Females						
	Resting	**Foraging**	**Traveling**	**Resting**	**Foraging**	**Traveling**
Average Step-lengths ± SE (m)	11.4 ± 7.38	37.70 ± 23.24	244.30 ± 220.97	19.25 ± 13.08	67.29 ± 48.32	276.62 ± 227.91
Average Turn Angles (radians)	3.14	3.11	0.001	-3.11	3.14	0.07
Mean Parameters - Males						
Average Step-lengths ± SE (m)	9.68 ± 6.31	33.00 ± 23.11	398.43 ± 385.81	14.27 ± 9.56	52.46 ± 34.67	420.70 ± 406.12
Average Turn Angles (radians)	-3.12	-3.12	-0.04	3.11	3.13	0.02

Table 2.6. Standardized coefficient estimates (±SE) and 95% confidence intervals for second-order selection (population-level) of male and female wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability (i.e., low-forage availability (January – April) and high-forage availability (May – December)).

Season	**Sex**	**Variable**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
Low-Forage	Female	Distance to upland hardwoods	-0.1749 ± 0.0102	-0.1950	-0.1550
		Distance to upland pines	-0.6287 ± 0.0225	-0.6730	-0.5848
		Distance to shrub/herb	-0.4026 ± 0.0131	-0.4286	-0.3771
		Distance to streams	-0.0911 ± 0.0082	-0.1071	-0.0752
		Distance to primary road	0.1573 ± 0.0077	0.1422	0.1723
		Distance to Secondary road	0.1879 ± 0.0118	0.1649	0.2110
		% Canopy cover	-0.0687 ± 0.0098	-0.0879	-0.0496
		Distance to bottomland hardwoods	-0.0896 ± 0.0088	-0.1068	-0.0724
Low-Forage	Male	Distance to upland hardwoods	-0.2649 ± 0.0106	-0.2857	-0.2441
		Distance to upland pines	-0.3284 ± 0.0204	-0.3685	-0.2886
		Distance to shrub/herb	-0.3846 ± 0.0131	-0.4103	-0.3590
		Distance to streams	-0.2546 ± 0.0088	-0.2718	-0.2374
		Distance to primary road	0.1055 ± 0.0082	0.0894	0.1215
		Distance to Secondary road	0.1047 ± 0.0119	0.0813	0.1281
		% Canopy cover	-0.0415 ± 0.0099	-0.0608	-0.0221
		Distance to bottomland hardwoods	-0.056 ± 0.0092	-0.0737	-0.0378
High-Forage	Female	Distance to upland hardwoods	0.0255 ± 0.0089	0.0080	0.0429
		Distance to upland pines	-0.3261 ± 0.0197	-0.3649	-0.2876
		Distance to shrub/herb	-0.5983 ± 0.0151	-0.6281	-0.5687
		Distance to streams	-0.2878 ± 0.0091	-0.3057	-0.2701
		Distance to primary road	-0.4510 ± 0.0109	-0.4725	-0.4296
		Distance to Secondary road	0.0577 ± 0.0123	0.0335	0.0819
		% Canopy cover	-0.0084 ± 0.0091	-0.0262	0.0095
		Distance to bottomland hardwoods	-0.0941 ± 0.0088	-0.1114	-0.0768

High-Forage	Male	Distance to upland hardwoods	0.0295 ± 0.0077	0.0145	0.0447
		Distance to upland pines	-0.1031 ± 0.0133	-0.1293	-0.0771
		Distance to shrub/herb	-0.3803 ± 0.0106	-0.4012	-0.3595
		Distance to streams	-0.1955 ± 0.0072	-0.2096	-0.1814
		Distance to primary road	-0.0034 ± 0.0075	-0.0181	0.0112
		Distance to Secondary road	0.0034 ± 0.0099	-0.0160	0.0228
		% Canopy cover	-0.055 ± 0.0078	-0.0704	-0.0397
		Distance to bottomland hardwoods	-0.044 ± 0.0073	-0.0578	-0.0293

Table 2.7. Standardized coefficient estimates (±SE) and 95% confidence intervals for third-order selection (behavioral state) of male and female wild pigs (*Sus scrofa*) on the Savannah River Site in South Carolina during two distinct seasons based on forage availability (i.e., low-forage availability (January – April) and high-forage availability (May – December)).

Model	**Season**	**Sex**	**Variable**	**Estimate ± SE**	**Lower 95% CI**	**Upper 95% CI**
Resting (State 1)	Low-Forage	Female	Distance to upland hardwoods	0.0003 ± 0.0195	-0.0379	0.0385
			Distance to upland pines	-0.0240 ± 0.0185	-0.0601	0.0122
			Distance to shrub/herb	-0.1462 ± 0.0184	-0.1823	-0.1102
			Distance to stream	0.0870 ± 0.0171	0.0535	0.1204
			Distance to primary road	-0.0586 ± 0.0193	-0.0964	-0.0208
			Distance to secondary road	0.0807 ± 0.0166	0.0481	0.1133
			% canopy cover	0.1693 ± 0.0185	0.1330	0.2057
			Distance to bottomland hardwoods	-0.3808 ± 0.0187	-0.4174	-0.3442
Foraging (State 2)	Low-Forage	Female	Distance to upland hardwoods	0.0693 ± 0.0188	0.0324	0.1062
			Distance to upland pines	0.0182 ± 0.0197	-0.0205	0.0568
			Distance to shrub/herb	0.0319 ± 0.0157	0.0012	0.0627
			Distance to stream	0.0075 ± 0.0161	-0.0240	0.0390
			Distance to primary road	-0.2293 ± 0.0173	-0.2631	-0.1954
			Distance to secondary road	0.1693 ± 0.0148	0.1402	0.1984
			% canopy cover	0.7363 ± 0.0261	0.6852	0.7874
			Distance to bottomland hardwoods	-0.5683 ± 0.0213	-0.6099	-0.5266
Traveling (State 3)	Low-Forage	Female	Distance to upland hardwoods	0.0224 ± 0.0152	-0.0075	0.0523
			Distance to upland pines	0.1283 ± 0.0145	0.0999	0.1567
			Distance to shrub/herb	0.0694 ± 0.0132	0.0434	0.0953

			Distance to stream	-0.0205 ± 0.0139	-0.0477	0.0067
			Distance to primary road	-0.0712 ± 0.0136	-0.0979	-0.0445
			Distance to secondary road	0.0007 ± 0.0125	-0.0237	0.0251
			% canopy cover	0.2479 ± 0.0164	0.2156	0.2801
			Distance to bottomland hardwoods	-0.4449 ± 0.0158	-0.4759	-0.4139
Resting (State 1)	Low-Forage	Male	Distance to upland hardwoods	-0.1216 ± 0.0165	-0.1540	-0.0893
			Distance to upland pines	0.2687 ± 0.0165	0.2364	0.3011
			Distance to shrub/herb	-0.1592 ± 0.0218	-0.2018	-0.1165
			Distance to stream	-0.2701 ± 0.0248	-0.3188	-0.2214
			Distance to primary road	-0.4467 ± 0.0413	-0.5277	-0.3657
			Distance to secondary road	0.2468 ± 0.0177	0.2121	0.2815
			% canopy cover	0.0697 ± 0.0187	0.0331	0.1063
			Distance to bottomland hardwoods	-0.2738 ± 0.0221	-0.3171	-0.2305
Foraging (State 2)	Low-Forage	Male	Distance to upland hardwoods	-0.0008 ± 0.0185	-0.0370	0.0353
			Distance to upland pines	0.1496 ± 0.0194	0.1117	0.1876
			Distance to shrub/herb	-0.053 ± 0.0210	-0.0943	-0.0120
			Distance to stream	-0.004 ± 0.0240	-0.0514	0.0426
			Distance to primary road	-0.2104 ± 0.0389	-0.2866	-0.1342
			Distance to secondary road	-0.0393 ± 0.0192	-0.0769	-0.0017
			% canopy cover	0.7822 ± 0.0322	0.7192	0.8453
			Distance to bottomland hardwoods	-0.4846 ± 0.0255	-0.5345	-0.4347
Traveling (State 3)	Low-Forage	Male	Distance to upland hardwoods	0.0498 ± 0.0130	0.0244	0.0752
			Distance to upland pines	0.1250 ± 0.0150	0.0955	0.1544

			Distance to shrub/herb	-0.1626 ± 0.0172	-0.1962	-0.1289
			Distance to stream	0.0292 ± 0.0196	-0.0093	0.0676
			Distance to primary road	-0.1294 ± 0.0308	-0.1897	-0.0691
			Distance to secondary road	-0.1961 ± 0.0160	-0.2275	-0.1647
			% canopy cover	0.2095 ± 0.0168	0.1765	0.2425
			Distance to bottomland hardwoods	-0.3702 ± 0.0179	-0.4053	-0.3351
Resting (State 1)	High-Forage	Female	Distance to upland hardwoods	-0.3794 ± 0.1907	-0.7532	-0.0057
			Distance to upland pines	-0.2719 ± 0.0148	-0.3009	-0.2429
			Distance to shrub/herb	-0.0053 ± 0.0138	-0.0325	0.0218
			Distance to stream	-0.1325 ± 0.0145	-0.1609	-0.1042
			Distance to primary road	0.2204 ± 0.0154	0.1903	0.2505
			Distance to secondary road	-0.1956 ± 0.0122	-0.2195	-0.1717
			% canopy cover	0.0721 ± 0.0128	0.0470	0.0972
			Distance to bottomland hardwoods	0.4200 ± 0.0161	0.3885	0.4514
Foraging (State 2)	High-Forage	Female	Distance to upland hardwoods	-0.3463 ± 0.0151	-0.3758	-0.3167
			Distance to upland pines	-0.0749 ± 0.0170	-0.1081	-0.0416
			Distance to shrub/herb	0.0317 ± 0.0168	-0.0012	0.0646
			Distance to stream	0.1333 ± 0.0195	0.0950	0.1715
			Distance to primary road	-0.3230 ± 0.0156	-0.3536	-0.2924
			Distance to secondary road	0.0643 ± 0.0157	0.0335	0.0951
			% canopy cover	0.5632 ± 0.0233	0.5175	0.6089
			Distance to bottomland hardwoods	-0.2882 ± 0.0197	-0.3268	-0.2496
Traveling (State 3)	High-Forage	Female	Distance to upland hardwoods	-0.1999 ± 0.0134	-0.2262	-0.1737

			Distance to upland pines	-0.0271 ± 0.0129	-0.0523	-0.0018
			Distance to shrub/herb	0.0104 ± 0.0131	-0.0153	0.0361
			Distance to stream	0.1528 ± 0.0151	0.1233	0.1823
			Distance to primary road	-0.1890 ± 0.0114	-0.2114	-0.1667
			Distance to secondary road	0.0648 ± 0.0115	0.0423	0.0872
			% canopy cover	0.2767 ± 0.0141	0.2491	0.3044
			Distance to bottomland hardwoods	-0.2710 ± 0.0139	-0.2982	-0.2438
Resting (State 1)	High-Forage	Male	Distance to upland hardwoods	-0.1152 ± 0.0144	-0.1434	-0.0871
			Distance to upland pines	0.2054 ± 0.0162	0.1737	0.2372
			Distance to shrub/herb	-0.2508 ± 0.0190	-0.2880	-0.2135
			Distance to stream	0.0266 ± 0.0188	-0.0103	0.0634
			Distance to primary road	-0.2176 ± 0.0314	-0.2791	-0.1561
			Distance to secondary road	0.1562 ± 0.0158	0.1252	0.1872
			% canopy cover	0.3785 ± 0.0175	0.3442	0.4128
			Distance to bottomland hardwoods	-0.2933 ± 0.0173	-0.3272	-0.2595
Foraging (State 2)	High-Forage	Male	Distance to upland hardwoods	0.0963 ± 0.0159	0.0652	0.1275
			Distance to upland pines	0.1670 ± 0.0185	0.1308	0.2033
			Distance to shrub/herb	-0.018 ± 0.0183	-0.0542	0.0173
			Distance to stream	0.1050 ± 0.0205	0.0649	0.1451
			Distance to primary road	-0.0203 ± 0.0309	-0.0808	0.0401
			Distance to secondary road	0.0516 ± 0.0167	0.0188	0.0843
			% canopy cover	0.6411 ± 0.0254	0.5914	0.6908
			Distance to bottomland hardwoods	-0.4063 ± 0.0209	-0.4473	-0.3652

Traveling (State 3)	Low-Forage	Male	Distance to upland hardwoods	-0.0145 ± 0.0109	-0.0358	0.0068
			Distance to upland pines	0.1127 ± 0.0127	0.0878	0.1375
			Distance to shrub/herb	-0.1358 ± 0.0138	-0.1629	-0.1087
			Distance to stream	0.1466 ± 0.0148	0.1176	0.1756
			Distance to primary road	-0.0373 ± 0.0229	-0.0822	0.0075
			Distance to secondary road	-0.1980 ± 0.0129	-0.2232	-0.1727
			% canopy cover	0.1758 ± 0.0125	0.1512	0.2003
			Distance to bottomland hardwoods	-0.1890 ± 0.0124	-0.2133	-0.1647

CHAPTER 3

INFLUENCE OF BIOTIC AND ABIOTIC FACTORS ON HOME RANGE SIZE AND SHAPE OF INVASIVE WILD PIGS (*SUS SCROFA*)

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ABSTRACT

Determining factors influencing animal movements at a temporal scale that is similar to the temporal scale at which management actions are conducted (e.g., weekly) is crucial for identifying efficient methods of wildlife conservation and management. Using GPS data from 49 wild pigs in the southeastern U.S., we constructed weekly 50% and 95% utilization distributions to quantify the effects of biotic and abiotic factors on core area and home range size, as well as home range and shape. We found vegetative composition (i.e., proportion of bottomland hardwoods), meteorological conditions (i.e., temperature and pressure), and sex influenced wild pig weekly home range and core area size, while landscape features (i.e., distance to streams) also impacted core area size. Vegetative composition (i.e., proportion of upland pines) and landscape features (i.e., distance to streams) also were important factors influencing home range shape. At close distances to streams, wild pigs had more elongate home ranges when their home ranges comprised less upland pine habitat; however, at far distances to streams, there was no change in home range shape across fluctuating proportions of upland pines. These results demonstrate that the extent of wild pig home ranges and movements are variable and influenced by several habitat, landscape, and meteorological attributes that can easily be quantified from available land use and meteorological databases. Results are important for designing monitoring studies, identifying high risk zones for diseases, planning response to disease emergence events, and allowing more effective and efficient short-term management planning.

KEYWORDS

animal movements, core area, home range, invasive species, spatial ecology

INTRODUCTION

Understanding how animals move throughout landscapes while interacting with resources and responding to shifts in weather is critical for understanding basic ecology and life-history strategies of a species. For species of management or conservation concern, knowledge of the underlying factors influencing animal movement and space use patterns is often a fundamental component of developing management plans or modeling population persistence and expansion, especially on a temporal scale that is similar to the scale at which management decisions are implemented. Numerous factors affect animal space use and movement at varying spatial and temporal scales, such as: (1) the distribution of required resources (i.e., food, water, cover) (Tufto et al. 1996, Borger et al. 2006, Gray et al. 2020), (2) meteorological conditions (i.e., temperature, rain, atmospheric pressure) (Webb et al. 2010, Kay et al. 2017), (3) memory-based foraging and site-fidelity (Wauters et al. 2001, Horne et al. 2008, Merkle et al. 2014), and (4) the density and location of other animals (i.e., mates, competitors, etc.) (Horne et al. 2008). An important concept describing animal space use and providing insight on animal behavior is the home range; defined by Burt (1943) as the ‘area traversed by the individual in its normal activities of food gathering, mating, and caring for young.’ While there are consistent patterns depicted for where and how these normal activities occur irrespective of geography, movement behavior of most wildlife species is dictated by landscape complexity (i.e., heterogeneity) and/or composition of resources (Mcloughlin and Ferguson 2000, Borger et al. 2006, Clontz et al. 2020), as most animals often live in complex and heterogenous landscapes relative to habitat quality and resource availability.

The composition and configuration of habitat attributes can have a profound influence on the movement patterns and home ranges of animals (Mcloughlin and Ferguson 2000, Miller et al. 2000, Beasley and Rhodes 2010, Hillen et al. 2011, Castillo-Contreras et al. 2018, Clontz et al. 2020). Generally, higher quality habitats, which coincide with highly productive biotic communities, are associated with smaller home ranges because animals have the ability to satisfy energetic requirements in a smaller area (Harestad and Bunnel 1979). Meteorological conditions (i.e., temperature and precipitation) also can influence home range size via physiological restraints and energetic tradeoffs (Webb et al. 2010, McClure et al. 2015, Schlichting et al. 2016, Kay et al. 2017). For example, Kay et al. (2017) demonstrated that wild pig home ranges at the monthly scale were negatively related to temperature and pressure. Landscape complexity and the distribution of vegetation and required resources across the landscape also can influence home range shape, irrespective of size (Metzgar 1973, Singer et al. 1981, McIlroy 1989, Gray et al. 2020). For example, topography, vegetation, and landscape characteristics such as streams and roads can influence home range shape by acting as linear barriers to movement (Armitage 2009). Also, in relation to these barriers of animal movement is the distribution of required resources such as food, water and cover, which can also direct animal movement and influence home range shape (Larivière et al. 2007). Therefore, knowledge of home range size and shape is critical for making management decisions, especially when considering invasive species, which often cause widespread ecological and economic impacts and are thus subject to extensive population control and eradication efforts.

Invasive species often are highly adaptable, habitat and/or resource generalists, and have few predators or competitors outside of their native range (Shea and Chesson 2002, Garza et al. 2017, Pitt et al. 2018). These attributes facilitate the efficient exploitation of novel habitats by invasive species, allowing them to occupy landscapes in climates that do not occur in their native range as well as rapidly expand in population size and distribution once established (Broennimann and Guisan 2008). Among invasive vertebrates, wild pigs (*Sus scrofa*; Keiter et al. 2016) are one of the most widespread and successful species in the world (Garza et al. 2017, VerCauteren et al. 2020). Introduced globally as a food source and for hunting, wild pigs have effectively established invasive populations throughout North and South America, Australia, New Zealand, and Africa, in addition to numerous island nations (Barrios-Garcia and Ballari 2012, Lewis et al. 2017). Within the United States, wild pigs originated through introduction of domestic pigs in the 1500s by Spanish explorers as a source of meat (Seward et al. 2004), which later hybridized with introduced Eurasian wild boar (Goedbloed et al. 2013, Keiter et al. 2016, Mayer and Beasley 2018). Wild pig populations have continued to increase due to both intentional and accidental methods of introduction such as translocation for hunting, escapees from confinement operations, and dispersal from other established populations (Witmer et al. 2003, Tabak et al. 2017, Hernández et al. 2018). The surges in invasive wild pig populations in the U.S. and around the world have created increasing ecological and economic damages to environmental, agricultural, and anthropogenic ecosystems (Pimental 2007, Bevins et al. 2014, Keiter and Beasley 2017). Even in their native range, wild boar impose threats on other native fauna and flora (Massei and Genov 2004). Given the continued growth in abundance and geographic spread of wild pigs and resulting impacts on humans, plants, and animals (i.e., environmental damage, agricultural damage, reservoir for disease, etc.; Barrios-Garcia and Ballari 2012), wild pigs have become a serious issue for wildlife managers (Mayer and Brisbin 2009). Thus, understanding the impact of biotic and abiotic attributes on the movement behavior of wild pigs at a spatial and temporal scale that most management occurs is important to aid in control efforts for this destructive invasive species through fine-tuning the efficiency of management techniques based on local environmental conditions.

Home range sizes of wild pigs are influenced by individual-level attributes, vegetation or habitat (Franckowiak and Poche 2018), distance to water (Kay et al. 2017, Gray et al. 2020), and meteorological conditions (Schlichting et al. 2016, Kay et al. 2017). In particular, although a generalist species, wild pigs have limited thermoregulatory capabilities and often are associated with areas proximal to water and associated vegetation types (Clontz et al. 2020, Gray et al. 2020). However, most studies that have quantified the influence of environmental attributes on wild pig movements have done so at relatively coarse temporal scales (e.g., annual, bimonthly, monthly) (Schlichting et al. 2016, Kay et al. 2017, Gray et al. 2020) relative to the temporal scales at which many management activities and decisions occur. Throughout much of their invasive range, wild pigs are subject to extensive control with adaptive management decisions often occurring on a weekly or even daily basis. For example, most management techniques such as trapping, toxicant deployment, and aerial gunning occur across days or weekly periods targeting individuals or social groups. Therefore, determining the underlying attributes that drive home range shape and size at a fine temporal scale (i.e., weekly) would provide managers with the ability to understand wild pig behavior and adapt management strategies more often and consistently to allow for more efficient and effective management.

Therefore, the objective of this paper is to quantify wild pig movements at a fine temporal scale (i.e., weekly) to provide a better understanding of how landscape composition, meteorological conditions, and individual-level attributes affect movements, and ultimately, home range size and shape compared to other temporal scales. Specifically, we examined the influence of sex, vegetation composition, distance to streams, and effects of weather (e.g., maximum temperature, average precipitation, and average atmospheric pressure) as factors that impact wild pig home range and core area size. In addition, we tested the effect of sex, vegetation composition, and distance to streams on the shape of wild pig home ranges. Based on prior studies of wild pig home range size, we hypothesized males would travel more than females resulting in larger home ranges, even at the weekly scale. We also hypothesized wild pig home ranges would increase in size when the proportion of low-quality habitat (e.g., upland pines) increased within home ranges, and become more elongate at closer distances to streams because these areas would most likely represent the highest quality habitat and sources of water embedded in a larger matrix of other vegetative communities. In addition, we expected an inverse response of a decreasing home range size when the proportion of high-quality habitat (e.g., bottomland hardwoods) increased within home ranges, as well as more circular home ranges at farther distances from streams and in low-quality habitat. Lastly, we expected to see shifts in home range size as a result of fluctuations of weather (i.e., maximum temperature and average precipitation). Specifically, we expected wild pigs to have smaller home ranges during weeks with higher temperatures and precipitation and lower pressure.

METHODS

Study area

Our work was conducted on the Savannah River Site (SRS), a ~800 km^2 site managed by the United States Department of Energy (DOE) on the border of Georgia and South Carolina (Fig. 3.1). Although established for industrial activities, facilities and infrastructure comprise a small proportion of the landscape, with most of the landscape being managed by the United States Forest Service for timber production and wildlife conservation. The SRS was comprised of approximately 50% upland pine including loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), and slash pine (*Pinus elliottii*), 25% was bottomland hardwood forest (*Taxodium sp., Liquidambar sp., Quercus sp., Nyssa sp.*), 10% shrub/herbaceous-dominated areas, 8% upland hardwoods (*Carya sp., Acer sp., Quercus sp.*), 2% open water, and the rest was mixed forest, developed, and barren land. These habitats were heterogeneously distributed across the site, with extensive areas of bottomland hardwood forest and other areas that had riparian drainages embedded within a matrix of mostly pine habitat. Wild pigs have been managed on the SRS since the early 1950s, when an active live-trap-and-removal program was initiated to mitigate damages caused by wild pigs (Mayer et al. 2020*a*). Despite this control, there are several thousand wild pigs inhabiting the SRS that are distributed throughout the site (Keiter et al. 2017). The diversity of habitat types of the SRS combined with the limited public access, diversity of other wildlife species present, and high wild pig densities make the SRS an ideal location to study how habitat configuration influences variability of home range shape and size of this species.

Field methods

We captured wild pigs throughout the SRS from January 2017 – May 2020 using baited-corral traps equipped with a combination of remote-operated and trip-wire mechanisms. We used a dart rifle (X-Caliber, Pneu-Dart Inc., Pennsylvania, USA) to anesthetize captured pigs using a combination of butorphanol [0.077 mg/kg], azaperone [0.026 mg/kg], medetomidine [0.031 mg/kg] (BAM; 0.031 ml/kg; Wildlife Pharmaceuticals Inc., Colorado, USA) and Ketamine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., Colorado, USA) or Xylazine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., Colorado, USA) and Telazol (4.4 mg/kg; MWI Veterinary Supply, Idaho, USA). While under anesthesia, we recorded sex and assessed age through examination of tooth eruption (Mayer et al. 2020*b*). We placed uniquely identifiable ear tags in both ears of all captured wild pigs and fit the largest adult female in each sounder (i.e., social unit) and breeding-aged males with an Iridium GPS collar (Telonics Gen4 GPS/Iridium System, Telonics, Inc., Mesa, Arizona or VECTRONIC GPS PLUS Globalstar-3, VECTRONIC Aerospace, Coralville, Iowa). On three occasions, more than one GPS collar was deployed within the same social unit. Anesthetized wild pigs were allowed to recover at the capture site after reversed with a combination of Atipamezole (25mg/ml; Wildlife Pharmaceuticals Inc.) and Naltrexone (50 mg/ml; Wildlife Pharmaceuticals Inc., Colorado, USA). Collars were programmed to record GPS locations at 30-minute or one-hour intervals and equipped with a mortality sensor that became activated after 12 hours with no movement by the animal. All capture and handling procedures were conducted in compliance with the University of Georgia's Animal Care and Use Committee (Protocols: A2012 08-004, A2015 05-004, and A2018 08-013).

To estimate location error of GPS transmitters, we left a subset of three collars out for 10 days in fixed locations, five days in open vegetation and five days in forest vegetation. We used these data to calculate the average error among fixes for each habitat type.

Data Processing

We subset data for wild pigs with a 30-minute GPS fix rate to one-hour intervals to maintain a comparable temporal resolution within our dataset. We also removed the first 48 hours of GPS fixes to account for any potential bias associated with residual anesthetic effects, as well as locations associated with non-pig movements (e.g., locations after mortality). We were unable to determine the dilution of precision or number of satellites used to obtain fixes for non-retrieved collars as these data were not transmitted via Iridium satellites. However, from collars we were able to retrieve during the course of the study and manually download, less than 0.01% of locations were 2-Dimensional fixes (i.e., locations collected with three satellites). Therefore, we included all locations regardless of dimensional fix within our dataset to be consistent across all individuals. We combined each individuals' locations for every seven-day weekly period separately for each year. In addition, we excluded any weeks within an individual's data that did not have at least 65% of the locations obtained for that week to ensure home ranges were representative of the weekly scale.

Response Variables

We quantified home range size and shape for each weekly home range for inclusion in our analyses as dependent variables. We constructed 50% and 95% fixed kernel utilization distributions (hereafter 'core area' and 'home range') to quantify home range size; however, to avoid over inflation of shape due to polygon smoothing and multiple disparate polygons characteristic of kernels, we constructed 95% minimum convex polygons (hereafter '95% MCP') to quantify home range shape for each week for each individual. We used the adehabitat package with the reference bandwidth (href) smoothing parameter (Calenge 2006) in the statistical computing software R 3.6.1 (R Core Team 2019) for kernel construction. Any individuals that did not have at least two consecutive weeks of home range data were removed from the analyses. We quantified home range shape using a shape index (McGarigal and Marks 1994) to evaluate the circularity of the home range using the following formula:

$$\text{shape index} = \text{perimeter} / (2 * \sqrt{(\text{pi} * \text{area})}).$$

A smaller outcome is indicative of a more circular home range (i.e., 1.0) and a larger value is indicative of a more elongate or linear home range (i.e., 4.0). Therefore, this index allowed us to compare home range shape on a continuous scale.

Habitat and Weather Covariates

We reclassified the 2016 National Land Cover Database (NLCD) raster layer (30 x 30 m-resolution; Jin et al. 2019) to include two classifications of vegetative cover representative of low- and high-quality habitat for our home range analyses: 1) upland pines and 2) bottomland hardwoods, respectively. In addition, we obtained temperature and precipitation variables from the nearest weather station in Aiken, SC (USC00380072) and recovered any missing data with data from the next closest station in Graniteville, SC (USC00383665; www.ncdc.noaa.gov). We acquired atmospheric pressure data from the Aiken Municipal Airport, SC (WBAN: 72060100193; www.ncdc.noaa.gov). We used the mean of average daily values over each corresponding week for precipitation (cm), maximum temperature (°C), and atmospheric pressure (Pa) as continuous, fixed covariates. We quantified the proportion of upland pine and bottomland hardwood vegetation types for all core areas, home ranges, and 95% MCPs by systematically sampling (every pixel, i.e., 30 m), extracting vegetation classifications for each sampled point, and then dividing the total number of pixels classified for each vegetation type by the overall total number of pixels for the relative home range. We also characterized the distribution of streams within our study area from existing SRS geospatial layers and generated a distance to stream layer using the Euclidean distance tool in ArcGIS 10.7.1 (Environmental System Research Institute, Inc., Redlands, CA, USA). We then took the average of the distances from all locations within each home range to obtain a single value associated with distance to stream for each core area, home range, and 95% MCP.

Statistical Analyses

We calculated Pearson's correlation coefficients to test for collinearity (i.e., Pearson's $|r| > 0.5$) between each of our habitat and weather covariates and did not include any correlated covariates within the same model in subsequent analyses (Roever et al. 2014). To quantify the effects of our habitat and weather covariates on wild pig home range size and shape, we used generalized linear mixed-effect models (GLMMs) with a Gamma distribution and a log-link because home range size and shape are non-negative and right-skewed. In order to best represent pressure in models, we conducted a preliminary analysis on the relationship of average pressure with home range size to determine if average pressure would be represented best as a quadratic term or a single covariate in relevant models since wild pigs have demonstrated variable patterns at different temporal scales (Kay et al. 2017). The use of a quadratic for average pressure did not improve model fit based on Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002); therefore, we included average pressure in models as a single covariate. Next, we generated 29 biologically relevant *a priori* models including the null models and interactions to examine the influence of sex and six environmental and meteorological variables (i.e., proportion of bottomland hardwoods, proportion of upland pines, average distance to stream, average weekly maximum temperature, average weekly precipitation, and average weekly atmospheric pressure) on home range and core area size at the weekly scale. We also generated 15 *a priori* models including the null model and interactions to determine the influence of sex, vegetation type (i.e., proportion of bottomland hardwoods and proportion of upland pines), and average distance to stream on 95% MCP shape. We accounted for repeated observations by specifying each individual pig as a random effect. We created two null models, one with a random effect for individual and one with a nested random effect with social group and individual, and we used model selection to test for the importance of a nested random effect with social group. We ranked models using AIC_c (Burnham and Anderson 2002), and assessed absolute goodness-of-fit using the trigamma-estimate of the marginal ($R^2_{GLMM(m)}$; i.e., represents variance explained by fixed effects) and conditional ($R^2_{GLMM(c)}$; i.e., represents variance explained by overall model including both random and fixed effects) pseudo-coefficient of determination for GLMMs

(Nakagawa and Schielzeth 2013). We performed calculations using the MnMIn package in R version 3.6.1 (R Core Team 2019, Barton 2020). We standardized all variables prior to model development [(x_i - $\bar{x}$)/s] (Table 3.1), and used the lme4 package in R version 3.6.1 for all analyses (Bates et al. 2014, R Core Team 2019).

RESULTS

Descriptive Statistics

We determined average collar error in forested vegetation to be 22.3 m and in open vegetation to be 11.9 m. We used a sample of 49 collared wild pigs (27 females and 22 males) tracked between January 2017 and August 2020, which provided 157 weekly periods and a total sample of 980 home ranges for modeling wild pig home range size and shape. The weekly sample size of individuals throughout the 157-week period ranged from 4 to 18 for females and from 4 to 22 for males per week, with a median of 8.5 individuals for both females and males separately. Average weekly fixed kernel core area and home range sizes (±SE) for female wild pigs in this study were 1.05 ± 0.32 km^2 and 4.75 ± 1.35 km^2, respectively, and for males they were 2.90 ± 0.62 km^2 and 13.81 ± 2.76 km^2, respectively. Home range shape index ranged from 1.03 (most circular) to 1.84 (most elongate) with a median of 1.13, indicating more individuals had circular home ranges compared to semi-elongate home ranges (Fig. 3.2).

The model including individual as a nested random effect within social group had a larger ΔAIC_c than the model with individual as a sole random effect and was associated with warnings of overfitting. Therefore, we only included individual as a random effect in subsequent models. Also, proportion of bottomland hardwoods and upland pines were correlated (R = -0.58), so we did not include them in the same model but tested them independently (Table 3.2).

Home Range Size

The highest ranked model for estimating weekly home range size included average maximum temperature, average atmospheric pressure, average precipitation, and an interaction between sex and bottomland hardwoods (Table 3.3). No other models were within Δ2 AIC$_c$ (Table 3.2). For weekly home ranges, males had a larger weekly home range compared to females. In addition, the interaction between sex and bottomland hardwoods was significant indicating the effect of bottomland hardwoods on home range size was dependent upon sex (Table 3.3; Fig. 3.3). Home range size had a negative relationship with proportion of bottomland hardwoods for both females and males. However, female home range size exhibited more dependence on bottomland hardwoods than males (Fig. 3.3). In addition, weekly home range size also displayed a negative relationship with average maximum temperature (Table 3.3; Fig. 3.1) and, conversely, a positive relationship with average atmospheric pressure (Table 3.3; Fig. 3.1). Although included in the top model for home range size, average precipitation was not significant in the model (i.e., $p \geq 0.05$; Table 3.3). The top model for estimating weekly home range size had a marginal $R^2_{GLMM(m)} = 0.25$ and a conditional $R^2_{GLMM(c)} = 0.35$.

Core Area Size

For weekly core areas, the highest ranked model included proportion of bottomland hardwoods, average maximum temperature, average atmospheric pressure, average precipitation, and an interaction between sex and average distance to stream (Table 3.4). No other models were within Δ2 AIC$_c$ (Table 3.5). Similar to weekly home ranges, males maintained larger weekly core areas than females. The interaction between sex and average distance to streams was significant indicating the effect of distance to streams on core area size was dependent upon sex (Table 3.4; Fig. 3.4). Male core area size was negatively associated with increasing distances to streams; however, females showed no substantial change in core area size across different distances to streams (Fig. 3.4). In addition, core area size maintained the same positive relationship with average atmospheric pressure as at the weekly home range scale (Fig. 3.4). Lastly, average precipitation and average maximum temperature were included in the top model, but they were not statistically significant (i.e., $p \geq 0.05$) predictors for core area size (Table 3,4). The top model for estimating core area size had a marginal $R^2_{GLMM(m)} = 0.18$ and a conditional $R^2_{GLMM(c)} = 0.28$.

95% MCP Home Range Shape

The analysis investigating the influence of sex, habitat, and environmental attributes on home range shape produced a single top model that included an interaction between average distance to stream and proportion of upland pines (Table 3.6). No other models were within $\Delta 2$ AIC$_c$ (Table 3.7). The interaction between proportion of upland pines and average distance to streams was significant, indicating that wild pig 95% MCP weekly home range shape was affected differently by the proportion of upland pines within the home range across varying distances to streams. For example, at close distances to streams (i.e., $\leq$250 m), wild pigs had more elongate home ranges that were comprised of less upland pine habitat and more circular home ranges comprised of a higher proportion of upland pines. However, at far distances to streams (i.e., $\geq$ 900 m), there was no change in home range shape across fluctuating proportions of upland pines (Fig. 3.5).

DISCUSSION

Using GPS data from wild pigs collected within a matrix of heterogeneously distributed bottomland hardwood (i.e., high-quality habitat) and upland pine (i.e., low-quality habitat) habitat, we demonstrated that home range size and shape were influenced by a combination of biotic (i.e., vegetation types) and abiotic (i.e., temperature, precipitation, pressure, streams) environmental factors. Similar to previous research that has quantified home ranges of wild pigs at more coarse temporal scales (i.e., monthly, bimonthly, annually), males exhibited larger weekly home ranges and core areas compared to females (Dexter 1999, Kay et al. 2017, Gray et al. 2020). In addition, the extent of movement by both males and females was strongly influenced by the availability of high-quality habitat, with individuals maintaining smaller home range and core area sizes in areas dominated by bottomland hardwood vegetation. However, at the home range scale this pattern was slightly more pronounced for females than males. Furthermore, temperature and pressure were found to influence both female and male home range size, while pressure was the only influential meteorological variable for both sexes at the core area scale. In addition, males had larger core areas at closer distances to streams, while females maintained consistent core area sizes across all distances to streams. Home range shape was also driven by vegetation and landscape characteristics via an interaction between low-quality habitat and average distance to stream in this study system.

The larger home range size of males observed in this study compared to females is consistent with our hypotheses, as well as most other wild pig research conducted at broader temporal scales (McIlroy 1989, Dexter 1999, Kay et al. 2017, Gray et al. 2020); although Singer et al. (1981) reported no difference in home range size between sexes. Male wild pigs are generally larger than females, and their body mass does not fluctuate as drastically as females (Saunders and McLeod 1999, Gray et al. 2020). In addition, wild pigs have a promiscuous mating strategy and are reproductively active year-round (Snow et al. 2020). Therefore, unlike other ungulates that experience one short-term rut annually, mate-seeking movements in wild pigs likely occur throughout the year with gradual peaks at certain temporal periods based on forage availability (Gray et al. 2020, Snow et al. 2020). Therefore, larger home range sizes of male wild pigs in this study could be a result of allometric effects or the process of maximizing reproductive fitness (Dexter 1999, Gray et al. 2020).

At the weekly scale, our results suggest landscape vegetation composition plays an important role in influencing the extent of wild pig movements. Landscape vegetation was intended to act as a proxy for habitat quality in our models and was represented by two dominant vegetation types within our study area, bottomland hardwoods (high-quality) and upland pines (low-quality). Bottomland hardwoods was an important predictor variable of home range and core area size with smaller home ranges and core areas associated with higher proportions of bottomland hardwoods. However, at the home range scale, the effect of bottomland hardwoods on home range size was moderated by sex, with male home range size being less influenced by the proportion of bottomland hardwoods than females. Bottomland hardwoods offer an abundance of resources important to wild pigs including dense cover, areas proximal to water, and a diversity of food resources (Ditchkoff and Mayer 2009, Ballari and Barrios-García 2014, Beasley et al. 2014, Gray et al. 2020, Mayer et al. 2020*a*). Therefore, increased availability of bottomland hardwoods likely facilitates reduced movements associated with important behaviors such as foraging, wallowing, searching for a mate, etc., and simplifies the process of acquiring necessary resources. However, the difference in social dynamics and reproductive responsibilities between males and females may produce differences in the dependence on and selection of bottomland hardwood habitat. For example, depending on the stage of reproduction, females may require more energy and/or cover or be limited to an area by their offspring and occupy habitats that offer the best conditions while males may be more mobile (Hillen et al. 2011, Gray et al. 2020).

The interaction between distance to streams and sex was an influential predictor variable for core area size but not for home range size. Male core area size was inversely related to distance to streams (i.e., core areas are smaller at farther distances from streams), while female core area size was not influenced by distance to streams. Previous literature has shown wild pigs have an affinity for water and associated vegetation types, which are generally associated with higher quality habitat (Gray et al. 2020); therefore, densities of wild pigs are potentially higher in areas with water-associated vegetation types than in areas with lower quality habitat. In other ungulates, both positive and negative relationships between home range size and population densities have been observed (Saunders and McLeod 1999, Kjellander et al. 2004, Kilpatrick et al. 2011). The association between male core area size and distance to streams could be influenced by population density and/or age, which were two variables we were unable to evaluate in our models and should be considered in further research.

The influence of meteorological conditions (i.e., temperature and pressure) on weekly home range size was also evident in our models. Average weekly maximum temperature and average atmospheric pressure were both important explanatory variables in weekly home range models, while atmospheric pressure alone was important in describing core area size. As predicted, warmer conditions were associated with smaller weekly home ranges, which is consistent with previous research (Dexter 1999, Kay et al. 2017). Since wild pigs have limited thermoregulatory capabilities, smaller home range sizes that coincide with warmer temperatures demonstrate a biological tradeoff between the need to increase movements for foraging purposes and the need to limit exertion and stay near areas with reliable thermal cover (Dexter 1999, Garza et al. 2017). This limited thermoregulatory ability of wild pigs thus may not only constrain wild pig movements at the home range scale (Kay et al. 2017), but may limit their ability to colonize new areas and proliferate throughout their overall invasive range (McClure et al. 2015). Therefore, quantifying the extent and relationship of temperature at the weekly scale is important for predicting movement capacity of wild pigs, which could provide input for managers on optimal timing for management strategies. For example, aerial gunning may be more effective when temperatures are cooler because wild pigs will be more active.

Wild pigs exhibited a positive relationship with atmospheric pressure at the weekly home range and core area scales, with home range sizes increasing as atmospheric pressure increased. Low pressure is generally associated with bad weather following frontal boundaries such as rain and storms, while high pressure is generally associated with clear, fair weather. Therefore, the positive association with pressure is likely explained by wild pigs restricting movements to areas with reliable cover in times of bad weather (i.e., low pressure). Similarly, movements of other species such as moose (Dussault et al. 2006), domestic cattle (Malechek and Smith 1976), deer (Webb et al. 2010), and red fox (Ables 1969) have been shown to respond to changes in atmospheric pressure. For invasive wild pigs, Kay et al. (2017) described a concave relationship between daily maximum distance moved and pressure for wild pigs, suggesting there is an optimal range of atmospheric pressure associated with wild pig movements. These patterns were evident through investigation of daily movement rates, but monthly averages of pressure were deemed less reliable for predicting animal movement patterns (Kay et al. 2017). However, averaging daily pressure readings across weekly periods produced a reliable relationship with estimated home range and core area size. Therefore, using averages of atmospheric pressure at fine temporal and spatial scales as an indicator for weather can provide insights into the extent of wild pig movements on a weekly scale, which can be used to implement effective management strategies. Additionally, precipitation was an important predictor variable in the top models of home range and core area size for wild pigs, but it was not statistically significant. This finding coincides with other studies that have found precipitation to be insignificant for both direct, real-time (i.e., animal's response to precipitation) (Garza et al. 2017) and delayed effects (i.e., animal's response to increased productivity in vegetation growth caused by precipitation) on wild pig movements (Schlichting et al. 2016).

Home range shape of wild pigs is highly variable and has been described as circular to elongate or irregular (Singer et al. 1981, McIlroy 1989, Gray et al. 2020). Our results suggest short-term wild pig home ranges are more circular than linear, but variance in home range shape may reflect the distribution of preferred habitats on the landscape, as the interaction between upland pines (i.e., low-quality habitat) and distance to streams was the most important factor influencing home range shape in our study. Wild pigs inhabiting areas at closer distances to streams with home ranges comprised of lower proportions of upland pines exhibited more elongate home ranges than those in areas close to streams with high proportions of upland pines. Given that upland pines and bottomland hardwoods were negatively correlated in our study area, and that most streams were buffered by bottomland hardwood habitat, this finding likely reflects more constrained movements of wild pigs along riparian corridors. Wild pigs tend to seek out river systems and riverine woodlands in hot and humid environments like the southeast United States in order to thermoregulate when heat loads are high (Dexter 1998). This biological restriction confines wild pigs to areas close to riparian areas; therefore, the composition of the landscape and distribution of riparian areas may have a substantial influence on the shape and distribution of wild pig home ranges. Also, linear landscape features such as streams that are buffered by productive, high-quality habitat have been shown to direct animal movement (Kay et al. 2017, Abouelezz et al. 2018, Gray et al. 2020). As a result, wild pigs with home ranges closer to streams are more likely to have elongate home ranges coinciding with intermixed high-quality habitat boundaries along streams in a matrix of low-quality habitat. However, at farther distances from streams wild pigs maintained consistent semi-circular home ranges across all proportions of upland pines, suggesting when possible, wild pigs can optimize movements to be centered on streams taking advantage of pockets of high-quality habitat in landscapes dominated by low-quality habitat. Therefore, streams can be important predictors of home range shape in heterogeneous landscapes. For example, Clontz et al. (2020) demonstrated wild pigs select for areas near streams at a population or second-order scale (Johnson 1980). Similarly, other linear landscape and anthropogenic features such a roads and edges of agricultural fields have been shown to influence home range shape or act as barriers to animal movement (Gray et al. 2020).

MANAGEMENT IMPLICATIONS

As an intensively managed invasive species, effective wild pig control requires insights into the ecology of this species that can be used by managers to make real-time decisions regarding where and when to best implement trapping, aerial gunning, toxicants, or other management approaches to maximize their efficacy. The temporal scale and covariates incorporated in this study were intended to be easily classified and estimated on a visual and/or knowledge-based foundation, making it practical to make informed, small-scale management decisions on a week-by-week basis. When managing wild pigs near streams, techniques such as trapping and toxicants can be distributed along stream corridors to efficiently target the flow of wild pig movement. In conjunction, implementing more traps and bait stations in high quality habitat (i.e., bottomland hardwoods) may be necessary to ensure multiple social groups and solitary boars have access since home range sizes are smaller in these areas. Also, accounting for meteorological conditions in short-term management has the potential to increase success and reduce costs. For example, it may not be practical to trap or deploy bait for wild pigs during certain weeks out of the year due to decreased movement caused by real-time or delayed effects of weather. Lastly, our data provide spatial ecology insight on wild pig movement and influential parameters to aid in disease risk assessment and control planning.

LITERATURE CITED

Ables, E. D. 1969. Activity studies of red foxes in southern Wisconsin. The Journal of Wildlife Management 33:145–153.

Abouelezz, H. G., T. M. Donovan, R. M. Mickey, J. D. Murdoch, M. Freeman, and K. Royar. 2018. Landscape composition mediates movement and habitat selection in bobcats (Lynx rufus): implications for conservation planning. Landscape Ecology 33:1301–1318.

Armitage, K. B. 2009. Home range area and shape of yellow-bellied marmots. Ethology Ecology & Evolution 21:195–207.

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

Barton, K. 2020. MuMIn: multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software. <http://arxiv.org/abs/1406.5823>. Accessed 6 Jan 2020.

Beasley, J. C., T. E. Grazia, P. E. Johns, and J. J. Mayer. 2014. Habitats associated with vehicle collisions with wild pigs. Wildlife Research 40:654–660.

Beasley, J., and O. Rhodes. 2010. Influence of patch- and landscape-level attributes on the movement behavior of raccoons in agriculturally fragmented landscapes. Canadian Journal of Zoology 88:161–169.

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.

Borger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168:471–485.

Broennimann, O., and A. Guisan. 2008. Predicting current and future biological invasions: both native and invaded ranges matter. Biology Letters 4:585–589. Royal Society.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Sociological Methods & Research 33:261– 304.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Castillo-Contreras, R., J. Carvalho, E. Serrano, G. Mentaberre, X. Fernández-Aguilar, A. Colom, C. González-Crespo, S. Lavín, and J. R. López-Olvera. 2018. Urban wild boars prefer fragmented areas with food resources near natural corridors. Science of The Total Environment 615:282–288.

Clontz, L., K. M. Pepin, K. C. VerCauteren, and J. C. Beasley. 2020. Connecting the dots: behavioral state resource selection in wild pigs in the southeast United States. preprint, In Review. <https://www.researchsquare.com/article/rs-58909/v1>. Accessed 6 Nov 2020.

Dexter N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment, Wildlife Research 25:547–559.

Dexter, N. 1999. The influence of pasture distribution, temperature and sex on home-range size of feral pigs in a semi-arid environment. Wildlife Research 26:755.

Ditchkoff, S. S., and J. J. Mayer. 2009. Wild pig food habits. Pages 105–143 in. Wild pigs: biology, damage, control techniques and management. Savannah River Nuclear Solutions LLC, Savannah River Site Aiken, SC, USA.

Dussault, C., M. Poulin, R. Courtois, and J.-P. Ouellet. 2006. Temporal and spatial distribution of moose-vehicle accidents in the Laurentides Wildlife Reserve, Quebec, Canada. Wildlife Biology 12:415–425.

Franckowiak, G., and R. Poche. 2018. Short-term home range and habitat selection by feral hogs in Northern Texas. The American Midland Naturalist 179:28–37.

Garza, S. J., M. A. Tabak, R. S. Miller, M. L. Farnsworth, and C. L. Burdett. 2017. Abiotic and biotic influences on home-range size of wild pigs (*Sus scrofa*). Journal of Mammalogy 99:97–107. American Society of Mammalogists.

Goedbloed, D. J., H. J. Megens, P. V. Hooft, J. M. Herrero-Medrano, W. Lutz, P. Alexandri, R. P. M. A. Crooijmans, M. Groenen, S. E. V. Wieren, R. C. Ydenberg, and H. H. T. Prins. 2013. Genome-wide single nucleotide polymorphism analysis reveals recent genetic introgression from domestic pigs into northwest European wild boar populations. Molecular Ecology 22:856–866.

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. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Harestad, A. S., and F. L. Bunnel. 1979. Home range and body weight--A reevaluation. Ecology 60:389–402.

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.

Hillen, J., T. Kaster, J. Pahle, A. Kiefer, O. Elle, E. M. Griebeler, and M. Veith. 2011. Sex-Specific Habitat Selection in an Edge Habitat Specialist, the Western Barbastelle Bat. Annales Zoologici Fennici 48:180–190.

Horne, J. S., E. O. Garton, and J. L. Rachlow. 2008. A synoptic model of animal space use: Simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. Ecological Modelling 214:338–348.

Jin, S., C. Homer, L. Yang, P. Danielson, J. Dewitz, C. Li, Z. Zhu, G. Xian, and D. Howard. 2019. Overall methodology design for the United States national land cover database 2016 products. Remote Sensing 11:2–32.

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

Kay, S. L., J. W. Fischer, 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. <http://proxy-remote.galib.uga.edu/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=edswsc&AN=000403549100001&site=eds-live>.

Keiter, D. A., and J. C. Beasley. 2017. Hog heaven? Challenges of managing introduced wild pigs in natural areas. Natural Areas Journal 37:6–16.

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

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 40:384–387.

Kilpatrick, H., S. Spohr, and K. Lima. 2011. Effect of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79:949–954.

Kjellander, P., A. Hewison, O. Liberg, J.-M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home-range size in roe deer (Capreolus capreolus L.): A comparison of two long-term studies. Oecologia 139:478–85.

Larivière, S., D. Howerter, and F. Messier. 2007. Influence of gender and den type on home range shape for striped skunks, Mephitis mephitis, in Saskatchewan. The Canadian Field-Naturalist 121:261–264.

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 7:44152.

Malechek, J. C., and M. Smith. 1976. Behavior of range cows in response to winter weather. Journal of Range Management 29:9–12

Massei, G., and P. Genov. 2004. The environmental impact of wild boar. Galemys 16:135-145.

Mayer, J. J., J. C. Beasley, R. Boughton, and S. S. Ditchkoff. 2020a. Wild Pigs in the southeastern North America. Pages 369–402 in. Invasive Wild Pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, USA.

Mayer, J. J., and I. L. Brisbin. 2009. Wild pigs in the United States: their history, comparative morphology, and current status. University of Georgia Press.

Mayer, J. J., T. J. Smyser, A. J. Piaggio, and S. M. Zervanos. 2020b. Wild pig taxonomy, morphology, genetics, and physiology. Pages 7–32 in. Invasive Wild Pigs in North America: Ecology, Impacts, and Management. CRC Press, Boca Raton, FL, 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 the Probability of Occurrence of Invasive Wild Pigs across the Contiguous United States. PloS One 10:e0133771.

McGarigal, K., and B. J. Marks. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Forest Science Department, Oregon State University, Corvallis, Oregon, USA.

McIlroy, J. C. 1989. Aspects of the ecology of feral pigs (Sus scrofa) in the Murchison Area, New Zealand. New Zealand Journal of Ecology 12:11–22.

Mcloughlin, P. D., and S. H. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Écoscience 7:123–130.

Merkle, J. A., D. Fortin, and J. M. Morales. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. Ecology Letters 17:924–931.

Metzgar, L. H. 1973. Home Range Shape and Activity in Peromyscus leucopus. Journal of Mammalogy 54:383–390.

Miller, D. A., B. D. Leopold, G. A. Hurst, and P. D. Gerard. 2000. Habitat selection models for eastern wild turkeys in central Mississippi. The Journal of Wildlife Management 64:765–776.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Pimental, D. 2007. Environmental and economic costs of vertebrate species invasions into the United States. Managing Vertebrate Invasive Species 38:2–8.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Roever, C. L., H. L. Beyer, M. J. Chase, and R. J. van Aarde. 2014. The pitfalls of ignoring behaviour when quantifying habitat selection. Diversity and Distributions 20:322–333.

Saunders, G., and S. McLeod. 1999. Predicting home range size from the body mass or population densities of feral pigs, Sus scrofa (Artiodactyla: Suidae). Australian Journal of Ecology 24:538–543.

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

Seward, N. W., K. C. VerCauteren, G. W. Witmer, and R. M. Engeman. 2004. Feral swine impacts on agriculture and the environment. Sheep & Goat Research Journal 19:34–40.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17:170–176.

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.

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

Tufto, J., R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715–724.

VerCauteren, K. C., J. J. Mayer, J. C. Beasley, S. S. Ditchkoff, G. J. Roloff, and B. K. Strickland. 2020. Introduction. Pages 1–5 in. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA.

Wauters, L. A., J. Gurnell, D. Preatoni, and G. Tosi. 2001. Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. Ecography 24:525–538.

Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. DeYoung. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology 2010:1–12.

Witmer, G. W., L. Avenue, F. Collins, R. B. Sanders, and A. C. Taft. 2003. Feral swine---are they a disease threat to livestock in the United States? Proceedings of the 10th Wildlife Damage Management Conference 316–325.

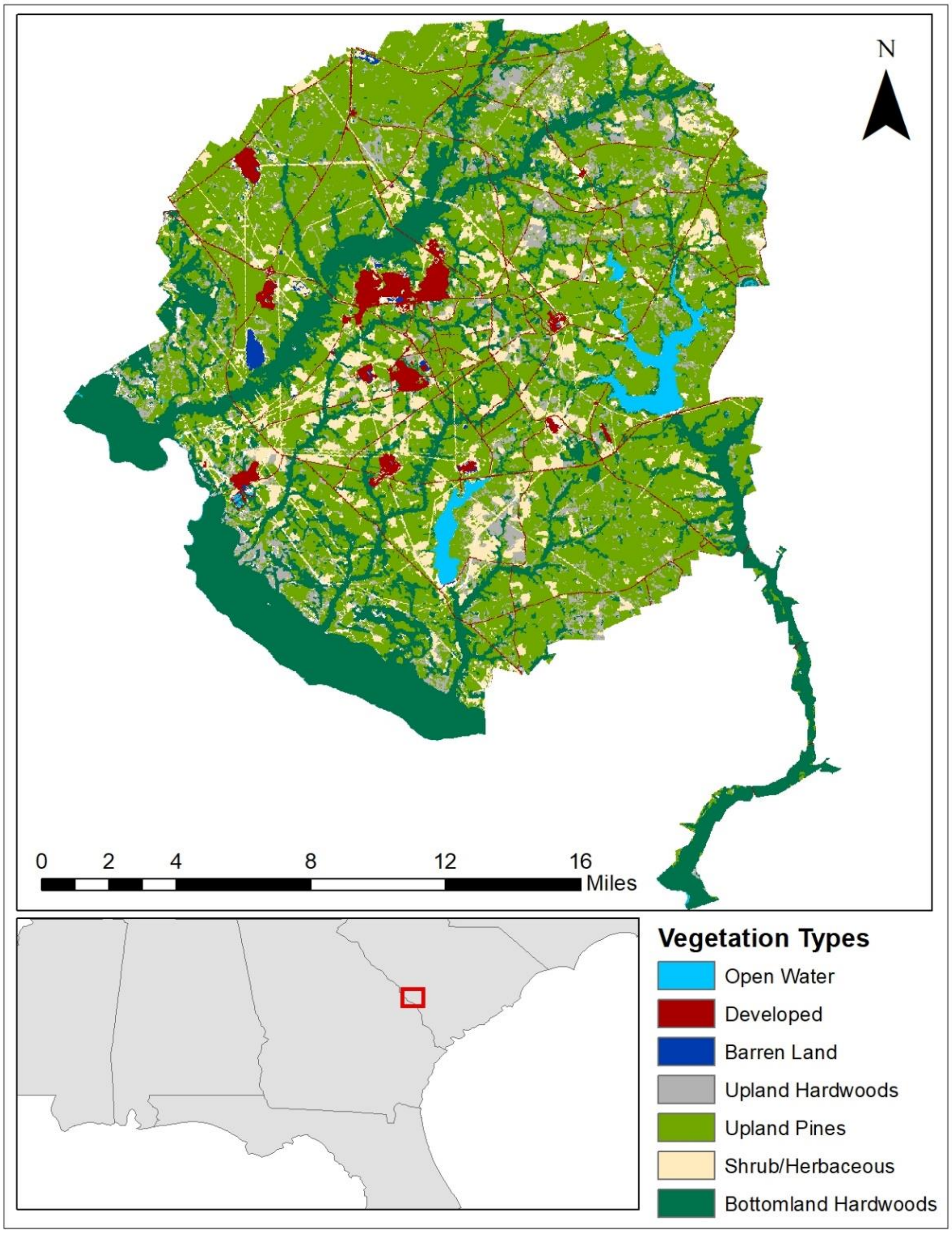

Figure 3.1. The Study area with all represented vegetative communities used to extract dominant vegetation types (i.e., Upland Pines and Bottomland Hardwoods) which were used to model the effect of low- and high-quality habitat within male and female wild pig (*Sus scrofa*) weekly home ranges between Janurary 2017 – August 2020 in South Carolina, USA.

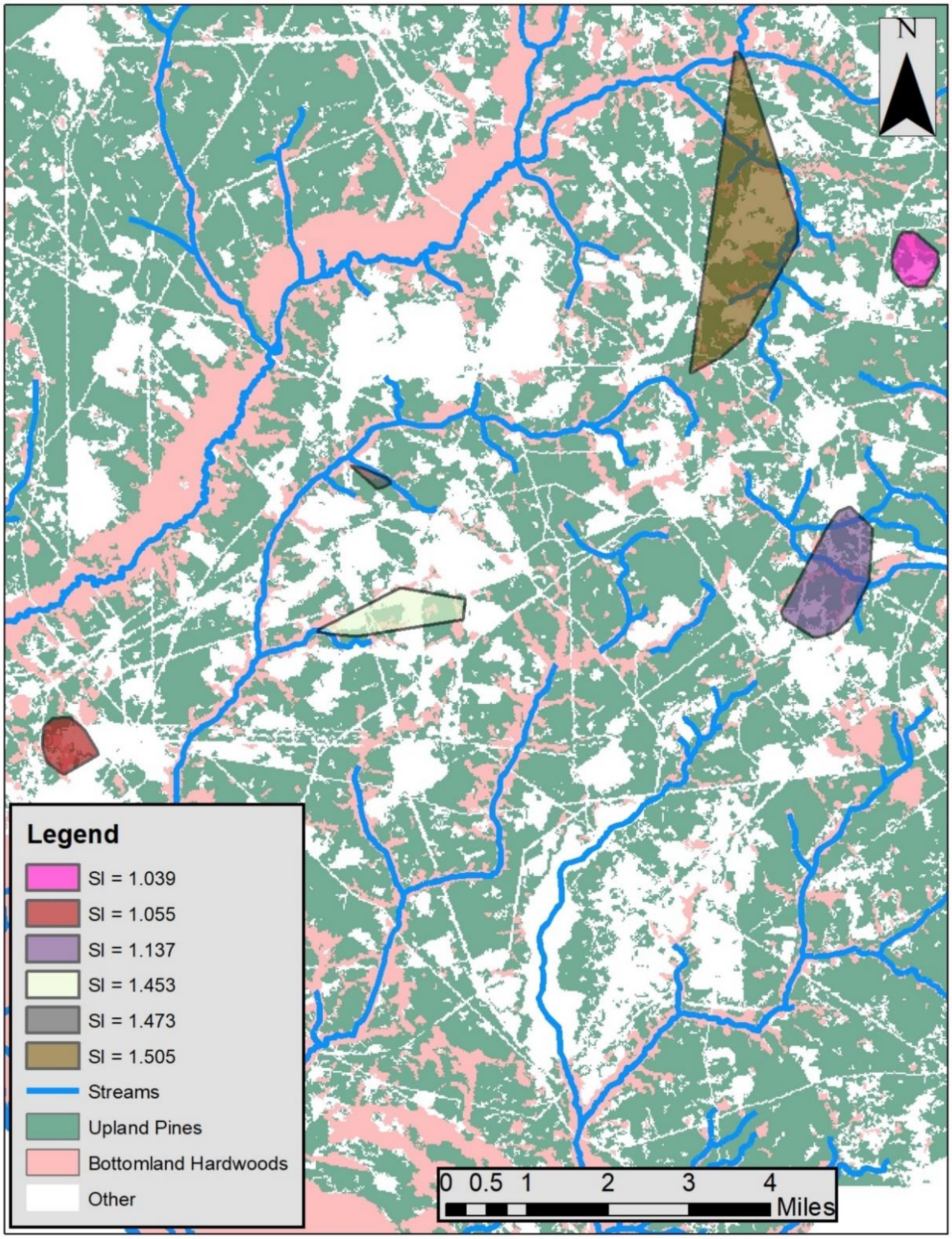

Figure 3.2. Examples of female wild pig (*Sus scrofa*) 95% minimum convex polygon (MCP) weekly home ranges illustrating variance in home range shape among individuals. Values for 95% home range shape are based on a shape index (perimeter / (2* √(pi * area)) which represents a spectrum from circular (smaller values) to elongate (larger values). Individuals were tracked between Janurary 2017 – August 2020 in South Carolina, USA.

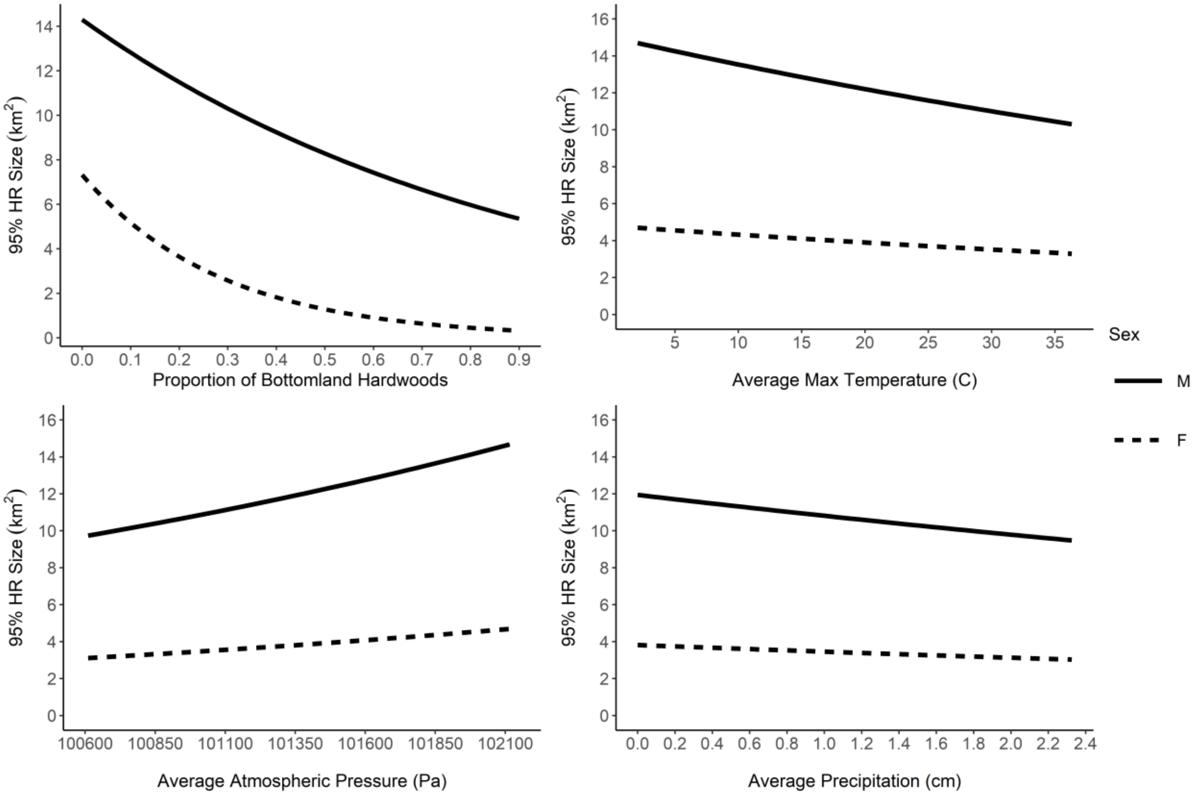

Figure 3.3. Relationships between back-transformed covariates for weekly home range size for both females and males from wild pig location data on the Savannah River Site in South Carolina based on GPS locations from January 2017 – August 2020.

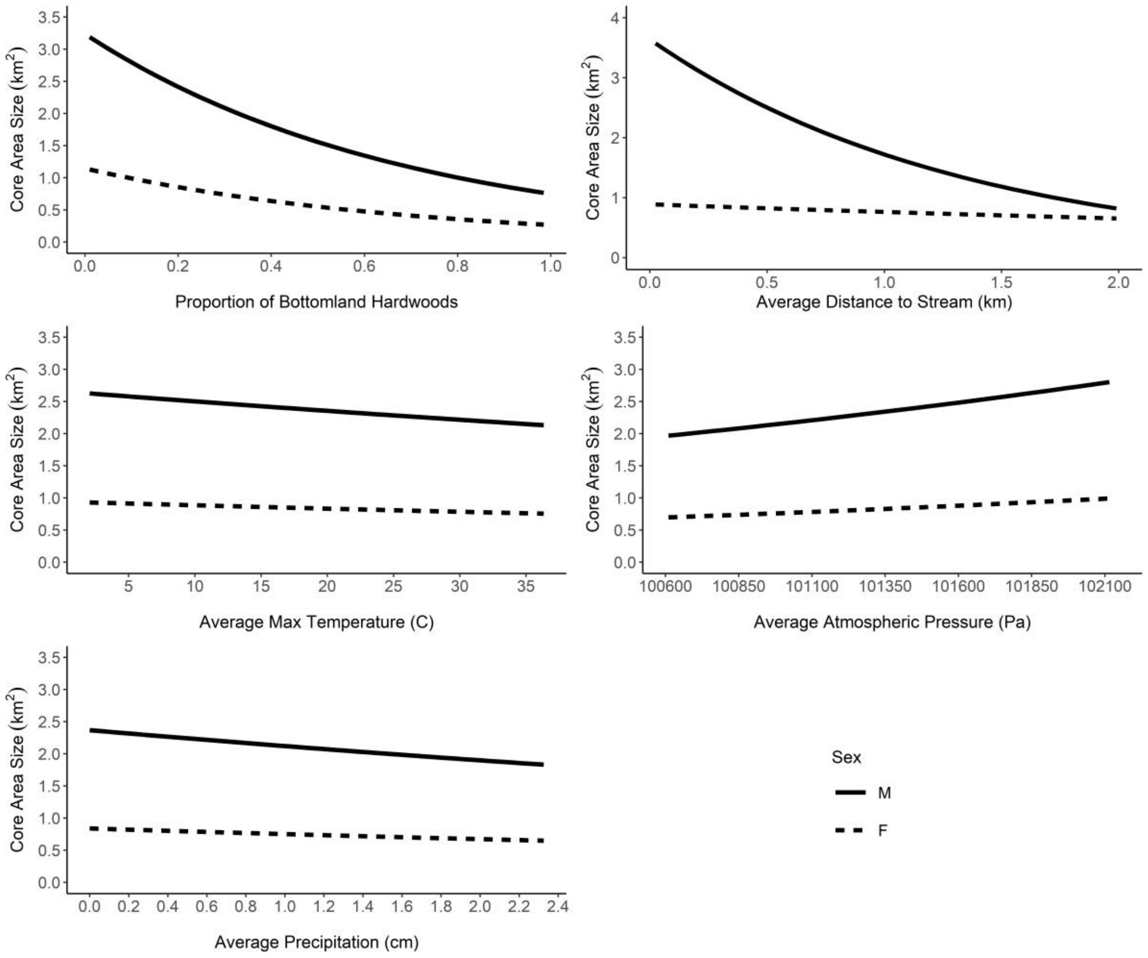

Figure 3.4. Relationships between back-transformed covariates for core area home range size for both females and males from wild pig location data on the Savannah River Site in South Carolina based on GPS locations from January 2017 – August 2020.

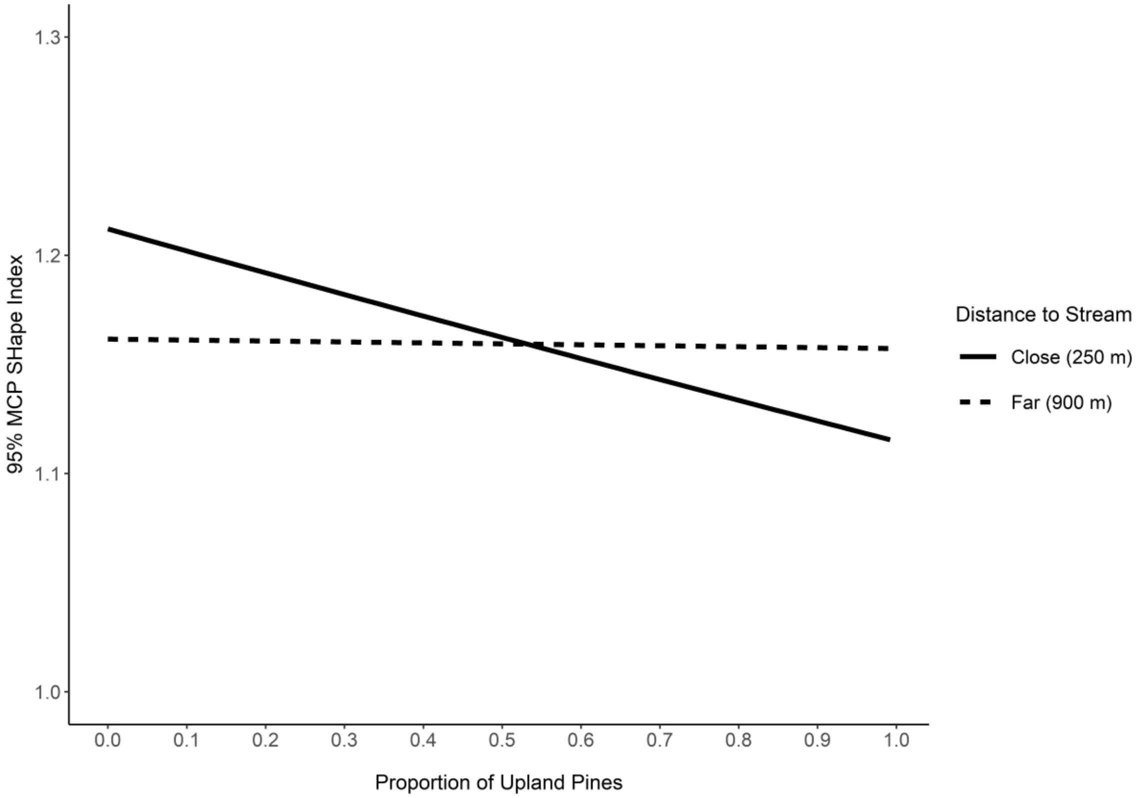

Figure 3.5. The relationship between 95% minimum convex polygon (MCP) home range shape and the interaction between back-transformed distance to streams and proportion of upland pine values from wild pig location data from the Savannah River Site in South Carolina based on GPS locations collected from January 2017 – August 2020. The values for 95% MCP home range shape are based on a shape index (perimeter/(2* √(pi * area)) which represents a spectrum from circular (smaller values) to elongate (larger values).

Table 3.1. Covariate statistics including mean, standard deviation, minimum, and maximum values for all observed data used to standardize and back-transform covariates used in models for A) core area size, B) weekly home range size, and C) 95% minimum convex polygon (MCP) home range shape for wild pigs in the southeast United States between January 2017 and August 2020. Covariates include proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), proportion of upland pines within the home range (Prop. Up. Pines), average maximum weekly temperature (Tmax), average weekly precipitation (Precip), average weekly atmospheric pressure (Avg. Pressure), and average distance to stream (Avg. Dist. Stream).

A.

Covariate	**Mean**	**SD**	**Min**	**Max**
Avg. Dist. Stream	0.63	0.45	0.02	2.11
Avg. Pressure	0.45	0.20	0.00	1.00
Prop. Up. Pines	0.24	0.18	0.00	1.00
Prop. B. Hardwoods	77.88	11.86	35.71	97.57
Tmax	0.14	0.16	0.00	0.92
Precip	29.89	0.11	29.69	30.17

B.

Covariate	**Mean**	**SD**	**Min**	**Max**
Avg. Dist. Stream	0.65	0.35	0.06	2.10
Avg. Pressure	29.89	0.11	29.69	30.17
Prop. Up. Pines	0.47	0.13	0.01	0.94
Prop. B. Hardwoods	0.20	0.12	0.00	0.90
Tmax	77.88	11.86	35.71	97.57
Precip	0.14	0.16	0.00	0.92

C.

Covariate	**Mean**	**SD**	**Min**	**Max**
Avg.Dist.Stream	0.66	0.39	0.05	2.14
Prop. Up. Pines	0.48	0.16	0.00	1.00
Prop. B. Hardwoods	0.19	0.14	0.00	0.93

Table 3.2. Model selection results for variation in weekly home range size for wild pigs in the southeast United States between January 2017 and August 2020. Model variables include sex, proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), proportion of upland pines within the home range (Prop. Up. Pines), average maximum weekly temperature (Tmax), average weekly atmospheric pressure (Avg. Pressure), and average weekly precipitation (Precip). Model output includes the number of parameters (*K*), AIC$_c$ values, ΔAIC$_c$ values, and AIC$_c$ weights (ω_i).

Model	**K**	**AIC*c***	**ΔAIC*c***	**ωi**
Sex * Prop. B. Hardwoods + Tmax + Precip + Avg. Pressure	9	5782.33	0.00	0.73
Sex * Avg. Dist. Stream + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	10	5785.08	2.75	0.18
Sex + Avg. Dist. Stream + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	9	5787.96	5.63	0.04
Sex + Prop. B. Hardwoods + Tmax + Avg. Pressure	7	5789.56	7.23	0.02
Sex + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	8	5789.62	7.30	0.02
Sex * Prop. B. Hardwoods + Tmax + Precip	8	5791.81	9.48	0.01
Sex * Prop. B. Hardwoods + Tmax	7	5794.59	12.26	0.00
Sex + Prop. B. Hardwoods + Tmax + Precip	7	5799.01	16.68	0.00
Sex * Tmax + Prop. B. Hardwoods + Precip	8	5800.71	18.39	0.00
Sex + Prop. B. Hardwoods + Tmax	6	5801.36	19.03	0.00
Sex * Prop. B. Hardwoods	6	5805.35	23.02	0.00
Sex + Avg. Dist. Stream + Prop. B. Hardwoods	6	5811.54	29.21	0.00
Sex + Prop. B. Hardwoods	5	5813.32	31.00	0.00
Sex * Prop. Up. Pines + Tmax + Precip + Avg. Pressure	9	5826.15	43.83	0.00
Sex + Prop. Up. Pines + Tmax + Precip + Avg. Pressure	8	5830.06	47.74	0.00
Sex + Prop. Up. Pines + Tmax + Avg. Pressure	7	5830.43	48.10	0.00
Sex + Prop. Up. Pines + Avg. Dist. Stream + Tmax + Avg. Pressure + Precip	9	5832.06	49.73	0.00
Sex * Prop. Up. Pines + Tmax + Precip	8	5836.06	53.73	0.00
Sex * Prop. Up. Pines + Tmax	7	5838.97	56.64	0.00
Sex + Prop. Up. Pines + Tmax + Precip	7	5839.82	57.50	0.00
Sex * Tmax + Prop. Up. Pines + Precip	8	5841.74	59.41	0.00
Sex + Prop. Up. Pines + Tmax	6	5842.96	60.63	0.00
Sex * Prop. Up. Pines	6	5846.92	64.59	0.00
Sex + Prop. Up. Pines	5	5850.94	68.61	0.00
Sex + Prop. Up. Pines + Avg. Dist. Stream	6	5852.84	70.51	0.00
Sex + Avg. Dist. Stream	5	5855.37	73.04	0.00
Null (1|Pig ID)	3	5880.59	98.26	0.00
Avg. Dist. Stream	4	5882.60	100.27	0.00

Null (1|Social Group/Pig ID)	4	5883.71	101.38	0.00

Table 3.3. Standardized coefficient estimates ± standard error, p-values (*p)*, and 95% confidence intervals for the covariates included in the top generalized linear mixed-effects model for weekly 95% fixed-kernel home range estimates of wild pigs on the Savannah River Site in South Carolina based on GPS locations from January 2017 – August 2020. Covariates include the intercept (represents females as reference level), SexM (males), proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), average maximum weekly temperature (Tmax), average weekly atmospheric pressure (Avg. Pressure), and average weekly precipitation (Precip).

Covariate	**Estimate ± SE**	**Pr(>|z|)**	**Lower 95% CI**	**Upper 95% CI**
Intercept	1.30 ± 0.10	<0.001	1.10	1.51
SexM	1.14 ± 0.16	<0.001	0.84	1.45
Prop. B. Hardwoods	-0.44 ± 0.06	<0.001	-0.54	-0.33
Tmax	-0.07 ± 0.03	0.033	-0.13	-0.01
Avg. Pressure	0.10 ± 0.03	0.001	0.04	0.16
Precip	-0.04 ± 0.03	0.133	-0.09	0.01
SexM:Prop. B. Hardwoods	0.299 ± 0.10	<0.001	0.10	0.50

Table 3.4. Standardized coefficient estimates ± standard error, p-values (*p*), and 95% confidence intervals for the covariates included in the top generalized linear mixed-effects model for 50% fixed-kernel home range estimates of wild pigs on the Savannah River Site in South Carolina based on GPS locations from January 2017 – August 2020. Covariates include the intercept (represents females as reference level), SexM (males), proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), average maximum weekly temperature (Tmax), average weekly atmospheric pressure (Avg. Pressure), and average weekly precipitation (Precip).

Covariate	**Estimate ± SE**	**Pr(>|z|)**	**Lower 95% CI**	**Upper 95% CI**
Intercept	-0.22 ± 0.11	0.044	-0.42	-0.01
SexM	1.04 ± 0.16	<0.001	0.73	1.35
Avg. Dist. Stream	-0.07 ± 0.06	0.237	-0.18	0.05
Prop. B. Hardwoods	-0.27 ± 0.05	<0.001	-0.37	-0.17
Tmax	-0.04 ± 0.04	0.258	-0.11	0.03
Avg. Pressure	0.09 ± 0.03	0.008	0.02	0.15
Precip	-0.05 ± 0.03	0.131	-0.10	0.01
SexM:Avg. Dist. Stream	-0.27 ± 0.09	0.005	-0.45	-0.08

Table 3.5. Model selection results for variation in core area home range size for wild pigs in the southeast United States between January 2017 and August 2020. Model variables include sex, proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), proportion of upland pines within the home range (Prop. Up. Pines), average maximum weekly temperature (Tmax), average weekly atmospheric pressure (Avg. Pressure), and average weekly precipitation (Precip). Model output includes the number of parameters (*K*), AIC_c values, ΔAIC_c values, and AIC_c weights (ω_i).

Model	**K**	**AIC*c***	**ΔAIC*c***	**ωi**
Sex * Avg. Dist. Stream + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	10	2855.97	0.00	0.94
Sex + Avg. Dist. Stream + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	9	2861.73	5.76	0.05
Sex + Prop. B. Hardwoods + Tmax + Avg. Pressure + Precip	8	2870.06	14.09	0.00
Sex + Prop. B. Hardwoods + Tmax + Avg. Pressure	7	2870.39	14.42	0.00
Sex * Prop. B. Hardwoods + Tmax + Precip + Avg. Pressure	9	2871.36	15.40	0.00
Sex + Avg. Dist. Stream + Prop. B. Hardwoods	6	2871.80	15.83	0.00
Sex + Prop. B. Hardwoods + Tmax + Precip	7	2876.07	20.10	0.00
Sex * Prop. B. Hardwoods + Tmax + Precip	8	2877.29	21.33	0.00
Sex * Tmax + Prop. B. Hardwoods + Precip	8	2877.87	21.91	0.00
Sex + Prop. B. Hardwoods + Tmax	6	2878.73	22.76	0.00
Sex * Prop. B. Hardwoods + Tmax	7	2880.00	24.03	0.00
Sex + Prop. B. Hardwoods	5	2882.06	26.09	0.00
Sex * Prop. B. Hardwoods	6	2883.12	27.16	0.00
Sex * Prop. Up. Pines + Tmax + Precip + Avg. Pressure	9	2883.94	27.97	0.00
Sex + Prop. Up. Pines + Avg. Dist. Stream + Tmax + Avg. Pressure + Precip	9	2886.05	30.08	0.00
Sex + Prop. Up. Pines + Tmax + Precip + Avg. Pressure	8	2886.42	30.45	0.00
Sex + Prop. Up. Pines + Tmax + Avg. Pressure	7	2887.07	31.10	0.00
Sex * Prop. Up. Pines + Tmax + Precip	8	2889.18	33.22	0.00
Sex + Prop. Up. Pines + Tmax + Precip	7	2891.30	35.33	0.00
Sex * Prop. Up. Pines + Tmax	7	2891.51	35.54	0.00
Sex * Tmax + Prop. Up. Pines + Precip	8	2893.25	37.28	0.00
Sex + Prop. Up. Pines + Tmax	6	2894.18	38.21	0.00
Sex + Avg. Dist. Stream	5	2894.51	38.54	0.00
Sex * Prop. Up. Pines	6	2895.43	39.46	0.00
Sex + Prop. Up. Pines + Avg. Dist. Stream	6	2896.43	40.46	0.00
Sex + Prop. Up. Pines	5	2897.88	41.91	0.00
Avg. Dist. Stream	4	2918.05	62.08	0.00
Null (1|Pig ID)	3	2919.91	63.94	0.00
Null (1|Social Group/Pig ID)	4	2922.89	66.93	0.00

Table 3.6. Standardized coefficient estimates ± standard error, p-values (*p)*, and 95% confidence intervals for every one unit of standard deviation for the covariates included in the generalized linear mixed-effects models for 95% Minimum Convex Polygon (MCP) home range shape estimates of wild pigs on the Savannah River Site in South Carolina based on GPS locations from January 2017 – August 2020. Covariates include the intercept (represents females as reference level), SexM (males), proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), proportion of upland pines within the home range (Prop. Up. Pines), and average distance to stream (Avg. Dist. Stream).

Covariate	**Estimate ± SE**	**Pr(>|z|)**	**Lower 95% CI**	**Upper 95% CI**
Intercept	0.150 ± 0.007	<0.000	0.14	0.16
Avg. Dist. Stream	-0.002 ± 0.004	0.483	-0.01	0.00
Prop. Up. Pines	-0.005 ± 0.004	0.151	-0.01	0.00
Avg. Dist. Stream:Prop. Up. Pines	0.007 ± 0.002	0.004	0.00	0.01

Table 3.7. Model selection results for variation in home range shape for wild pigs in the southeast United States between January 2017 and August 2020. Model variables include proportion of bottomland hardwoods within the home range (Prop. B. Hardwoods), proportion of upland pines within the home range (Prop. Up. Pines), average distance to stream (Avg. Dist. Stream). Model output includes the number of parameters (*K*), AIC$_c$ values, ΔAIC$_c$ values, and AIC$_c$ weights (ω_i).

Model	**K**	**AIC*c***	**ΔAIC*c***	**ωi**
Avg. Dist. Stream * Prop. Up. Pines	6	-1949	0.00	0.80
Prop. Up. Pines	4	-1944	5.17	0.06
Avg. Dist. Stream + Prop. Up. Pines	5	-1943	6.16	0.04
Null(1|Pig ID)	3	-1942	7.26	0.02
Avg. Dist. Stream	4	-1941	7.56	0.02
Sex + Avg. Dist. Stream + Prop. Up. Pines	6	-1941	8.18	0.01
Sex * Avg. Dist. Stream + Prop. Up. Pines	7	-1940	8.54	0.01
Sex * Prop. Up. Pines + Avg. Dist. Stream	7	-1940	9.16	0.01
Avg. Dist. Stream * Prop. B. Hardwoods	4	-1940	9.26	0.01
Sex	4	-1940	9.28	0.01
Avg. Dist. Stream + Prop. B. Hardwoods	5	-1939	9.50	0.01
Avg. Dist. Stream * Prop. B. Hardwoods	6	-1938	10.68	0.00
Sex * Avg. Dist. Stream + Prop. B. Hardwoods	7	-1937	11.49	0.00
Sex + Avg. Dist. Stream + Prop. B. Hardwoods	6	-1937	11.52	0.00
Sex * Prop. B. Hardwoods + Avg. Dist. Stream	7	-1936	12.82	0.00

CHAPTER 4

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Despite the growing importance of wild pigs (*Sus scrofa*) as an invasive species, research investigating fine-scale behaviors and spatial ecology is relatively scarce. This is an important literature gap to fill because understanding the behaviors and spatial ecology of invasive wild pigs provides the ability to understand invasions as well as refine strategies to manage this destructive invasive species more effectively and efficiently. Within this Master’s thesis, using an extensive dataset of GPS locations for wild pigs, I evaluated common behaviors of wild pigs and how these behaviors corresponded with resources on the landscape, as well as, how wild pig home ranges are affected by vegetative composition, meteorological conditions, landscape characteristics, and demographic attributes. The results provide unique knowledge of specifics on behavioral state resource selection, activity patterns, and influencing factors of fine-scale movements for an invasive, generalist species that is adaptively managed yet understudied. Therefore, this thesis represents a contribution to the scientific literature of wild pig behavioral and spatial ecology.

In chapter 2, I used an extensive dataset of wild pig GPS data to demonstrate the variance in resource selection strategies employed by wild pigs at both a broad and fine spatial scale across two distinct seasons in the Southeastern U.S. I found that step-lengths and turning angles of wild pigs in our study were influenced by habitat attributes such as bottomland and upland hardwoods, streams, secondary roads, and shrub/herbaceous vegetation communities. Males and females selected similar vegetation types at the population scale; however, there were notable differences in the fine-scale use of habitats within home ranges between sexes and seasons. However, both males and females selected bottomland hardwood habitats and areas with extensive canopy cover consistently. Also, in using movement characteristics to define behavioral patterns, I found that females and males differed in daily activity patterns across seasons depending on forage availability. For example, females demonstrated a crepuscular activity pattern in the high-forage season and a variable pattern in the low-forage season, while males exhibited nocturnal activity patterns across both seasons. In addition, I found that wild pigs exhibited variance in selection of landscape attributes among behavioral states. For example, males selected for diversity in vegetation types while foraging in the low-forage season compared to the high-forage season and demonstrated an increased use of linear anthropogenic features across seasons while traveling. Furthermore, females selected areas near primary roads and bottomland hardwoods during the low-forage season, yet during the high-forage season they selected areas near upland hardwoods, upland pines, bottomland hardwoods, and areas near primary roads. Collectively, these results demonstrate that unique behavioral states provide unique insights into the relative importance of environmental attributes critical to the invasion of an ecosystem or management of a species that may otherwise be obscured through more coarse-scale resource selection, which in turn showed that male and female pigs exhibit clear differences in movement behavior and there are key resources associated with common behaviors that can be targeted to improve the efficiency of management programs.

In Chapter 3, using GPS data from wild pigs collected within a matrix of heterogeneously distributed bottomland hardwood (i.e., high-quality habitat) and upland pine (i.e., low-quality habitat) habitat, I have shown that weekly home range size and shape were influenced by a combination of biotic (i.e., vegetation types) and abiotic (i.e., temperature, precipitation, pressure, streams) environmental factors. Males demonstrated larger weekly home ranges and core areas compared to females. In addition, individuals maintained smaller home range and core area sizes in areas dominated by bottomland hardwood vegetation. However, at the home range scale this pattern was more pronounced for females than males. In addition, meteorological conditions including temperature and pressure were found to influence both female and male home range size, while pressure was the only influential meteorological variable at the core area scale. Furthermore, males had larger core areas at closer distances to streams, but females maintained consistent core area sizes across all distances to streams. Lastly, home range shape was driven by an interaction between low-quality habitat and average distance to streams in this study system. These results demonstrate the extent of wild pig home ranges and movements are variable and influenced by several abiotic and biotic factors that can easily be quantified from available land use and meteorological databases. Unique insights from this fine-scale study may be useful for monitoring populations, identifying high risk zones for diseases, and allowing more effective and efficient short-term management planning.

The conclusions of this research provide building blocks to build upon and continue to fill critical knowledge gaps regarding the ecology and management of wild pigs. Understanding how wild pigs use the landscape can provide an advantage for managers and/or disease biologists when trying to deploy traps, toxicants, attractants, etc. to ensure visitations occur quickly and consistently, and to predict areas of high risk for disease transmission. This knowledge, in conjunction with the knowledge of how the shape and size of wild pig weekly home ranges are influenced by vegetative composition, meteorological conditions, demographic attributes, and landscape characteristics, provides insight on the intricacies of wild pig spatial ecology that can better inform fine-scale management decisions to control this widespread invasive species. For all these reasons, this thesis represents an important contribution to the literature on wild pig spatial ecology, which should further contribute to the improvement of management for this widespread generalist species.