Spatial Ecology of Wild Pigs in Southwest Florida

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Abstract (Academic)

Wild pigs *(Sus scrofa*) are among the world's most destructive mammalian invasive species, and mitigating farther range expansion will require a thorough understanding of movement behavior, diel activity patterns, space use, and resource selection. Currently, limited empirical evidence is available on the ecology of wild pigs in Southwest Florida. Therefore, I examined how wild pigs behaviorally modified their movements and diel activity patterns in response to individual and environmental covariates. I investigated space use dynamics (e.g., home range size and seasonal variation) and evaluated how individual and environmental variation influenced home range size. Next, I determined how fine-scale movement patterns and resource selection of wild pigs are affected by temperature and time of day, and how those resources changed at broad and fine-scales, given their availability. I found that as temperature increased, the probability of foraging increased while the probability of traveling decreased. Foraging behavior occurred predominately between 8:00 and 17:00, and traveling behavior occurred predominately between 18:00 and 7:00, thereby indicating wild pigs were cathemeral. Home range size ranged from 2.6 to 35.8 km^2 and averaged 13.0 km^2 (n=16). Finally, home range size increased as the proportion of pasture increased and decreased as the proportion of wetlands increased, indicating that resources in agricultural areas were more diffuse than in natural habitats. At the broad (i.e., home range selection) and fine-scale (i.e., within home range) wild pigs selected for wetlands, forests, and pastures. Wild pig movement tended to be tortuous in forested and cropland habitats, but more directed in pasture habitats. Slower movements (i.e., smaller steps) and more directed (i.e., fewer turning) steps were observed during warmer temperatures, particularly avoiding croplands

when temperatures were warmer. Wild pigs avoided wetland habitats during dusk and night hours and cropland habitats during dawn hours. Wild pigs selected for forested habitats during night and dawn hours, possibly in response to human activity. In addition, I found that wild pigs were less likely to step into a location with a daily temperature of 35.7°C than 16.1 C°. Wild pigs were less likely to choose warmer locations and more likely to select intermediate temperatures, thus avoiding locations with extremely low or high daily temperatures. Also, I found that wild pigs were more likely to select home ranges nearer to wetlands, forests, and pastures, while avoiding areas near cropland habitats. However, within their home ranges they were more likely to select habitats farther from croplands, forests, and wetlands. My findings reinforce the importance of wetlands, forests and pastures to wild pig selection of home ranges, where they likely utilize these landcover types for thermoregulation (e.g. forests and wetlands) and for foraging resources (e.g. pastures). Within their home ranges wild pigs may avoid forests and wetlands due to perceived predation risk being higher in those habitats, thus causing wild pigs to forgo higher quality resources to reduce risk. These results contribute information useful to wildlife managers to better predict which landcover types provide refuge (e.g., wetlands and forests) or potential movement corridors (e.g., pasture and cropland habitats) for wild pigs. In Southwest Florida, wild pigs have broad inter-individual variation in home range size, are strongly regulated by temperature, and are largely dependent on wetlands and forests to meet their energetic demands.

Spatial Ecology of Wild Pigs in Southwest Florida

Christopher B. Satter

Abstract (Public)

Wild pigs are one of the world's most destructive invasive species. Although, hunters often oppose efforts to reduce wild pig populations, agricultural and natural resource managers support reduction efforts because they cause major economic and ecological damage. In addition, wild pigs carry a plethora of diseases and pose direct health risks to livestock, wildlife, and humans. Therefore, a better understanding of how environmental and landscape factors influence wild pig movements and space use is of broad interest to multiple stakeholder groups. I found that wild pigs mostly foraged during daytime and traveled at night, indicative of irregular activity patterns. Home range size averaged 13.0 km^2 across 16 individuals and tended to increase as the proportion of pasture habitat increased and decreased as herbaceous wetlands increased. This indicated that resources were more abundant in natural habitats. Wild pigs preferred wetlands, forests, and pastures, and avoided croplands. However, they were more likely to forage in forests and croplands, and travel in pastures. Wild pigs avoided wetlands during dusk and night hours and croplands at dawn, while selecting forests during night and dawn hours. Wild pigs tended to move slower with less turning during warmer temperatures, particularly avoiding croplands when temperatures were hot. In general, wild pigs avoided locations with extremely low or high daily temperatures. I found wild pigs were more likely to select home ranges nearer to wetlands, forests, and pastures, while avoiding areas near cropland habitats. Wild pigs likely utilized these landcover types for thermoregulation (e.g. forests and wetlands) and for foraging resources (e.g. pastures), while avoiding open areas (e.g. croplands) due to a lack of shade. However, within their home ranges they were more likely to select habitats farther from

croplands, forests, and wetlands, possibly because they perceived these areas to have higher predation risk. I highlight differences in space use among individuals and identify habitat types that are most likely to meet energetic demands. By understanding how environmental factors (e.g., habitat type and temperature) influence home range movement behaviors of wild pigs, land managers can focus on scale-dependent population control efforts. My results will aid land managers in better predicting which landcover types are providing refuge (e.g., wetlands and forests) or serving as potential movement corridors (e.g., pasture and cropland habitats).

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Chapter 1: Introduction – Wild pig space use and resource selection in Southwest Florida

Where wild pigs *(Sus scrofa*) are nonnative they are among the world's worst vertebrate species and cause significant damage to agriculture and the environment. Wild pigs are nonnative to Florida and are a major source of economic and ecological damage in the state. Negative interactions between the public and wild pigs are increasing with well-documented cases including digging up lawns and aggression toward residents. Nonetheless, in Southwest Florida, wild pigs are also important potentially as a sustaining prey species for endangered Florida panthers (*Puma concolor coryi*) and they are often considered prized by hunters (Maehr et al. 1990, Dalrymple and Bass, 1996). Florida's invasive wild pig populations occur statewide and are estimated to consist of at least 500,000 individuals, second only to Texas (Giuliano, 2010). These generalists are highly adaptive and occur in a variety of habitat types, usually preferring mesic conditions. Wild pigs are prolific breeders, and this creates challenges for population managers due to their short gestation period, early maturation, and large litter sizes (Caplenor et al. 2017). Multiple stakeholders with differing priorities regarding wild pigs can make consensus on management decisions difficult. For example, hunters often oppose efforts to reduce wild pig populations, whereas agricultural producers and natural resource managers support efforts to reduce wild pig populations because they annually inflict billions of dollars in damage to crops, livestock, native species, and ecosystem resources (Timmons et al. 2012; Krull et al. 2013; Pimental, 2007). Moreover, wild pigs also are known to carry at least 30 zoonotic diseases, and 37 types of parasites, highlighting how expanding populations may pose a direct health risk to livestock, especially domestic swine production, wildlife and humans (Centner and Shuman, 2015; Leiser et al. 2013). Therefore, factors influencing space use and behaviorally mediated movement patterns are of broad interest to land managers, the agricultural sector, and other stakeholder groups.

Understanding space use and movement pattern dynamics of wild pigs in Southwest Florida will provide information relevant to managers to aid in mitigating further range expansion and to manage wild pigs on a scale-dependent basis. Environmental conditions (e.g., temperature, precipitation, etc.) influence the space use, movement behavior, and resource selection of wild pigs (Clontz et al, 2021; Hartley et al. 2014; Thurfjell et al. 2014, Kay et al. 2017, Dexter, 1998). In addition, high-temperature avoidance behavior is thought to drive nocturnal or crepuscular diel activity patterns in wild pigs (Thurfjell et al. 2014; Gray et al. 2020; Clontz et al. 2021), which has been well-documented (Reinke et al. 2021; Johann et al. 2020; Gray et al. 2020; Thurfjell et al. 2014; Hartley et al. 2014). In addition, wild pigs can exhibit cathemeral activity patterns in the absence of hunting pressure by humans (Johann et al. 2020; Ohashi et al. 2013; Keuling et al. 2008). Nationally, wild pigs have a home range size of about 4.9 km^2 (McClure et al. 2015), which is the smallest area necessary to meet energy demands with the lowest cost of energy (Harestad and Bunnel, 1979). However, in the Southeastern Coastal Plain of the United States average home range size is 12.4 km^2 (Kay et al. 2017), which is closer to their range-wide estimate of about 10 km^2 (Mayer and Brisbin, 2009). Understanding home range size and factors that influence space use in Southwest Florida will equip wildlife managers with the information necessary to mitigate population growth and range expansion.

The United States Fish and Wildlife Service (USFWS) recovery criteria for the Florida panther (*Puma concolor coryi*) require the establishment of three panther populations, each with a minimum of 240 individuals. Thus, panther conservation efforts aim to increase the number of Florida panthers and encourage the populations to expand northward into unoccupied portions of the species’ historic range. From a sociological perspective, panther recovery is partially dependent on society understanding the effects of the panther population on resources that people value, as well as the intrinsic value of the panther itself. Research should facilitate the societal discussion regarding human-predator coexistence by providing information on the effects of panthers on the ecosystems they inhabit, with acute focus on the interactions that influence resources valued by society. Wild pigs are an important prey species for the endangered Florida panther, and are a natural host for a plethora of zoonotic diseases (e.g. pseudorabies) which can be spread to native wildlife (Cunningham et al. 2021). For example, pseudorabies was found to be the cause of death for an estimated 9% of radio-collared panthers in Southwest Florida (Cunningham et al. 2021). In addition, due to reports of recreational sport hunters being concerned about anecdotal declines in wild pig populations, which they’ve associated with increased Florida panther populations, coupled with declines in pig harvests through time, Florida state wildlife agencies had interest in better understanding the space use and resource selection of wild pigs in Southwest Florida on a landscape shared with the Florida panther.

The goal of my project was to study the spatial ecology of wild pig populations in Okaloacoochee Slough and Dinner Island Ranch Wildlife Management Areas in Southwest Florida, USA, across heterogeneous habitat types and environmental conditions (Figure 1). Specifically, I investigated wild pig space use (i.e. home range), behavioral modification of movement in response to environmental variation, and resource selection at broad and fine-scales. I had 5 objectives: 1) I examined spatial and temporal (e.g., hourly) movement behaviors as a function of environmental and individual covariates using hidden Markov models; 2) I investigated space use dynamics (e.g., seasonal variability in home ranges within and among individuals) using continuous-time stochastic process movement models; 3) I used generalized linear models to evaluate individual and environmental variation in home range size; 4) I evaluated integrated step selection to better understand how movement patterns and resource selection of wild pigs are affected by temperature and time of day; and 5) I estimated population-level resource selection patterns at the second and third order to evaluate habitat selection, given availability.

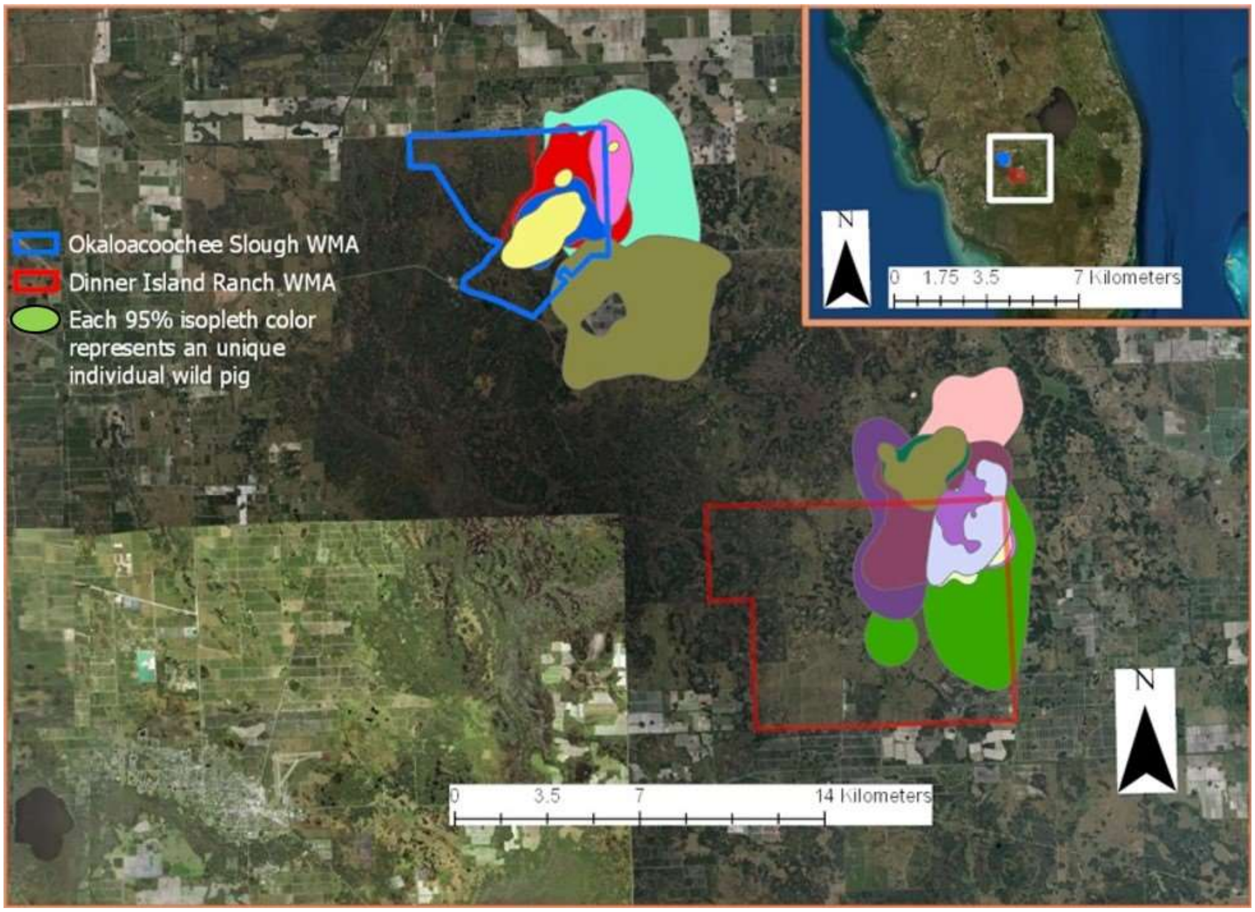

Figure 1. Study sites and 95% isopleth home ranges for 16 individual wild pigs (Sus Scrofa) in Okaloacoochee Slough and Dinner Island Ranch Wildlife Management Areas in Southwest Florida, USA, 2019-2021.

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Chapter 2. Wild pig movement behavior and influence of habitat type on seasonal space use in Southwest Florida.

Abstract

Quantifying animal space use patterns and spatiotemporal movement behaviors allows investigators to better understand how home range and movement varies across heterogeneous landcover types and diel activity periods. Wild pigs *(Sus scrofa*) are among the world's worst vertebrate pests in their nonnative range, and control efforts require an understanding of habitat associations, diel activity patterns, and space use. However, this information is lacking in many areas, including Southwest Florida, where pigs are particularly destructive to agricultural and ecological resources. Therefore, to study wild pig movement behavior and space use in Southwest Florida, we quantified diel activity patterns using hidden Markov models to infer movement path characteristics (resting, foraging, rooting, traveling) and recorded activity and temperature using collar-mounted sensors. We used autocorrelated kernel density estimation to evaluate differences in seasonal space use and assess the effects of landcover on variation in home range size to better understand which habitats were most energetically productive. We found that as activity level increased, the probability of traveling increased, and the probability of resting or foraging decreased. As the temperature increased, the probability of foraging increased, whereas the probability of traveling decreased. Foraging behavior occurred predominately between 8:00 and 17:00, and traveling behavior occurred predominately between 18:00 and 7:00, thereby indicating wild pigs were cathemeral. Home range size ranged from 2.6 to 35.8 km^2 and averaged 13.0 km^2 km^2 (n=16) for all individuals. Finally, home range size increased as the proportion of pasture landcover type increased and decreased as herbaceous wetlands increased, indicating that resources in agricultural areas were more diffuse than in natural habitats. Our results highlight broad inter-individual variation in space use and species-habitat association, which will help fill knowledge gaps by increasing the efficacy of control efforts in Southwest Florida.

Key words: Habitat, ctmm, hidden Markov models, home range, movement behavior, wild pigs

Introduction

Understanding the movement behavior of invasive species offers insight into mitigating potential ecological issues, including zoonotic disease spread, ecosystem disruption, and economic burden (Shackleton et al. 2019; Mazza et al. 2014; Crowl et al. 2008). The global risk potential of invasive species to inflict widespread changes to the environment underlines the importance of research on their ecology to guide policy formulation and management decisions (Pejchar and Mooney, 2009; Shackleton et al. 2019). Native to Eurasia and north Africa, the wild pig *(Sus scrofa*) now has one of the largest geographic distributions among terrestrial mammals and currently occupies all continents except Antarctica (Garza et al. 2017). In Florida, USA, wild pigs occur statewide across a landscape mosaic of vegetative types. These generalists are highly adaptive and occur in a variety of habitat types usually preferring forested areas with abundant food sources (e.g., acorns), interspersed with mesic habitats (e.g., forested wetlands, marshes, sloughs) to keep from overheating by wallowing in mud (Giuliano, 2010). In addition, wild pigs are a major source of economic (Pimental, 2007; Krull et al. 2013) and ecological damage and pose a direct health risk to wildlife and humans through disease transfer (Leiser et al. 2013;

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Centner and Shuman, 2015). Thus, a better understanding of their spatial ecology across different spatial and temporal scales is of broad interest to land and agricultural managers and other stakeholder groups (e.g., hunters), particularly in Southwest Florida where anecdotal evidence suggests a possible decline in wild pig populations.

Wild pig movement ecology is understudied across Southwest Florida, with limited information available on their spatiotemporal distribution. The distribution of resources is partly what drives those spatiotemporal distributions. Therefore, by studying how environmental covariates (e.g., sex, temperature, precipitation) and resources (e.g., habitat types) influence space use and movement behavior (i.e., spatial distributions) of wild pigs, we can inform management decisions on public and private lands. Also, by studying the diel activity of wild pigs and their responses to environmental variations in the climate (e.g., season and temperature), we can further understand potential drivers of short (e.g., foraging) and long-distance (e.g., traveling behavior) movements of wild pigs. This information will help equip wildlife managers with the necessary knowledge to mitigate range expansion and disease spread in the population (Clontz et al. 2021).

Home range is typically defined as the space traversed by an animal in its daily activities, which contains resources essential to finding food, reproduction, and caring for young (Burt 1943). Conversely, this area may shift through time if those critical resources change, in which case, it may be referred to as a seasonal range. Factors influencing space use dynamics are typically a direct function of landscape productivity and indicate geographic regions on the landscape where energy demands are being met in smaller areas of high productivity (Harestad and Bunnel, 1979). Therefore, animals are then likely to exploit resources in more productive habitats, thus reducing long distance movement behaviors (Smith et al. 2022), ultimately leading to smaller home range sizes. A knowledge gap of empirical evidence depicting inter-individual changes in space use over time and space (e.g. over wet and dry seasons) will lead to challenges in mitigating species population growth and further range expansion (Schlichting et al. 2016). Wild pigs are known to exhibit site fidelity, but space use is influenced by climate (e.g., water availability and temperature), food and resource availability, reproductive opportunities, and hunting pressure (Froehly et al. 2020; Kay et al. 2017; McClure et al. 2015). Male and female wild pigs typically establish home ranges and become residents (i.e., remain within their home range) for varying periods of time (Gatson et al. 2008), with sounders (groups of females and young) typically staying together (Sparklin et al. 2009; Kaminski et al. 2005), whereas males compete with one another for females and territory and will travel long distances to establish their own home ranges (Rosell et al. 2004). Wild pig home range size varies across their geographic range, but on average is about 10 km^2 across their native and nonnative ranges (Mayer and Brisbin, 2009). In the United States, home range size tends to be smaller than their geographic range, with a national average estimated to be 4.9 km^2 (McClure et al. 2015), although a more recent meta-analysis across six states in the Southeastern United States estimated an average home range size of 12.4 km^2 (Kay et al. 2017).

Fine-scale GPS data allow investigators to interpret movement patterns by observing the unique behavioral characteristics of a species, which can then be classified into behavioral responses or movement states (Goodall et al. 2019). Hidden Markov models are state-transition models that categorize the underlying movement process (i.e., time-series movement data) or behavior during the time period between successive GPS locations, into distinct behavioral states (Michelot et al. 2016; Goodall et al. 2019). Therefore, animals exhibiting short or intermediate step length measurements (e.g., slow-moving state) may be indicative of resting or foraging behavior. Conversely, animals exhibiting long step length measurements (e.g., faster movement state) may be indicative of transitory or traveling behavior. Associated with the speed of each movement state are directional changes known as turning angles (Michelot et al. 2019). Thus, low rates of turning may be indicative of individuals exhibiting more directional or straightforward movements, whereas high rates of turning may be more indicative of exploratory or foraging behavior.

An important tool for quantifying space use patterns is continuous-time stochastic process movement models because they account for the inherent multiscale autocorrelation structure (e.g., position and velocity autocorrelation) of movement data (Fleming et al. 2015; Calabrese et al. 2016). Quantifying animal space use patterns allows investigators to better understand how animals utilize heterogeneous composition and configurations across different landscape types. Previous studies investigating home range size for wild pigs used older methods that resulted in sample size bias (Jennrich and Turner, 1969; Fleming et al. 2015), failed to account for autocorrelation in the data, (Silverman, 1986; Fleming et al. 2014a) and lacked methodology to identify non-range resident individuals, thus disregarding heterogeneity in space use (Morato et al. 2016).

Florida's rapid population growth and landscape changes (e.g., increased development), likely induce variation in space use and movements of wild pigs. Wild pigs are a highly adaptive species that will adapt to changes in their environment (e.g. climate, anthropogenic pressure, or season) by behaviorally modifying their movements and space use dynamics. Therefore, we predicted that individuals should exhibit larger movement patterns in the dry season (i.e., October to May) to utilize lower daily temperatures and to search for more abundant resources (e.g., water availability). Wild pigs are susceptible to heat stress (Johann et al. 2020) and rely on panting or external sources in the environment (e.g., shade and water) to regulate their body temperatures. Therefore, we explored diel activity in space use and predicted that wild pigs should exhibit nocturnal behavior due to thermoregulatory limitations. We predicted that the average home range size should vary with landcover types such that higher quality (i.e. more resource rich) habitats (e.g. wetlands, forests, croplands) should be smaller compared to lower quality (i.e. resource poor) habitats (e.g. pasture), given that energy demands should be met in smaller areas (Harestad and Bunnel, 1979). However, we expected some variation among and within individual home range sizes, resulting in home range shifts, potentially reflecting seasonal differences. Lastly, we predicted that the highest proportion of wild pig locations would occur in forested and wetland habitats that provided cover for thermoregulation and concealment from predators.

Materials and Methods

Study area

Our study took place in Okaloacoochee Slough Wildlife Management Area (WMA) and Dinner Island Ranch WMA, both of which were located south of the Caloosahatchee River in Clewiston, Southwest Florida (Figure 1). Okaloacoochee Slough WMA is managed by the Florida Forest Service (e.g., 34,722 acres; 140.5 km^2) and Florida Fish and Wildlife Conservation (FWC) (~8527 acres; 34.5 km^2), consists of recreational lands. Okaloacoochee Slough WMA is comprised of restored pasture lands, slough marsh, basin marsh, depression marsh, wet prairie, mesic hammocks, and mesic flatwoods. In addition, a portion of the area has been planted with Florida slash pine (*Pinus elliottii*), for timber production. Dinner Island Ranch WMA protects 21,714 acres (87.87 km^2) of recreational lands. The area was managed by FWC and was comprised of pasture, cypress (Taxiodium spp.), marsh, pine flatwoods, and hammocks consisting of various hardwood and palm species, such as live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*). Portions of Dinner Island Ranch WMA have active cattle grazing and citrus production contracts, whereas Okaloacoochee WMA contains abandoned pasture land and is not leased for cattle or citrus production. Although Dinner Island Ranch WMA used cattle grazing to manage plant succession, both sites were actively restoring portions of pasture to pine flatwoods, wetlands, hardwood hammocks, and natural hydrologic systems.

The carnivore guild that could potentially prey on wild pigs included the Florida panther (*Puma concolor coryi*), Florida black bear (*Ursus americanus floridanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and the American alligator (*Alligator mississippiensis*). General habitat management techniques on the WMAs included prescribed fires, cattle grazing, chemical or mechanical treatments, restoring natural hydrology regimes, citrus production, and removal of invasive exotic plant species. In addition, habitat and harvest management included hunting of species such as white-tailed deer (*Odocoileus virginianus*) and wild pigs to generate revenue and mitigate environmental damage.

Capture and monitoring

We captured and collared 16 adult and subadult pigs (≥ 23.0 kg) with ATS model G5-2D global positioning system (GPS) tracking collars (Advanced Telemetry Systems, Isanti, Minnesota, USA). Wild pigs were captured in Okaloacoochee Slough WMA, and Dinner Island Ranch WMA using open-topped corral and box traps. We assembled circular corral traps using 16' x 5' welded wire livestock panels with no larger than 4"x4" openings. We made box traps by welding a steel frame, 2.4 meters long, 1.8 meters wide, and 1.5 meters high, with a trigger mechanism attached to a guillotine door. This trap allows for quick assembly and breakdown in field settings and was set and checked twice daily (morning and evening). Traps were placed in shaded areas to prevent pigs from overheating or being exposed to extreme solar radiation. Because wild pigs typically travel in large family groups, large corral traps are more effective in capturing the entire group, which otherwise could cause stress to separated group members. Push doors were installed to allow additional hogs to enter the trap after the first animals were captured. Open-topped trap designs are advantageous over other trapping methods because they allow for the easy escape of most non-target wildlife that can climb or jump over livestock panels. However, any non-target species remaining in the trap were released as soon as possible. Traps were pre-baited with shelled corn to attract pigs. Trapping occurred during all seasons of the year, but traps remained closed if ambient temperatures were projected to rise above 32.2 C to avoid heat stress or below -7.7 C, which rarely occurs in Southwest Florida as temperatures rarely drop below 4.4 C. We estimated the body weights of pigs with a portable battery-operated digital veterinary scale.

We chemically immobilized wild pigs using a .22 caliber cartridge-fired rifle with a 5cc slow-inject disposable dart (Model 389, Pneu-Dart Inc., Williamsport, PA, USA) by injecting them with a mixture of Xylazine (4.4 mg/kg), Telazol (4.4 mg/kg), and Ketamine (2.2 mg/kg) intramuscularly (e.g., shoulder, rump). We reversed Xylazine with Tolazoline (2.0 mg/kg) administered via intravenous injection of half of the required Tolazoline dosage into the lateral auricular ear vein and intramuscular injection of the remaining dosage of Tolazoline into the hindquarter of the animal (Swindle 2015). We monitored wild pigs until full recovery to ensure the safety of the animals and researchers. We applied ophthalmic ointment to both eyes to prevent desiccation. We monitored heart rate, respiratory rate, and collar temperature every 10 minutes during anesthesia until full recovery. We handled pigs without administering anesthesia if they were < 7 kg in body weight. For all captured wild pigs, we recorded sex, weight, and morphological measurements. We programmed GPS collars to a fix rate at half-hour intervals recording 48 locations/day. The satellite transmission interval and mortality rate schedule were programmed at 4 hours intervals.

Florida Fish and Wildlife Conservation Commission Division of Hunting and Game Management issued a Special Purpose Permit for Dinner Island Ranch WMA for trapping periods: 4/2/2019 – 7/31/2019 (permit number: SPGS-19-24); 11/11/2019 – 7/31/2020 (permit number: SPGS-19-63). Okaloacoochee Slough WMA trapping periods included: 3/02/2020 – 7/31/2020 (permit number: SPGS-19-63-A1), and all procedures were permitted by Virginia Tech Institutional Animal Care and Use Committee Protocol number: 18-248. We conducted animal handling in accordance with the American Society of Mammologists (ASM) guideline (Sikes et al. 2016).

Data analysis

We used hidden Markov models (HMMs) in the R package moveHMM (Michelot et al. 2016) to model behavioral differences in movement among wild pigs, which implement Markov chains to generate a sequence of states. The hidden Markov models measure the speed of animal movement (i.e., step length) along with their associated turning angles or changes to the distribution of direction in movement (Michelot et al. 2016). The step length parameter was estimated with a gamma distribution, and the turning angle parameter with a von Mises distribution (Michelot et al. 2016). The maximum likelihood-based hidden Markov models assume animal locations are sampled at equally spaced points in time and are observed with zero or negligible error (Michelot et al. 2019). To maximize the likelihood function and avoid convergence issues, we chose initial parameter values for the state-dependent distributions by selecting values as close as possible to the true maximum likelihood (Michelot and Langrock, 2019). For all step length and turning angle parameters (e.g., mean, standard deviation, zero mass parameter, angle concentration), we simulated starting values at random from a distribution of plausible values and followed all data preparation and initial parameter value recommendations from Michelot and Langrock (2019).

We ran ten 3-state hidden Markov movement Models (HMM) across both sites and were parameterized according to a priori movement behavior hypotheses. For example, we expected that wild pigs' movement states would include: state 1 (A) = short steps and low rates of turning (i.e., resting state). State 2 (A) = intermediate steps and high rates of turning (i.e., foraging state), and state 3 (A) = long steps and low rates of turning (e.g., directional state); State 1 (B) = short steps and high rates of turning (i.e., rooting or wallowing state); state 2 (B) = intermediate steps and low rates of turning (i.e., walking state), and state 3 (B) long steps and high rates of turning (i.e., exploratory or transitory state). We modeled the state transition probabilities as functions of three continuous environmental predictor variables and one discrete individual predictor variable: activity (i.e., activity levels indicate the percentage of seconds that the collar detected significant movement between the previous fix until the current fix), collar temperature, rain, and sex (Figure 2). Rainfall data were obtained by aggregating the total daily rainfall values (meters) from June 2019 to February 2021, attained from hydrologic-well data provided by the Southwest Florida Water Management District's corporate environmental database (DBHYDRO, 2021; RAIN; DBKEY: VN400; Station: SIX L 3_R). We implemented GPS fix rate data at half-hour intervals into HMM models. To account for initial convergence failure, all initial values were tested randomly. All continuous covariates were standardized (i.e., scaled and centered) for numerical stability and to reduce convergence failure when trying to reach convergence of the global maximum of the likelihood function (Michelot et al. 2019). We used diagnostic plots

(Time Series, QQ-Plots, Autocorrelation Functions of the Pseudo-Residuals) to check model fit and used Akaike information criterion (AIC) in R-package ‘AIC.moveHMM’, as our model selection criterion (Burnham and Anderson, 2002).

We produced wild pig home range estimates using the autocorrelated kernel density estimator (AKDE) in the continuous-time movement modeling (ctmm) R package (Fleming et al. 2015; Fleming and Calabrese, 2021-R package version 0.6.1). To implement the AKDE method, we first used visual diagnostics (e.g., empirical variogram) to provide an unbiased means of visualizing the autocorrelation structure and distinguish between resident (i.e., the tendency of an animal to remain within its home range) or nomadic individuals (Calabrese et al. 2016). For example, evidence of range residency is typically depicted by a variogram that eventually reaches an asymptote, which is proportional to home range size (Calabrese et al 2016). Once individuals were confirmed to show evidence of range residence, we selected initial autocorrelation parameter estimates and chose the best-supported maximum likelihood-based movement model to identify the appropriate autocorrelation structure in the data (Calabrese et al. 2016). We estimated home range crossing (i.e., on average, the number of days an individual takes to cross their home range) and the effective sample size (i.e., the number of range crossings that occurred during the observation period), calculated as T/τ, where T is the total amount of time an individual was tracked, and τ is the average time required for an individual to cross the linear extent of its home range (Silva et al. 2021). To select the most appropriate candidate movement model, we used Akaike’s Information Criterion (Burnham and Anderson, 2002) to select from the following list of candidate models: independent identically distributed process (IID), Brownian Motion (BM), Ornstein Uhlenbeck (OU), Integrated Ornstein Uhlenbeck (IOU), or the Ornstein-Uhlenbeck Foraging (OUF) process. We used the most appropriate model given the data to estimate the 95% AKDE home range contours and confidence intervals for each individual wild pig. In addition, we compared 95% seasonal home range estimates for ten individuals that were tracked for at least two seasons (wet or dry) or longer, by dividing the year into wet (May-October) and dry (October-May) based on NASA'S MERRA-2 Modern-Era Retrospective Analysis models for Clewiston, Florida (https://gmao.gsfc.nasa.gov/reanalysis/MERRA-2/ ; Gelaro et al. 2017).

We estimated the effects of habitat type on variation in home range size by modeling environmental and individual predictor covariates (i.e., sex, body weight, collar temperature, and precipitation), as well as the proportions of landcover type within home ranges using the raster package in Program R (Hijmans, et al. 2015). We used the 2019 landcover data from the National Landcover Database (NLCD; Jin et al. 2019) to generate individual raster layers for 9 landcover variables including: (1) forest (i.e., deciduous forest, evergreen forest, mixed forest), (2) pasture hay, (3) cultivated cropland, (4) wetlands (i.e., woody wetlands, emergent herbaceous wetlands), (5) open water, (6) development (i.e., open space, low intensity, medium intensity, high intensity), (7) barren land (i.e., rock/sand/clay), (8) shrub/scrub, (9) grassland/herbaceous. To quantify the proportions of landcover within each wild pig home range we summed the cells for each landcover type and divided each by the total number of cells of all landcover types within the home range polygon to calculate a proportion of landcover types within each animal's home range. We used a forward stepwise model selection procedure to identify possible predictor variables. At each step, variables were added based on p-values and R^2, and AICc (e.g., eliminating variables with >2 delta AICc) of the top model was used to set a limit on the total number of variables in the final model. We fit generalized linear models (GLM) in the program R package lme4, with a Gaussian distribution to model additive and interactive effects on the home range size. We tested the response variable (individual home range size) against three habitat variables (pasture hay, woody wetlands, and herbaceous wetlands) using an alpha level of 0.05. We tested for multicollinearity using the Variance Inflation Factor (VIF) with (>10) indicating potential collinearity issues. Finally, we used diagnostic plots (residuals vs. fitted, normal Q-Q, scale-location, residual vs leverage plot) to check model fit and used log-likelihood based AIC, in R-package stats, as our model selection criterion (Burnham and Anderson, 2002).

Results

Summary statistics

Across both sites and years, we had a total sample size of 16 individual wild pigs (Table A1). We captured and collared ten pigs on Dinner Island Ranch WMA (8M, 2F) and six pigs on Okaloacoochee Slough WMA (5M, 1F). Collared pigs on Dinner Island Ranch WMA had an average functioning collar retainment rate of 6.85 months and 5.83 months in Okaloacoochee Slough WMA. Across both sites, the longest length of time an individual retained a functioning collar was 17.22 months and the shortest was 0.60 months. Across both sites, body weight ranged from 46.0 to 102.9 kg for males and 24.2 to 44.5 for females kg (Table A1).

Hidden-Markov Movement States

Our top two models generated estimates using three-state hidden Markov models (HMMs) to estimate step length distribution and turning angle distribution for wild pigs (Table A2). The top model incorporated covariate ‘activity’, and the second top model incorporated covariate ‘temperature’, which was measured by the deployed GPS collars (Table A3). Stationary state probabilities as a function of ‘activity’, with 95% confidence intervals, demonstrated that as activity level increases, the probability of being in states 1 and 2 decreases, and the probability of being in state 3 increases (Figure 3). However, as temperature increases the probability of being in state 3 decreases (Figure 3). Temporal diel activity distribution measured hourly for states 1-3 demonstrated that wild pigs were predominantly in state 2 (intermediate step lengths and high rates of turning) between ~ 8 am to 5 pm, and state 3 (i.e., long step lengths and low rates of turning) between ~ 6 pm to 7 am, indicative of foraging behavior during day time hours and nocturnal behavior during the night and early morning hours (Figure 4). Temporal distribution measured on a monthly scale demonstrated that wild pigs had the highest likelihood of being in state 3 (i.e., long step lengths and low rates of turning) between months February to August, with the largest movements between June to August months (Figure 5). Thus, wild pigs seem to show evidence of increased movements during the warmer months of the year. Throughout the study, wild pigs spent 19.2% of the time in a resting state, 34.1% of the time in a foraging state, and 46.7% of the time in a traveling state and thus were most frequently in state 3, indicative of overall larger movement rates.

Continuous-time Movement model (CTMM)

We estimated 95% AKDEs home ranges for 16 individual wild pigs (13 males, 3 females) across Dinner Island Ranch WMA and Okaloacoochee Slough WMA (Figure 6). Home range size ranged from 2.64 to 35.81 km^2 and averaged 13.0 km^2 (95% CI = 10.7 – 15.6 km^2) across individuals (Figure 7). Home range crossing time ranged from 0.33 to 2.91 days and on average took wild pigs 1.28 days to cross their home range. The effective sample size ranged from 25 to 218 and averaged 118.8 range crossings that occurred during the observation period. Most individual wild pigs demonstrated evidence of range residency, given the asymptotic relationship in their empirical variograms. However, three males and one female deviated from range residency (i.e., remained within their home range) starting between 3-5 months from being fitted with a GPS Collar (e.g., Figure 8). However, the effective sample size (i.e., the number of range crossings that occurred during the observation period) for all individuals still contained a sufficient number of range crossing estimates during the observation period to adequately estimate home range size. Therefore, we did not discard non-range residents from our average home range estimate (Silva et al. 2021). We selected the AIC OUF-Anisotropic top model for all 16 individuals. The OUF top model accounts for restricted space use, autocorrelated positions and autocorrelated velocities (Calabrese et al. 2016). After overlaying home ranges on a topographical base map in Arcgis Pro (ArcGIS, 2018), home range estimates show possible evidence of overlap among individuals (Figure 1). The majority of individuals had estimated 95% CIs for home range that overlapped zero (figure 7). For ten individuals that were tracked for a minimum of two seasons (wet or dry), 95% home range CIs did not overlap zero for one male and one female wild pig (Figure 9). Although the empirical variograms for those individuals demonstrated linear increases at intermediate time lags (i.e., within a few days) and asymptotic relationships (i.e., suggesting restricted space use), seasonal differences in home range seemed to occur during the transition from wet to dry season), or from dry to wet season for those two individuals.

Generalized Linear Model

To better understand how much variation in home range size was explained by landcover type and individual covariates we used a generalized linear model (GLM) in the program R package lme4, with a Gaussian distribution, to model all possible combinations of predictor variables, which included proportion of landcover types: pasture, woody wetlands, and herbaceous wetlands against response variable individual home range size, with additive and interactive effects (Table A4). The model explained ~ 97% (i.e., adjusted R^2) of the variation in home range size. Parameter estimates demonstrated significance in the main effect predictor variables pasture (β = 2.61; SE = 0.89; Pr(>|t|) = 0.02) and herbaceous wetlands (β = -7.85; SE = 2.34; Pr(>|t|) = 0.01). (Table A4, Figure A3-diagnostic plots). We found evidence that home range size increased as the proportion of pastures increased and decreased as herbaceous wetlands increased. Within each home range, 56% of landcover types were pasture, 20% herbaceous wetlands, 13% woody wetlands, 6% croplands, and ≥ 2% were composed of the remaining habitat types.

Discussion

The heterogenous landcover types in Southwest Florida likely induce variation in space use and movements of wild pigs, while shifts in diel activity patterns can influence movement behavior (Giuliano et al. 2010). Investigating space use, movement behavior and diel activity patterns of wild pigs will allow us to better understand their spatial ecology. Wild pigs are a highly adaptive species that will adapt to changes in their environment (e.g. temperature or anthropogenic pressure) by behaviorally modifying their movements and space use dynamics.

We conducted this study to better understand wild pig movement behavior and space use in Southwest Florida. Wild pigs are known to expand their home range in search of food and water during dry years (Finzel and Baldwin, 2015). Therefore, we predicted that individuals in Southwest Florida should exhibit larger movement patterns in the dry season (e.g., October to May) when various types of hard mast become most available in Southwest Florida. On the contrary, using a multi-state hidden Markov approach, we found evidence that the highest likelihood of large movements (e.g., traveling behavior) occurred in the warmer, wetter months from June to August (Figure 4). Wild pigs across both of their native and introduced ranges have been observed moving larger distances during summer months, likely in response to thermoregulatory limitations (e.g., increased water availability) and, in some places, increased food availability (Thurfjell et al. 2014). Given that one of our study sites is used for citrus production, and both sites are adjacent to private farmlands that were leased for grazing, hunting, farming, and other land management operations, it is plausible that nearby food sources (e.g., remaining watermelon and citrus crops left over after the last harvest) become more accessible during the warmer months of the year, thus influencing movement behavior (Dardaillon, 1987; Kay et al.2017). However, seasonal modifications in movement behavior could be driven by breeding behavior (e.g., males traveling large distances to search for females) (Giuliano, 2010) or to search for other seasonal food sources such as saw palmetto berries (*Serenoa repens*), which become ripe and abundant from August through October (UF|IFAS, 2021).

Poor thermoregulatory abilities in wild pigs are well-documented, as they are known to be sensitive to heat (Johann et al. 2020; VerCauteren et al. 2019; Bracke et al. 2011). Wild pigs will modify their movements in response to thermoregulation (Clontz et al, 2021; Hartley et al. 2014; Kay et al. 2017, Dexter, 1998). We observed a similar relationship between temperature and movement, where the probability of larger movements decreased as ambient temperatures increased (Figure 2). Heat thresholds have been documented for wild pigs in the Southern United States (Kay et al. 2017; Froehly et al. 2020); however, their populations are also limited by cold temperatures and the availability of water throughout the United States (McClure et al. 2015).

Our data provided evidence of cathemeral movement behavior in wild pigs, given that foraging behavior occurred predominately during daytime hours, and traveling behavior occurred predominately during night hours. Several studies of wild pigs across their range have reported nocturnal or crepuscular activity patterns (Reinke et al. 2021; Johann et al. 2020; Gray et al. 2020; Thurfjell et al. 2014; Hartley et al. 2014). Nocturnal behavior is commonly thought of as high-temperature avoidance behavior (Thurfjell et al. 2014; Gray et al. 2020; Clontz et al. 2021), where wild pigs spend more than half of the day resting (Johann et al. 2020). Wild pigs are known to exhibit diurnal activity patterns in colder months as a behavioral means of controlling their collar temperature (Mayer and Brisbin, 2009). Our study sites offer hunting opportunities for wild pigs, deer and other species. Therefore, anthropogenic disturbance may explain localized foraging behavior during the day and traveling behavior at night when hunting pressure is reduced (Johann et al. 2020; Ohashi et al. 2013; Keuling et al. 2008). Wild pigs living in areas with undisturbed conditions and low anthropogenic pressure may exhibit more cathemeral activity patterns (Johann et al. 2020). Although, differences in diel activity between males and females have been documented for wild pigs (Clontz et al. 2021), we did not find support for a sex effect on temporal distribution, potentially because of a low female sample size.

Home range size ranged from 2.6 to 35.8 km^2 and averaged 13.0 km^2 (10.7 – 15.6 km^2) across individuals. Our estimate is higher than the reported national average of 4.9 km^2 (McClure et al. 2015) but closer to the range-wide average of 10 km^2 (Mayer and Brisbin, 2009). In addition, our estimates are similar to those for other wild pigs in the southeastern United States ($\bar{x}$ =12.4 km^2), whose investigators implemented an AKDE approach (Kay et al. 2017). Previous home range estimates may be negatively biased because older methods did not account for autocorrelation in the data (Fleming et al. 2014a,b). In general, the literature suggests home range size varies widely across their geographic range, and the types of estimators used. In addition, home range sizes for wild pigs living in mesic environments tend to be smaller than that of wild pigs in xeric environments (Adkins and Harveson, 2007; Mayer and Brisbin, 2009; Schlichting et al. 2016). However, other factors such as wild pig population densities, availability of food, water, escape cover, and body weight, may contribute to overall home range size (Mayber and Brisbin, 2009). We expected seasonal home range differences within each individual home range, which we observed for two individuals. However, the majority of wild pigs had no observable differences in home range size between wet and dry seasons. The empirical variograms plotted for all 16 individual wild pigs indicated evidence that four individuals deviated from home range residency somewhere between 3 to 5 months while being monitored by GPS collars. Deviations from range residency could be the result of an individual not being tracked long enough to reveal their true home range extent (Calabrese et al. 2016). However, in our study, the effective sample size (i.e., the number of range crossings that occurred during the observation period) for the individual with the shortest duration of tracked data (i.e., ~ 0.6 months) still contained a sufficient number of range crossing estimates during the observation period to adequately estimate home range size. Wild pigs are known for wandering or drifting, but typically do exhibit site fidelity through time (Mayer and Brisbin, 2009). Thus, evidence of range shifts in wild pigs likely occur because of either opportunistic food sources, mating behavior, or seasonal resource change, which is well-documented in the literature (Singer et al. 1981; Dardaillon, 1987; Gatson et al, 2008; Kay et al. 2017).

We predicted wild pig home ranges would be a function of habitats that provided shade, concealment from predators, and mesic substrate for wallowing. Wild pig home ranges were comprised mostly of pasture (56%), followed by herbaceous wetlands (33%), croplands (6%), and remaining landcover types (e.g., ≤ 2%). We found evidence of pasture and herbaceous wetland habitats explaining the most variation in home range size (Table A5). For example, home range size increased as the proportion of pastures increased and decreased as herbaceous wetlands increased, indicating that resources in agricultural areas were more diffuse than in natural habitat. Thus, wild pigs likely utilized these more productive habitats because their energy demands were met with the lowest cost of energy (Harestad and Bunnel, 1979). The highly adaptive generalist ecology of wild pigs has allowed them to be successful in utilizing suitable habitats across their North American range (West et al. 2009). Wild pigs have been well-documented using wetland habitats (Kay et al. (2017; Gastson et al. 2008; Wood and Brenneman, 1980), pasture habitats (Mersinger and Silvy, 2007; Barrett, 1982) and cropland habitats (Kay et al. 2017). Each of these habitat types provide essential food resources ((Froehly et al. 2020; McClure et al. 2015; West et al. 2009), cover for shade, and concealment from predators for wild pigs. A meta-analysis that examined 31 different studies found a negative association between home range and rainfall (Schlichting et al. 2016). Similarly, we used rainfall as a proxy for surface water levels and did not find evidence of a relationship to home range size.

Wild pig space use and movement vary widely across their geographic range, largely due to their generalist life-history traits. However, our study largely aligns with results produced from other wild pig studies examining space use and movement. To the best of our knowledge, we produced the first estimates of home range and movement behavior in Florida. Our study sites undergo active cattle grazing (e.g., Dinner Island Ranch WMA), pasture restoration, and agriculture. Therefore, the high proportions of wild pig locations found in pasture, croplands, and wetland habitats is a reason for concern. Wild pigs are likely impacting habitat restoration, food production, native habitat ecology, and threatened or endangered plant and animal species due to rooting, trampling, and compaction of sensitive lands (West et al.2009). Another area of concern is that high proportions of wild pigs in pastures with active cattle management threaten the spread of zoonotic diseases (e.g., Pseudorabies) to cattle, hunting dogs, and native wildlife (Hernández et al. 2018). Our results highlight broad inter-individual variation in space use and species-habitat association, which will help fill knowledge gaps by increasing the efficacy of control efforts in Southwest Florida.

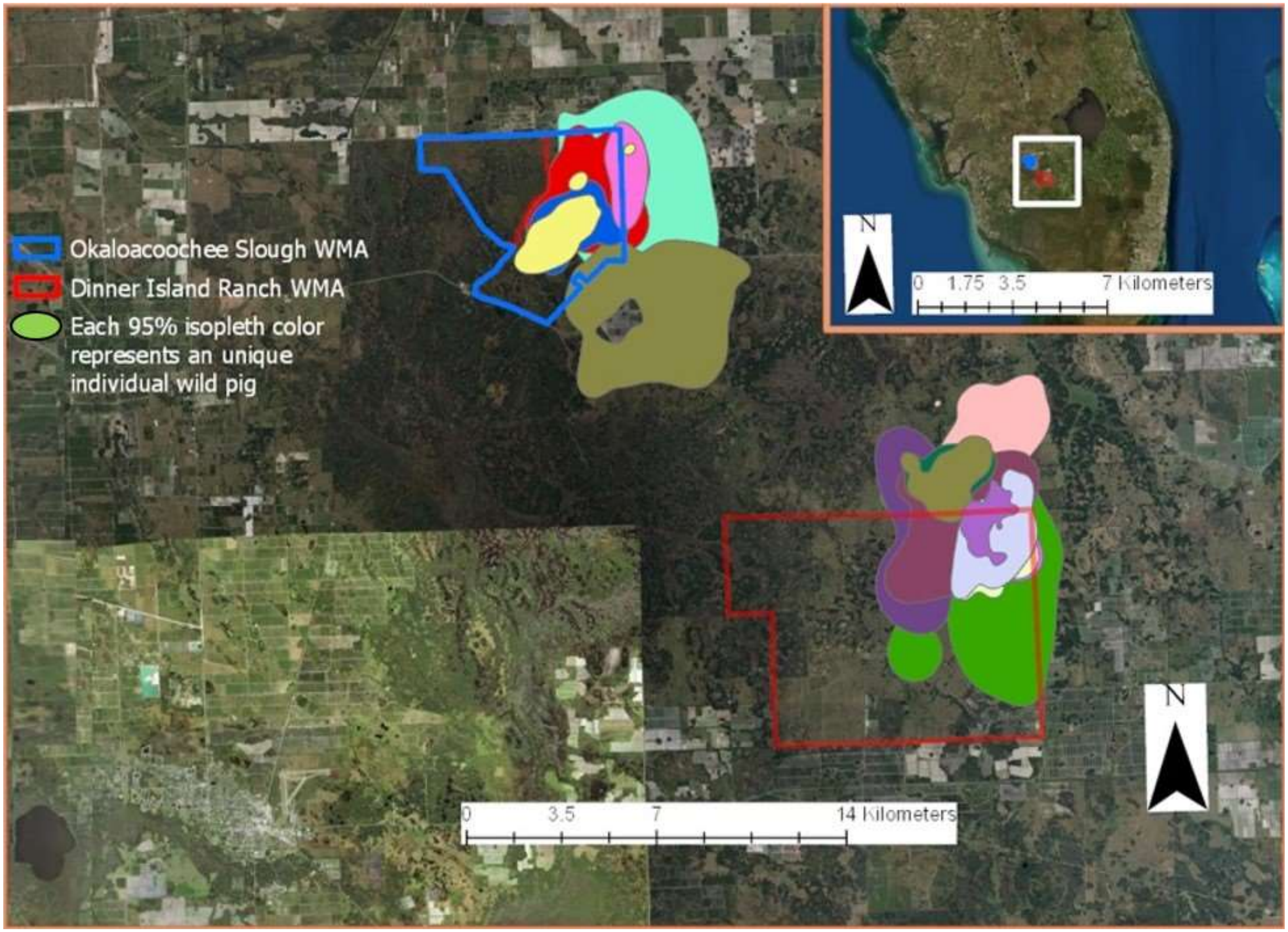

Figure 1. Study sites and 95% isopleth home ranges for 16 individual wild pigs (Sus Scrofa) in Okaloacoochee Slough and Dinner Island Ranch Wildlife Management Areas in Southwest Florida, USA, 2019-2021.

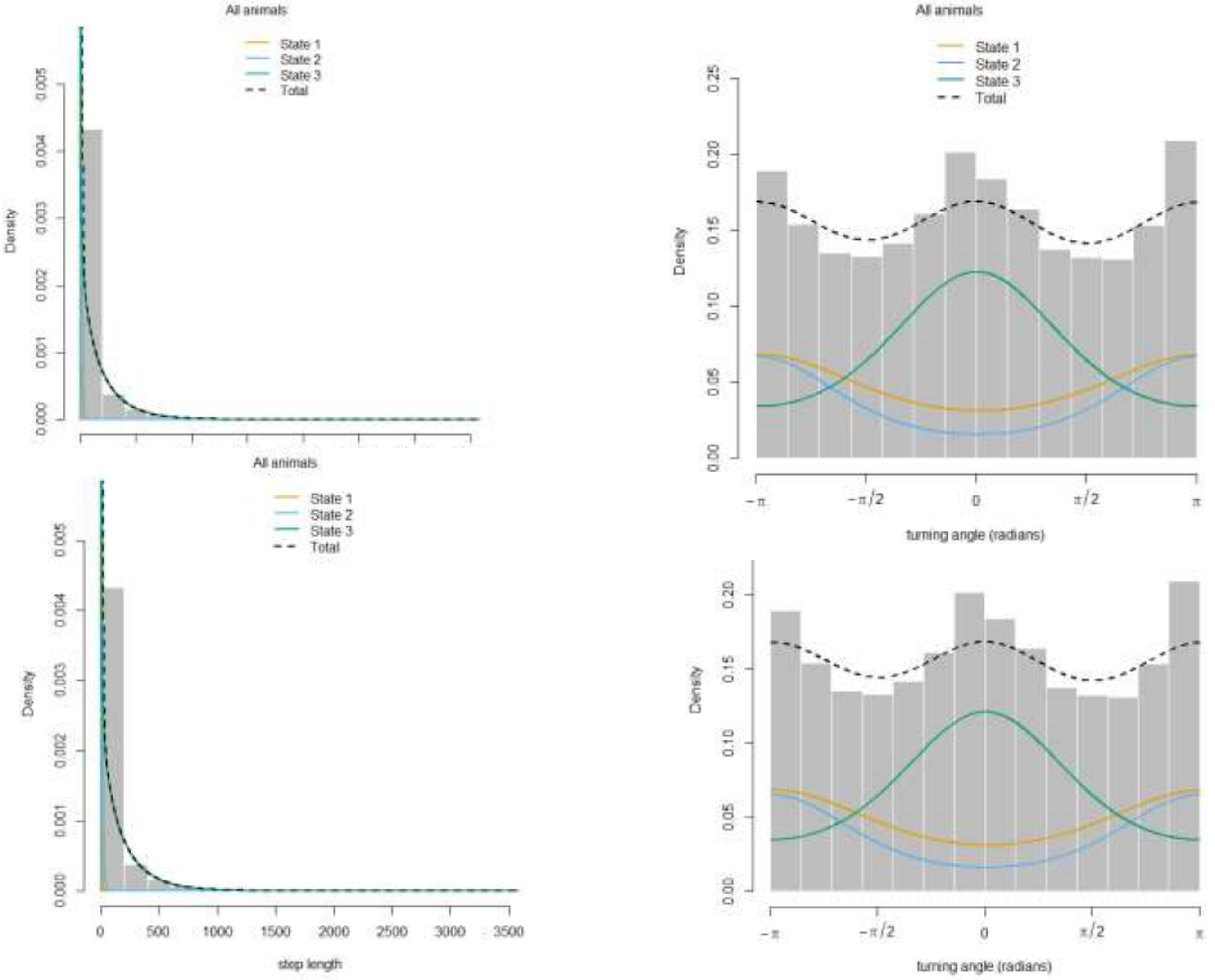

Figure 2. Histograms of observed step lengths and turning angles of fitted distributions as a function of activity (i.e., top model - upper) and temperature (competing model - bottom). Fitted distributions for both models were very similar, given that they were derived from three-state models with the same initial parameter values (e.g., models A). States are: 1 = resting, 2 = foraging, 3 = directional or traveling. Study was conducted in Okaloacoochee Slough and Dinner Island Ranch Wildlife Management Areas in Southwest Florida, USA, 2019-2021.

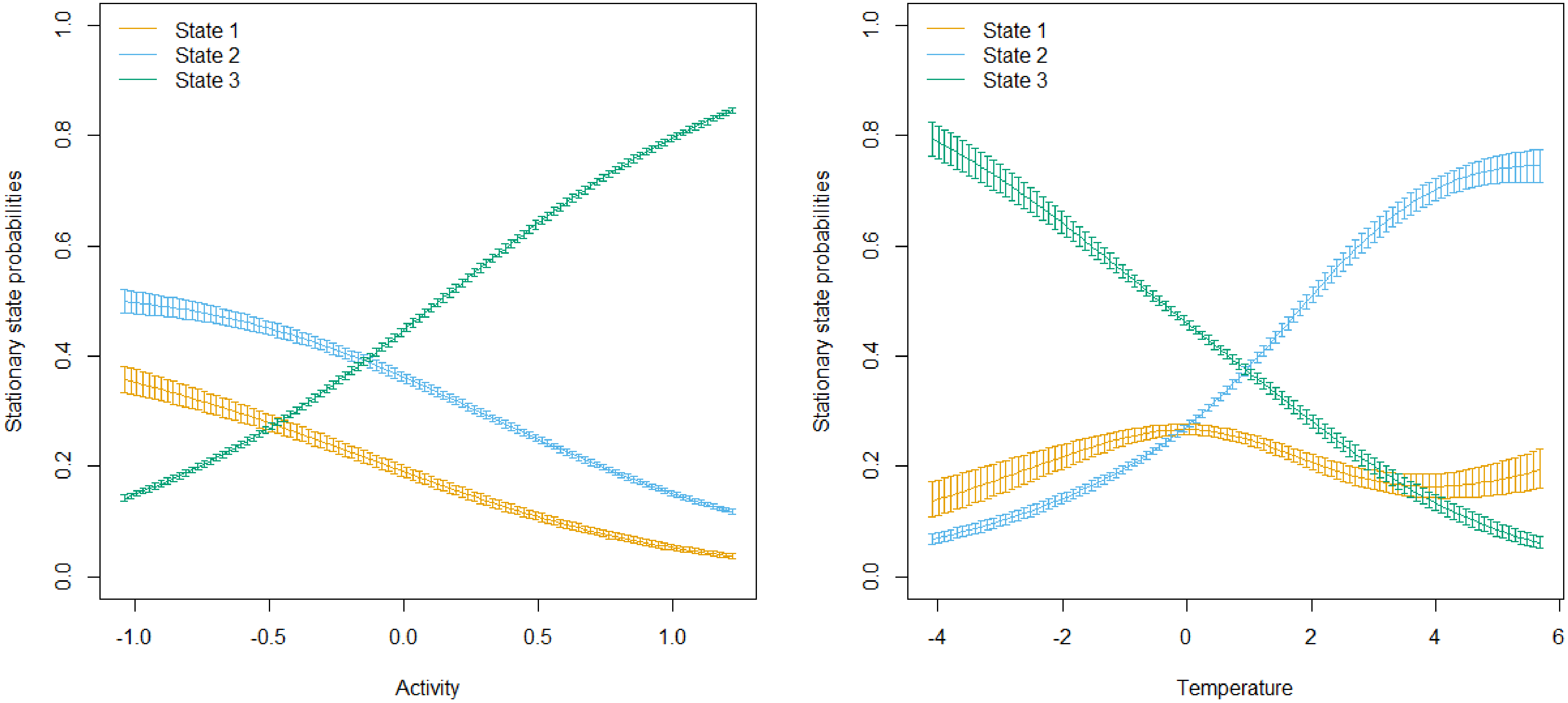

Figure 3. Stationary state probabilities as a function of ‘activity’, with 95% confidence intervals on Dinner Island Ranch and Okaloacoochee Slough wildlife management areas (WMAs) in Southwest Florida, USA, 2019-2020. As activity level (left) increases, the probability of being in states 1 and 2 decreases, and the probability of being in state 3 increases. As temperature (right) increases the probability of being in state 3 decreases, while the probability of being in state 1 remains constant and the probability of being in 2 increases. States are: 1 = resting, 2 = foraging, 3 = directional or traveling.

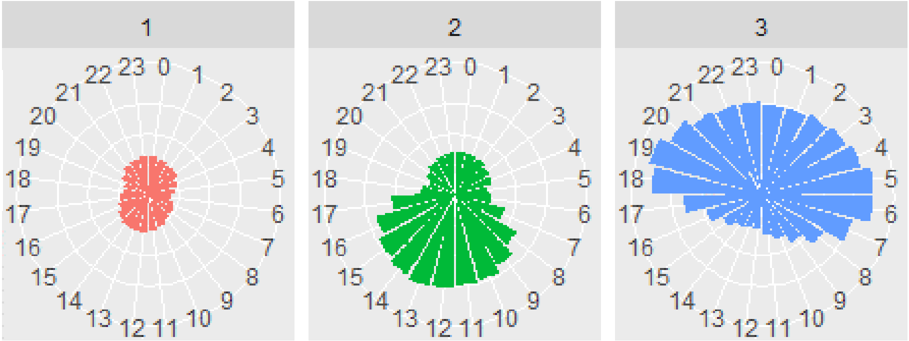

Figure 4. Temporal distribution (hour: 0-24) for states 1-3 for wild pigs on Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA in Southwest Florida, USA, 2019-2020. Wild pigs were predominantly in state 2 (intermediate step lengths and high rates of turning) between ~ 8 am to 5 pm and state 3 (i.e., large step lengths and low rates of turning) from ~ 6 pm to 7 am, indicative of transitory, exploratory behavior. States are: 1 = resting, 2 = foraging, 3 = directional or traveling.

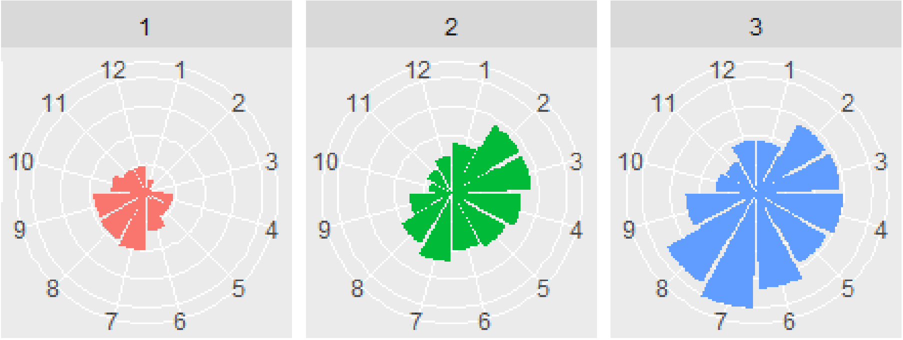

Figure 5. Temporal distribution (months: 1-12) for states 1-3 for wild pigs on Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA, Southwest Florida, USA, 2019-2020. Wild pigs were predominantly in state 3 (i.e., large step lengths and low rates of turning) between months February to August, with the highest probability of large movements occurring between June to August. States are: 1 = resting, 2 = foraging, 3 = directional or traveling.

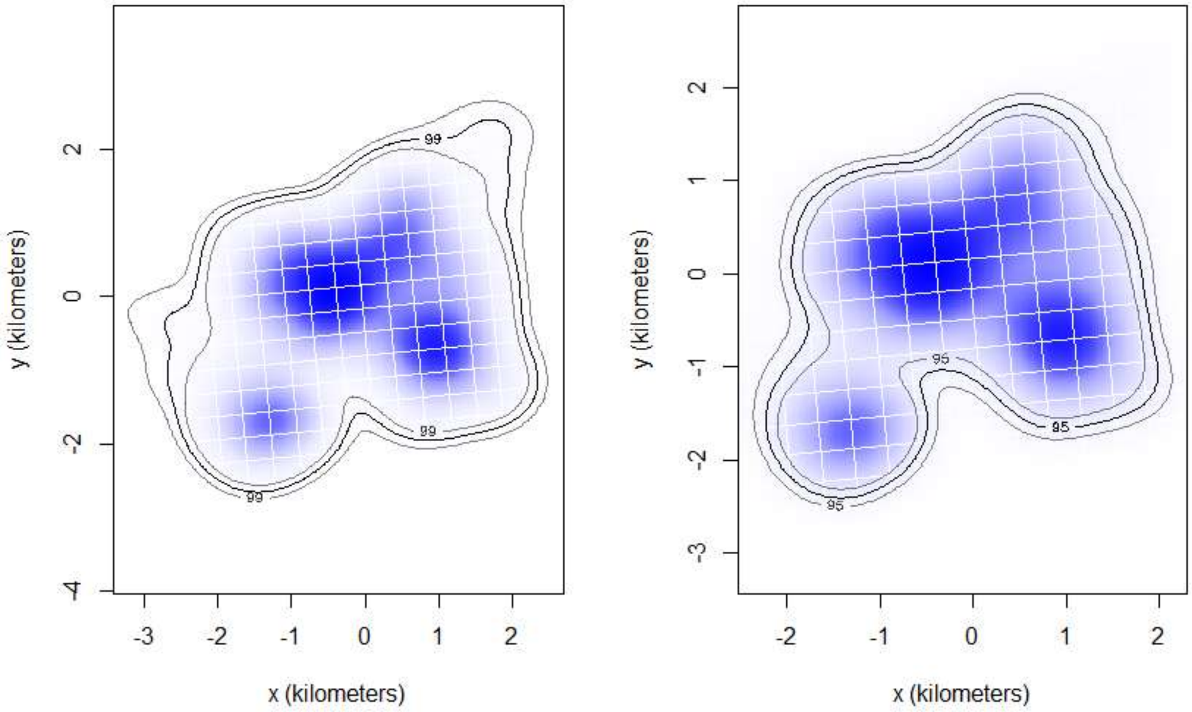

Figure 6. Autocorrelated kernel density (AKDE) plots depicting home range contours and 99 (left) and 95% (right) isopleths for individual 2. The middle black contour lines represent the home range area estimate, while the lighter contours represent 95-99% confidence intervals. The grid lines depict the bandwidth size and spatial resolution of the home range estimate. This individual was captured and collared in Dinner Island Ranch Wildlife Management Area, Southwest Florida, USA, 2019-2020.

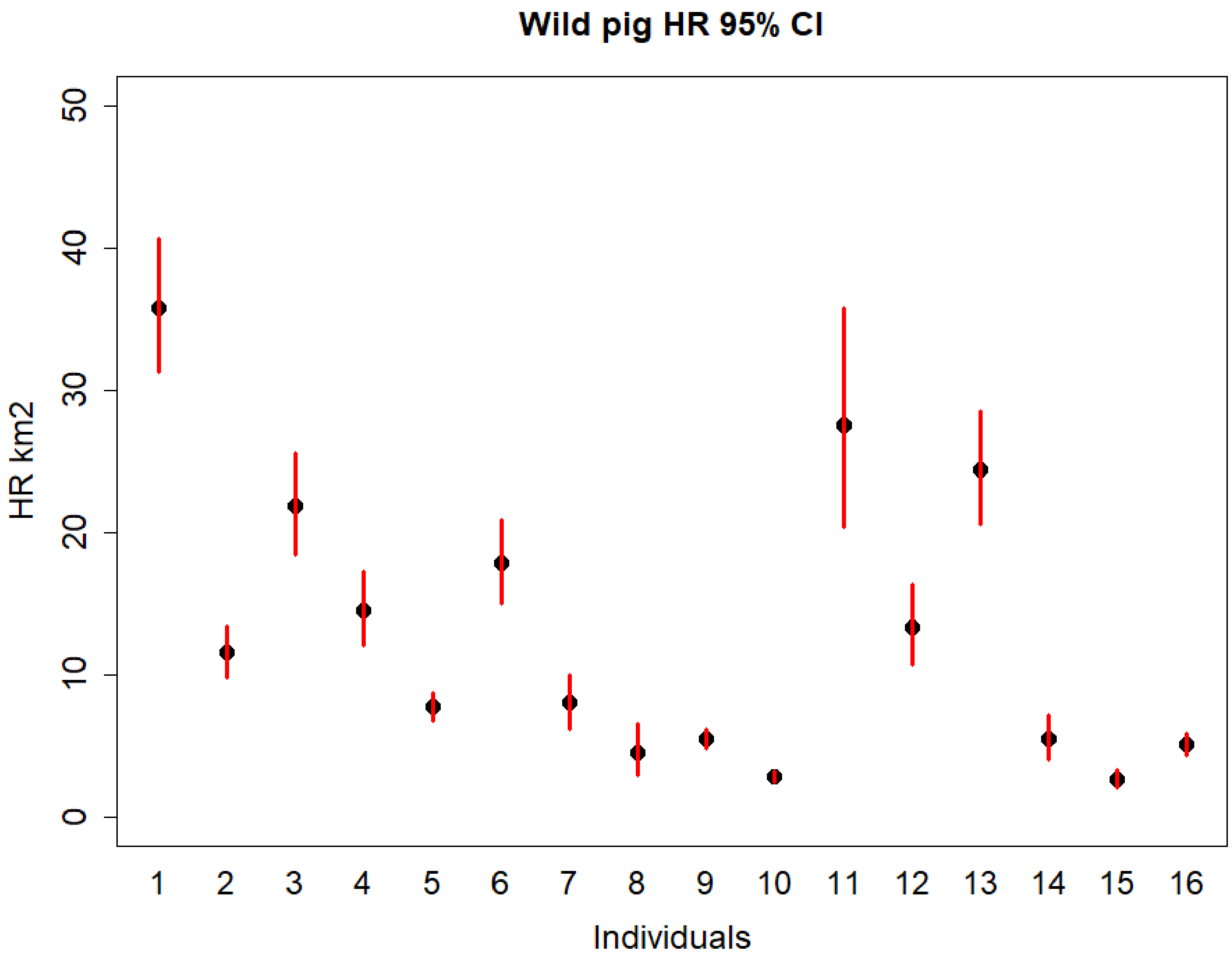

Figure 7. Home range point estimates (black dots) and 95% confidence intervals (CI; red lines) of 16 wild pigs on Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA in Southwest Florida, USA, 2019-2020.

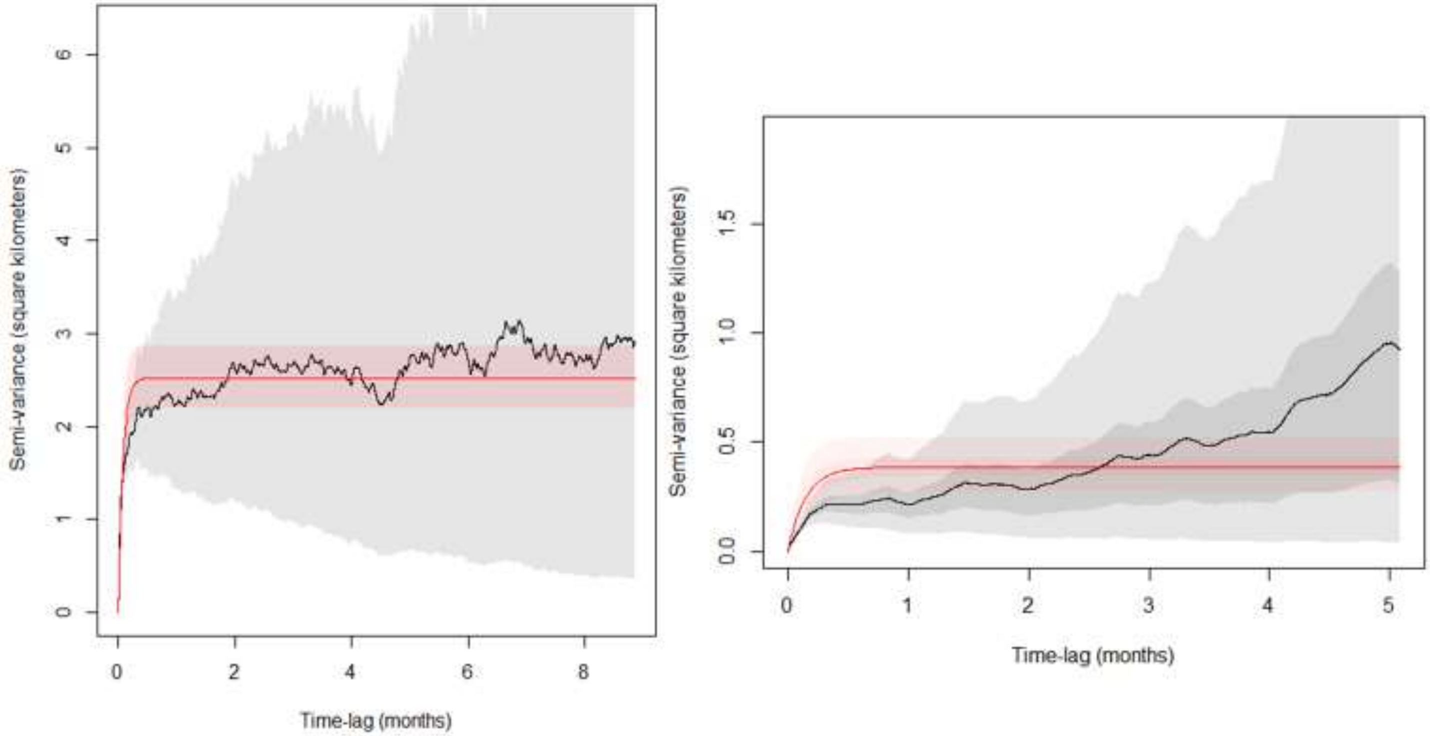

Figure 8. Empirical variograms depict the semivariance of a range resident wild pig (left) and a temporary resident wild pig (right). The individual in plot (left) shows evidence of reaching an asymptote within a few days, roughly representing the time it takes to cross its home range. Individual wild pig (right) reaches an asymptote for the first ~ 2 months but then appears to shift its home range after ~ 2.5 months. These individuals were captured and collared in Dinner Island Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

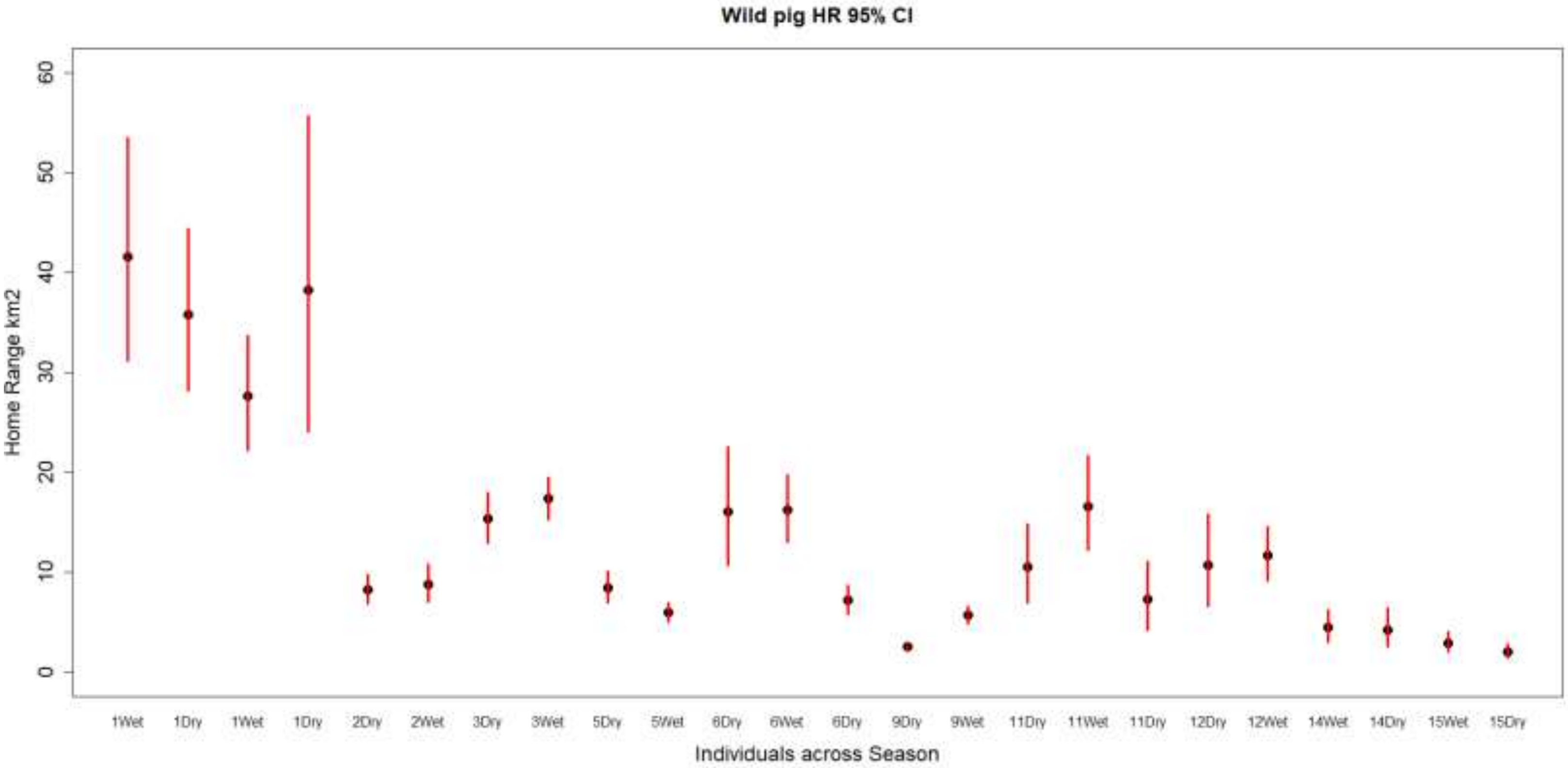

Figure 9. Seasonal home range point estimates (black dots) and 95% confidence intervals (CI; red lines) for 10 wild pigs on Dinner Island Ranch wildlife management area (WMA) and Okaloacoochee Slough WMA in Southwest Florida, USA, 2019-2020. Each point estimate refers to an individual and their home range size for that particular season (i.e., wet or dry). Some individuals were observed over multiple seasons but were tracked for a minimum of two seasons. Season were categorized into wet (May-October) and dry (October-May).

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Appendix A. Summary statistic and movement model figures and tables

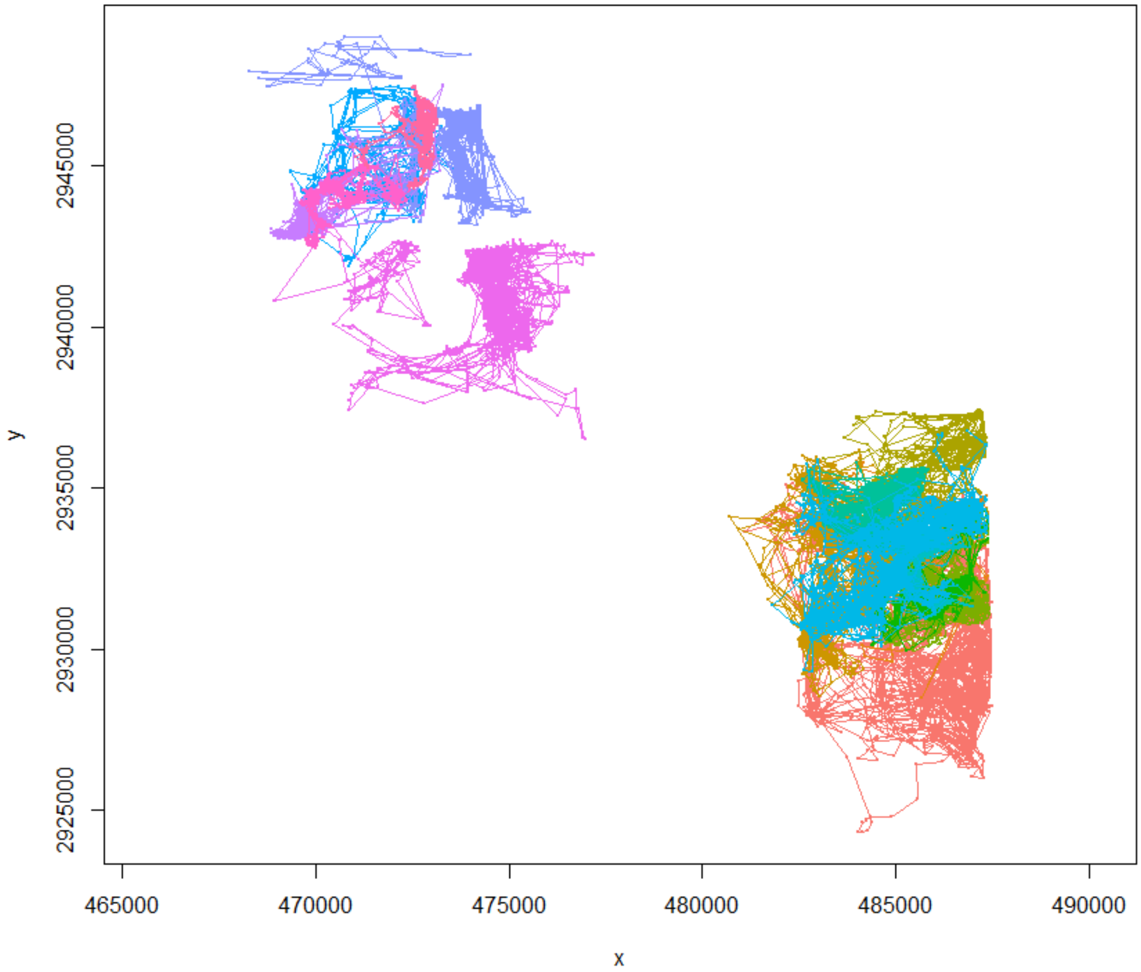

Figure A1. Movement patterns from all individuals on Dinner Island Ranch wildlife management area (WMA) and Okaloacoochee Slough WMA, Southwest Florida, USA, 2019-2020. Each color represents an individual wild pig.

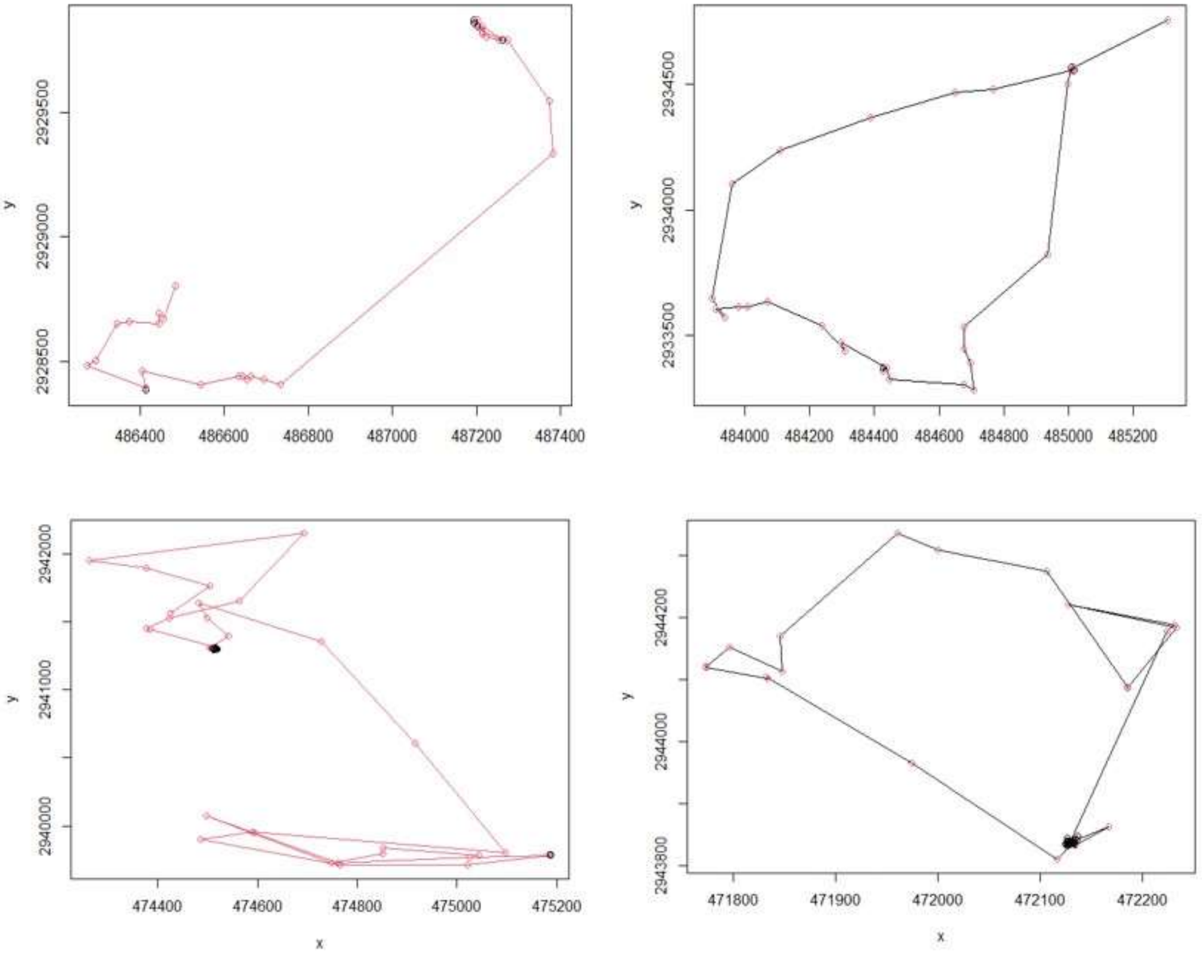

Figure A2. Twenty-four-hour movement tracks for 4 individuals from July 18, 2020 to July 19, 2020 from 7 am to 7 pm on Dinner Island Ranch wildlife management area (WMA) and Okaloacoochee Slough WMA, in Southwest Florida, USA, 2019-2020. The x-axis is in UTM coordinate system with tick marks 200 meters apart. Upper left = male in Dinner Island Ranch WMA; upper right = female in Dinner Island Ranch WMA, lower left = male in Okaloacoochee Slough WMA, lower right = female in Okaloacoochee Slough WMA.

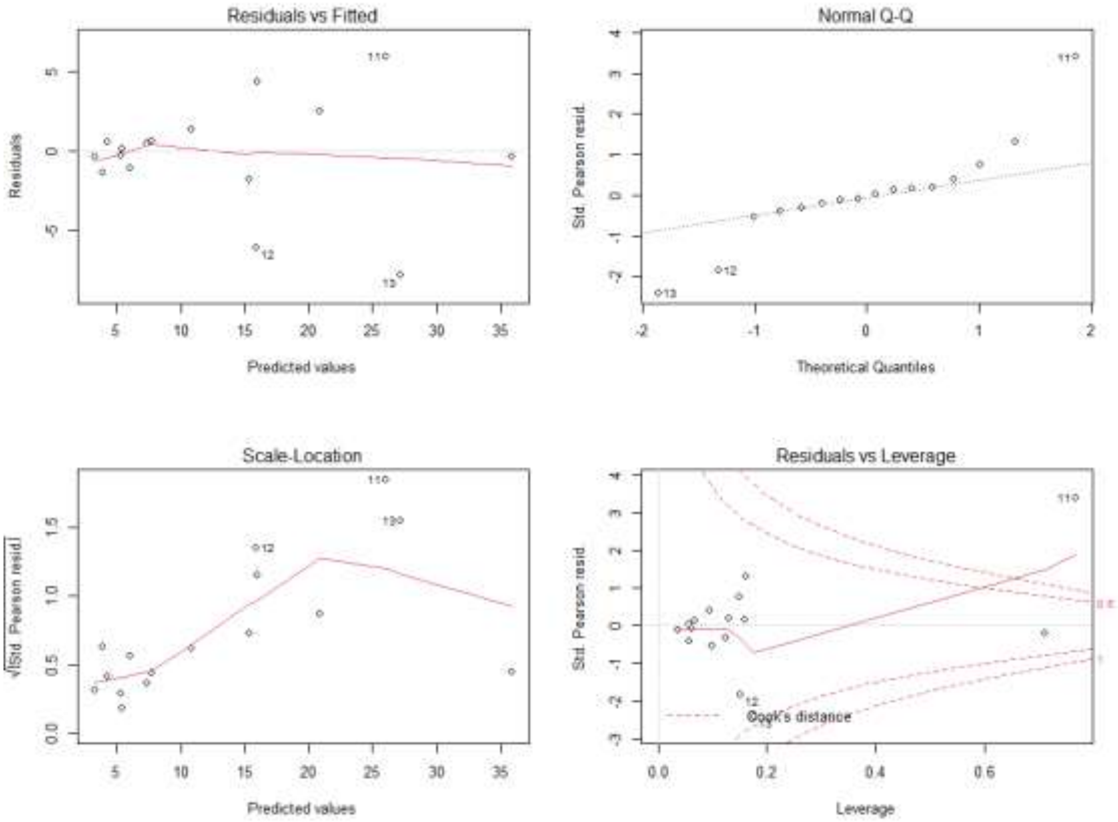

Figure A3. Diagnostic plots demonstrate model fit for the top AIC selected generalized linear model (GLM). In the Residuals versus Fitted plot, residuals appear to bounce randomly around the 0 line, indicating that the linearity assumption has been met. However, variances appear slightly left skewed with potential outliers (e.g., residual points, representing individuals: 11, 12, 13). The Normal Q-Q plot appears to demonstrate a normally distributed population, given majority of the data points fall into a straight line. Scale-Location plot demonstrates most residuals are randomly spread, indicative of homoscedasticity in the model. Finally, in the Residual vs Leverage plot, residual 11 is outside of the Cook's distance lines and may be an influential observation. Excluding that observation may have a small influence on the slope coefficient and R^2 estimates. Study was conducted on Dinner Island Ranch wildlife management area (WMA) and Okaloacoochee Slough WMA, Southwest Florida, USA, 2019-2020.

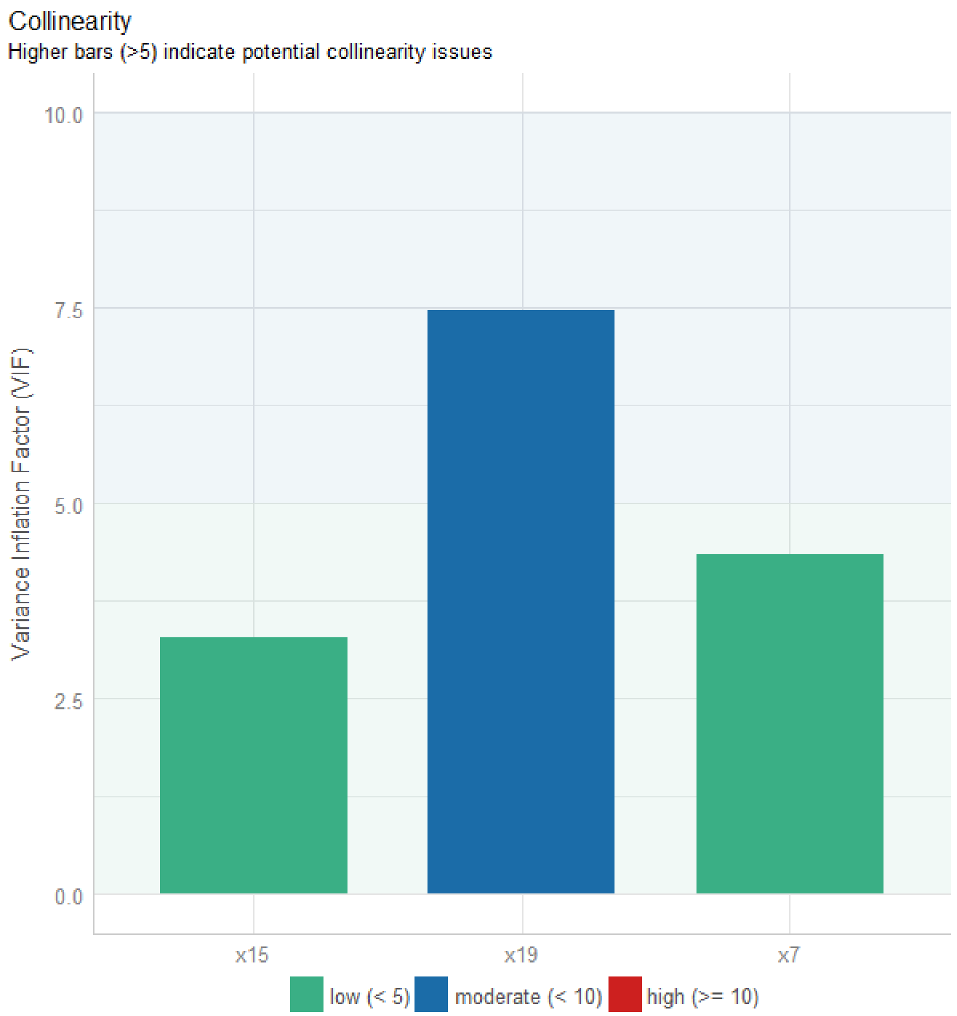

Figure A4. Variation inflation factor (VIF) plot for predictor variables x7 = pasture hay, x15 = woody wetlands, x19 = emergent herbaceous wetlands for GPS collared wild pigs on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Table A1. Wild pig summary statistics for GPS collared individuals on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020. The table includes: sex, weight (kg), dates of collar deployment, total months collared, number of fix locational points, and home range point estimates with 95% confidence intervals (CI). OUF = Ornstein-Uhlenbeck Foraging model used to estimate home range.

ID	Site	Sex	Weight	Start	End	Total Months	# of fix points	HR 95% CI	Effective sample size	Top Model
1	DIR	M	195.8	6/27/19	12/1/20	17.22	23, 718	35.81 (31.29 - 40.63)	218.32	OUF
2	DIR	M	144.8	12/5/19	8/2/20	7.96	11, 203	11.55 (9.81 - 13.43)	147.99	OUF
3	DIR	M	200	12/13/19	9/16/20	9.17	12, 635	21.87 (18.46 - 25.56)	145.52	OUF
4	DIR	M	154	12/20/19	2/27/20	2.3	4, 239	14.53 (12.08 - 17.21)	123.31	OUF
5	DIR	M	101.4	1/14/20	9/18/20	8.19	11, 771	7.71 (6.79 - 8.69)	10167.51	OUF
6	DIR	M	109.4	2/14/20	1/13/21	11.01	12, 823	17.84 (15.03 - 20.88)	135.03	OUF
7	DIR	M	114	1/29/20	3/19/20	1.68	2, 381	8.02 (6.23 - 10.03)	68.36	OUF
8	DIR	F	53.4	2/5/20	2/22/20	0.59	829	4.57 (2.95 - 6.53)	24.77	OUF
9	DIR	F	54.4	2/5/20	9/20/20	7.53	10, 505	5.48 (4.78 - 6.22)	214.99	OUF
10	DIR	M	211.8	2/7/20	5/3/20	2.86	4, 023	2.84 (2.47 - 3.22)	211.32	OUF
11	OK	M	132.8	4/3/20	1/24/21	9.76	5, 822	27.53 (20.39 - 35.72)	49.37	OUF
12	OK	M	171.6	3/27/20	10/3/20	6.28	9, 134	13.38 (10.69 - 16.38)	77.54	OUF
13	OK	M	163.2	6/17/20	10/17/20	4.04	7, 673	24.43 (20.63 - 28.55)	107.06	OUF
14	OK	F	98	7/5/20	12/29/20	5.85	10, 995	5.49 (4.00 - 7.21)	37.79	OUF
15	OK	M	140	7/24/20	2/11/21	6.67	12, 693	2.64 (2.05 - 3.30)	67.97	OUF

16	OK	M	226.8	6/1/20	8/13/20	2.43	4, 681	5.06 (4.33 - 5.85)	169.19	OUF

Table A2. Akaike information criterion (AIC), as our model selection criterion (Burnham and Anderson, 2002) for 10 three-state hidden Markov models on Okaloacoochee Slough Wildlife Management Area (WMA) and Dinner Island Ranch WMA in Southwest Florida, USA, 2019-2020. All 3-state models and their respective covariates were parameterized according to a priori hypotheses, as the following: state 1 (A) = short steps and low rates of turning (i.e., resting state). State 2 (A) = intermediate steps and high rates of turning (i.e., foraging state), and state 3 (A) = long steps and low rates of turning (i.e., directional or traveling state). State 1 (B) = short steps and high rates of turning (i.e., rooting or wallowing state); state 2 (B) = intermediate steps and low rates of turning (i.e., walking state), and state 3 (B) long steps and high rates of turning (i.e., exploratory or transitory state).

	Model Name	Model Description	AIC
1	m3.1	3-state model (A), formula=Activity	1498873
2	m3.2	3-state model (A), formula=Temperature	1506423
3	m3.3	3-state model (A), formula=Rain	1508196
4	m3	3-state model (A), formula=Null	1508209
5	m4.1	3-state model (B), formula=Activity	1540279
6	m4.2	3-state model (B), formula=Temperature	1548866
7	m4.4	3-state model (B), formula-Sex	1549798
8	m4.3	3-state model (B), formula=Rain	1550235
9	m4	3-state model (B), formula=Null	1550249
10	m3.4	3-state model (A), formula=Sex	1550665

Table A3. Hidden Markov model parameter estimates for top model (top) and competing model (bottom) on Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA in Southwest Florida, 2019-2020. Values represent the step length mean, step length standard deviation, step length zero-mass, and turning angle and angle concentration parameter estimates from the 3-state top model. States are: 1 = resting, 2 = foraging, 3 = directional or traveling.

Parameters	State 1	State 2	State 3
Step length mean	5.952 (5.876 – 6.029)	11.397 (11.370 – 11.423)	177.458 (175.909 – 179.021)
Step length SD	4.246 (4.164 – 4.330)	1.746 (1.726 – 1.767)	192.772 (190.903 – 194.659)
Step length Zero-mass	0.031 (0.029 – 0.034)	0.547 (0.542 – 0.552)	0.001 (0.001 – 0.002)
Turning angle mean	-3.101 (-3.13 – -3.068)	-3.119 (-3.141 – -3.097)	0.003 (-0.0186 – 0.025)
Turning angle concentration	0.567 (0.547 – 0.587)	1.244 (1.206 –1.282)	0.541 (0.529 – 0.554)

Value of the maximum log-likelihood: -749407.5

Parameters	State 1	State 2	State 3
Step length mean	3.431 (3.386– 3.477)	10.593 (10.375 – 10.816)	183.827 (181.988 – 185.685)
Step length SD	1.944 (1.906 – 1.982)	7. 111 (6.932– 7.293)	205.489 (203.369 – 207.631)
Step length Zero-mass	0.066 (0.063 – 0.068)	0.004(0.003 – 0.006)	0.002 (0.001 – 0.002)
Turning angle mean	-3.091 (-3.133 – -3.049)	-3.125 (-3.153 – -3.098)	0.005 (-0.014 – 0.024)
Turning angle concentration	0.391 (0.374 – 0.409)	0.699 (0.676– 0.723)	0.625 (0.612 – 0.639)

Value of the maximum log-likelihood: -754081.7

Table A4. Generalized linear model parameter estimates for wild pigs in Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA in Southwest Florida, 2019-2020. Table includes individual home range size as the response and proportion of landcover types within each home range as predictor variables. All models were weighted by 95% confidence intervals.

Covariate	β	SE	t value	Pr(>|t|)
Intercept	2.3104	2.2534	1.0250	0.3352
Pasture	2.6100	0.8918	2.9270	0.0191 *
Woody Wetlands	7.9300	4.1205	1.9250	0.0905
Herbaceous Wetlands	-7.8482	2.3418	-3.3510	0.0101 *
Pasture x woody wetlands	-1.1634	0.9698	-1.2000	0.2646
Pasture x herbaceous wetlands	1.0021	0.5383	1.8620	0.0997
Woody wetlands x herbaceous wetlands	4.0873	2.2580	1.8100	0.1079
Pasture x woody wetlands x herbaceous wetlands	-0.3462	0.4327	-0.8000	0.4468

Chapter 3. The influence of habitat selection, diel activity, and temperature on wild pig movement behavior in Southwest Florida.

Abstract

Since introduction in the late 1500's, wild pigs *(Sus scrofa*) have historically thrived in the warm tropical climate of Florida. The abundance of wetlands, forests, and dense vegetation is conducive to the omnivorous diet of wild pigs, which fosters high population densities throughout the state, especially north and west of Lake Okeechobee. However, anecdotal evidence suggests a decline in wild pig densities in Southwest Florida. In the last decade, the region has seen hundreds-of-thousands of new residences, substantial development, rebounding Florida panther (*puma concolor coryi*) populations, and a warming climate, which all have the potential to influence the movement and population ecology of wild pigs in Southwest Florida. The thick subcutaneous fat and an inability to dissipate heat by sweating and panting create physiological limitations for wild pigs in warm, tropical climates. Thus, their overall reproductive success is closely tied to shaded resource-rich habitats to raise young, find food, and protect from predators. Therefore, to evaluate how wild pigs adapt to external temperature and landscape, we used an integrated step selection process to investigate the effects of temperature on habitat selection and movement, habitat selection during different times of day, and changes to movement patterns in different habitat types. We found evidence of wild pigs selecting areas closer distances to wetland habitats. Wild pig movement was tortuous in forested and cropland habitats, but more directed in pasture habitats. Slower (i.e., smaller steps) and more directed (i.e., less turning) movements were observed during warmer temperatures, particularly staying farther from cropland when temperatures were warmer.

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[1] This chapter was formatted for the Journal of PLOS ONE.
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Wild pigs also stayed farther from wetland habitats during dusk and night hours, and cropland habitats during dawn hours. However, wild pigs selected for forested habitats during night and dawn hours. In addition, we calculated the relative selection strength for two locations and found that wild pigs were less likely to step into a location with a daily temperature of 35.7°C than 16.1°C. However, wild pigs were more likely to select intermediate temperatures and avoid locations with extremely low or high daily temperatures. A greater understanding of wild pig movement behavior will aid wildlife managers in controlling populations of an invasive species. For example, our results will help land managers to better predict which landcover types are providing refuge (e.g., wetlands and forests) or potential movement corridors (e.g., pasture and cropland habitats), to prevent expanding populations.

Key words: Integrated Step Selection, resource selection, *Sus scrofa*, wild pigs

Introduction

A better understanding of resource selection is relevant for conservation (Fagan and Lutscher, 2006), given its applicability to the spatial ecology of species (Morrison et al. 2012). Resource selection typically occurs on different spatial and temporal scales (Rettie and Messier, 2000). Therefore, identifying which habitats are most likely selected by nonnative and invasive species with economic relevance is important for developing population growth mitigation plans.

Though present on the landscape for > 500 years, wild pigs (*Sus scrofa*) are nonnative to Florida and are a significant source of economic and ecological damage. They are an important, perhaps sustaining, prey species for Florida panthers (Maehr et al. 1990, Dalrymple and Bass, 1996) and are the second most popular large animal hunted in Florida. However, Florida's invasive wild pig populations occur statewide and are estimated to be at least 500,000 individuals (Giuliano, 2010), second only to Texas with estimates of about 2.6 million

(Friesenhahn et al. 2022; Timmons et al. 2012) and at least 6.9 million wild pigs in the Unites States as of 2016 (Lewis et al. 2019). In Florida, these generalists are highly adaptive and occur in various habitat types, usually preferring mesic conditions (e.g., marshes) surrounded by large forested areas with abundant food sources (Hartley et al. 2014; Giuliano et al. 2010). In Southwest Florida, wild pig habitat typically encompasses restored pasture lands, wetland habitats, cypress forests (e.g. *Taxiodium* species), hardwood-cabbage palm hammocks (*Sabal palmetto*), and are adjacent to active cattle grazing and citrus production. Wild pigs are prolific breeders, and this creates challenges for population managers due to their short gestation period, early maturation, and large litter sizes (Caplenor et al. 2017). Multiple stakeholders with differing priorities regarding wild pigs can make management decisions difficult. For example, hunters often oppose efforts to reduce wild pig populations, whereas agricultural producers and natural resource managers support efforts to reduce wild pig populations because they annually inflict billions of dollars in damage to crops, livestock, native species, and ecosystem resources (Timmons et al. 2012; Krull et al. 2013; Pimental, 2007). Moreover, wild pigs also are known to carry at least 30 zoonotic diseases and 37 different parasites, highlighting how expanding populations may pose a direct health risk to livestock, especially domestic swine production, wildlife, and humans (Centner and Shuman, 2015; Leiser et al. 2013). Therefore, factors influencing resource selection and movement should be of interest to land managers, the agricultural sector, and other stakeholder groups.

The omnivorous diet of wild pigs allows them to be highly adaptive; however, they have relatively poor physiological cooling mechanisms, that often limits their use of resources in xeric habitats (Giuliano et al. 2010). In the warm, tropical climate of Southwest Florida, wild pigs are dependent on wet soil conditions for wallowing in mud and soaking in water to keep body temperatures cool and to rid themselves of external parasites (Giuliano et al. 2010). However, wild pigs may select more open warmer areas in the cooler winter months, range wider in search of food, and shift diel activity patterns to cathemeral feeding strategies (Giuliano et al. 2010). Shifts in movement are also tied to reproductive activity, while reproductive success is highly dependent on food availability (e.g., hard mast; Guiliano et al. 2010). When food availability is abundant and widely distributed wild pigs are likely to reduce their movements to conserve energy expenditure (Massei et al. 1997). Anthropogenic activities such as agricultural operations, hunting, and trapping, and the illegal translocation of wild pigs to establish new populations for hunting likely modify wild pig movement patterns (Kay et al. 2017; Hartley et al. 2014; Comer and Mayer, 2009).

Knowledge of resource selection is informative for wildlife managers and conservation planning (Schlichting et al. 2016) and also for understanding what resources are essential to the biological needs (reproduction and survival) of wildlife populations. With invasive species spreading throughout the globe, and a changing climate (e.g., global warming), it is imperative to study how environmental conditions (e.g., temperature) influence the distribution, movement, and spatial ecology of species, such as wild pigs. Quantifying the relationship between a species' movement and resource selection is informative because it provides evidence explaining how animals utilize their landscape under different conditions, and their physiological plasticity. Wild pigs are heat-sensitive animals with poor thermoregulatory abilities (Johann et al. 2020; VerCauteren et al. 2019; Bracke et al. 2011). Therefore, they likely use their landscape in a manner that does not exceed their physiological limits, by adjusting their movement, habitat selection, and diel activity patterns.

Step selection analysis (SSA) is advantageous over conventional resource selection models because they allow the conditional probability structure of the model to accommodate temporally dynamic environmental covariates (e.g., temperature), while including movement parameters directly into a conditional logistic regression model (Avgar et al. 2016; Fieberg et al. 2021). However, Integrated step selection analysis (iSSA) is advantageous over SSAs because they allow for simultaneous, rather than sequential, estimation of the movement and habitat-selection process. Therefore, iSSAs reduce bias in habitat-selection estimates by adequately accounting for the movement process (Avgar et al. 2016; Forester et al. 2009). The iSSA framework allows investigators to incorporate the effects of environmental covariates on the movement and selection process simultaneously, to model questions pertaining to traveling speed under different circumstances (Avgar et al. 2016; Potts et al. 2016a).

We evaluated the resource selection of wild pigs in two wildlife management areas in Southwest Florida. These sites provided an opportunity to better understand how movement and temperature effect the resource selection of wild pigs on landscapes used for cattle and citrus production. We predicted that wild pigs would take larger, more directed steps (i.e., faster straight movements) in open habitats (i.e., pasture and cropland) and habitats with lower resources (e.g. pasture), and smaller steps with more tortuous turning (i.e., slower movements) in resource rich forested and wetland habitats where energy demands can be met in smaller areas (Harestad and Bunnel, 1979). We predicted that wild pigs would take smaller steps, with more tortuous turning when temperatures were warmer, and stay in shadier forested and wetland habitats to keep body temperatures lower, given their thermoregulatory limitations (Johann et al. 2020; VerCauteren et al. 2019; Bracke et al. 2011). We predicted that wild pigs would choose locations with intermediate temperatures when two locations had wide daily temperature differences. Finally, we predicted that wild pigs would select for open habitats (e.g., pasture and cropland) during dusk and night hours for increased vigilance and lower perceived predation risk. We predicted that wild pigs would select wetland or forested habitats during dawn and day hours to keep collar temperatures lower. Our goal was to help equip wildlife managers to make informed recommendations regarding wild pig population control to mitigate farther nonnative range expansion.

Methods

Study area

We worked on two sites located south of the Caloosahatchee River in Clewiston, Southwest Florida (See Chapter 2 - Figure 2.1). We trapped wild pigs in Okaloacoochee Slough Wildlife Management Area (WMA) and Dinner Island Ranch WMA. Okaloacoochee Slough WMA was managed partly by the Florida Forest Service (~140.5 km^2) and the Florida Fish and Wildlife Conservation (FWC) (~ 34.5 km^2). The study site encompasses restored pasture lands, slough marsh, basin marsh, depression marsh, wet prairie, mesic hammocks, mesic flatwoods, and slash pine (*Pinus elliottii*) plantations. Dinner Island Ranch WMA is managed by FWC and encompasses 87.87 km^2 of pasture, cypress dome, marsh, pine flatwoods, and hammocks consisting of various hardwood and palm species, such as live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*). Portions of Dinner Island Ranch WMA experienced cattle grazing and citrus production contracts and grazing is used as a tool to manage plant succession and wildlife habitat diversity. Okaloacoochee WMA contained abandoned pasture land with no active agricultural production activity. However, both sites were actively restoring portions of pasture to pine flatwoods, wetlands, hardwood hammocks, and natural hydrologic systems. The area was comprised of restored pasture lands, slough marsh, basin marsh, depression marsh, wet prairie, mesic hammocks, and mesic flatwoods.

Field methods

Across Okaloacoochee Slough WMA and Dinner Island Ranch WMA, using open-topped corral and box traps. we captured and collared adult and subadult pigs (≥ 23.0 kg) with GPS collars and recorded sex, weight, and morphological measurements. We fitted each individual with a G5-2D Iridium GPS collar (Advanced Telemetry Systems, Isanti, Minnesota, USA)., weighing 0.7 kg, and programmed with a GPS fix rate at half-hour intervals (0.00, 0:30, 1.00, Etc.), recording 48 locations/day. The satellite transmission interval and mortality rate schedule were programmed at 4 hours intervals. Trapping occurred during all seasons of the year. However, traps remained closed if outside temperatures were projected to rise above 32.2 C to avoid heat stress or below -7.7 C, which rarely occurs in Southwest Florida as temperatures rarely drop below 4.4 C. We measured body weights of pigs with a portable battery-operated digital veterinary scale. We chemically immobilized wild pigs by injecting them with a mixture of Xylazine (4.4 mg/kg), Ketamine (2.2 mg/kg) and Telazol (4.4 mg/kg) intramuscularly (e.g., shoulder, rump) using a .22 caliber cartridge-fired rifle with a 5cc slow-inject disposable dart (Model 389, Pneu-Dart Inc., Williamsport, PA, USA). We reversed Xylazine with Tolazoline (2.0 mg/kg) administered via intravenous injection of half of the required Tolazoline dosage into the ear vein and intramuscular injection of the remaining dosage of Tolazoline into the hindquarter of the animal (Swindle 2015). A Special Purpose Permit was issued by the Florida Fish and Wildlife Conservation Commission Division of Hunting and Game Management for Dinner Island Ranch WMA for trapping periods: 4/2/2019 – 7/31/2019 (permit number: SPGS-19-24); 11/11/2019 – 7/31/2020 (permit number: SPGS-19-63). Okaloacoochee Slough WMA trapping periods included: 3/02/2020 – 7/31/2020 (permit number: SPGS-19-63-A1), and all procedures were permitted by Virginia Tech Institutional Animal Care and Use Committee Protocol number: 18-248. We conducted animal handling in accordance with the American Society of Mammologists (ASM) guideline (Sikes et al. 2016).

Data analysis

We used the 2019 landcover data from the National Landcover Database (NLCD; Jin et al. 2019) to generate individual raster layers into 4 habitat categories: (1) wetlands (i.e., woody wetlands, emergent herbaceous wetlands), (2) pasture/hay, (3) cultivated crops, and (4) forest (i.e., deciduous forest, evergreen forest, mixed forest). We transformed and projected the coordinate reference system of our GPS movement data to match that of the NLCD raster data, cropped the NLCD raster layers to a bounding box containing GPS movement data within our study area, and used an Euclidian distance-based approach to determine selection or avoidance of each habitat type by measuring the distance from each raster cell to the nearest cell with a value. A distance-based approach reduces edge effect and telemetry error biases (Thurfjell et al.2014; Conner et al. 2003). We then stacked the habitat-raster layers and extracted "distance-to" data to each step's start or end point for obtained locations of each wild pig. Following the same approach, we incorporated gridded minimum and maximum daily temperatures from the daymetr R package (Hufkens et al. 2018). We scaled (*SD* =1) and centered (mean = 0) all habitat variables and converted the response variable from a categorical (i.e., True or False) to a numeric variable (i.e., 1 = used or 0 = available points). Each step was assigned a step identifier within strata, and a cluster variable of animal ID to account for variation in individual movements (Fieberg et al, 2021; Prima et al. 2017). We included the time_of_day function in the amt package to test hypotheses related to diel activity patterns. This allowed us to test if wild pigs selected or avoided certain habitat types during dawn, day, dusk, and night hours. For all models, we used the car package (Fox and Weisberg, 2019) to check for multicollinearity by confirming that the variance inflation factors (VIFs) were (>5) between main-effects. We included movement parameters (log step length and cosine of the turn angle) in all models to update the selection free movement kernel, reduce bias in the habitat-selection parameters and improve estimates of movement (Fieberg et al. 2021; Avgar et al. 2016; Duchesne et al. 2015; Forester et al. 2009).

We used an iSSF to model wild pig resource selection and movement behavior. For our iSSF, we selected available points using a parameterized gamma distribution for step lengths and a von mises distribution for the observed distribution of turn angles (signer et al. 2018). We subsampled all GPS fix rates to half-hour intervals for iSSF models, given that step-selection models are scale-dependent and observations should be equally spaced in time (Munden et al. 2020). For our first population-level global model, we paired 90 random steps to each observed step to fit a mixed-effect conditional logistic regression model. Fieberg et al. (2021) provide evidence that increasing the number of available steps reduces Monte Carlo error. Interaction terms incorporated fine-scale temperature on an hourly scale by implementing 30-minute fix-rate collar temperatures. Because collar temperature (i.e. proxy for ambient temperature) did not vary for each observed and sequential, random step, it was not appropriate to use as a main-effect term but it was appropriate as an interaction term given that the link between wild pig locations (i.e., distribution) and habitat attributes can change as a function of temperature (Fortin et al. 2009). We then ran a model including both main-effect and interaction terms. The main-event terms directly tested hypotheses pertaining to habitat selection, whereas interaction terms directly tested hypotheses related to: (1) the effects of habitat cover types (e.g. pasture) and movement patterns (e.g. log step length) on resource selection, (2) the effects of hourly (i.e. collar) temperature and movement on resource selection, (3) effects of hourly temperature on resource selection, and (4) the effect of time of day on habitat selection. Our global model included the full set of covariates that were of interest for hypothesis testing and, to achieve direct comparison between coefficient estimates, we did not use a model selection technique to rank candidate models.

Additionally, we ran two main-effect conditional logistic regression models to investigate hypotheses regarding the relative selection strength (RSS) for two locations with different temperatures on the daily scale, along with non-linear effects. To do this, we calculated the log-relative intensity (referred to as the log-Relative Selection Strength; Avgar et al. 2017) by incorporating raster layers containing gridded minimum and maximum daily temperatures, which allowed for the temperature data to vary within the stratum, and thus was appropriate for modeling main-effect models. Due to computational restraints, we used ten random steps for each observed step, which is sufficient for interpreting slope coefficient estimates (Fieberg et al. 2021). We ran two main-effect iSSF models to determine the log-Relative Selection Strength of wild pigs choosing hypothetical locations with differing daily temperatures and the likelihood of choosing locations with extremely low or high daily temperatures. All iSSF models were fit using the amt-package to generate regression coefficients (Signer et al. 2018).

Results

Overall, we found evidence for three fixed effect terms and four interaction terms whose 95% CIs overlapped from our global mixed-effect integrated step selection model (Table A1). The results indicate that wild pigs, on average were approximately 50% more likely to have larger steps (sl_: β = 0.00033; 95%CI = 0.00023 – 0.00043) and approximately 55% more likely of directed turning (cos_ta_: β = -0.19710; 95% CI =-0.34654 – -0.04770). On average, wild pigs selected for closer distances to wetland habitats (wet_dist_end: β = -0.13970; 95% CI = -0.20434 – -0.07496), and the probability of use decreased approximately 47% for every 100 m increase from wetland habitats (Figure 1,2).

We found evidence to support that wild pig movement was tortuous when individuals started their movements (i.e., or remained) in forested (cos_ta_* fore_dist_start: β =0.00013; 95% CI = 0.00004 – 0.00022) and cropland habitats (cos_ta_* crop_dist_start: β =0.00002; 95%CI = 0.00000 – 0.00004), and directed in pasture habitat (cos_ta_* past_dist_start: β = -0.00134; 95% CI = -0.00198 – -0.00071). Therefore, wild pigs were approximately 50% more likely to have tortuous movements in forested and cropland habitats, and approximately 50% more likely to have directed movements in pasture habitat (Figures 1,2).

We found evidence that wild pigs took smaller steps (log_sl_* Temperature: -0.03483; 95% CI = -0.04801 – -0.02166) and more directed turning (cos_ta_:Temperature : β = -0.14800; 95% CI = -0.23191 – -0.06409) when collar temperatures were warmer. Therefore, for every one-unit increase in temperature wild pigs were approximately 49% more likely to take smaller steps and 46% more likely to have directed movement. In addition, wild pigs, on average stayed farther distances from croplands when collar temperatures were warmer (crop_dist_end * temperature: β = 0.03320; 95% CI = 0.00962 – 0.05678). Therefore, probability of use decreased approximately 51% for every 100 m increase from croplands when temperatures were warmer.

We found evidence to support that wild pigs stayed farther distances from wetland habitats during dusk hours (wet_dist_end * tod_end_dusk * β = 0.11862; 95% CI = 0.02786 – 0.20938) and night hours (wet_dist_end * tod_end_night: β = 0.07875; 95% CI = 0.02858 – 0.12893) relative to reference class daytime. Therefore, probability of use increased 53% and 52% for every 100 m increase from wetland habitats during dusk and night hours. Wild pigs stayed farther distances from cropland habitat during dawn hours (crop_dist_end * tod_end_dawn: β = 0.03722; 95% CI = 0.01804 – 0.05639) relative to reference class daytime. Therefore, probability of use increased 51% for every 100 m increase from cropland habitats during dawn hours. However, wild pigs selected for closer distances to forests during night hours (fore_dist_end:tod_end_night: β = -0.03373; 95% CI = -0.06745 – -0.01701) and dawn hours (fore_dist_end:tod_end_dawn: β = -0.02120; 95% CI = -0.04212 – -0.00027) relative to reference class daytime. Therefore, the probability of use decreased approximately 49% for every 100 m increase from forested habitats during night and dawn hours. (Figures 1,2).

Our main effect integrated step-selection model found that the log-relative selection was 0.98 times more likely (i.e., >1 indicates less likely) to step into a habitat with a temperature of 35.7° C than 16.1°C, therefore less likely to choose locations with warmer temperatures (Figure 3). We found evidence for three movement (e.g., log_sl_, cos_ta_, and sl_), and one habitat (e.g., wet_dist_end) main-effect terms whose 95% CIs overlapped zero (Table 2). We ran a quadratic non-linear main-effect iSSF model and found evidence for three movement terms (e.g., log_sl_, cos_ta_, and sl_), and three habitat terms (e.g fore_dist_end, past_dist_end, wet_dist_end) whose 95% CIs overlapped zero (Table 3). We found evidence that wild pigs selected for intermediate daily temperatures and avoided locations with extremely low or high temperatures (i.e., 35.7° C verse 16.1° C) given that a concave non-linear effect was visible (Figure 4).

Discussion

We conducted this study to address several ecological hypotheses related to the spatial ecology of wild pig populations in Southwest Florida. We investigated wild pig movement behavior as a function of habitat quality, temperature, and diel activity. Generally, we expected animals to utilize smaller areas of higher productivity if a majority of their energy demands are met (Harestad and Bunnel, 1979). Therefore, we predicted that wild pigs would have smaller steps and slower, more tortuous movements in natural wetland and forested habitats compared to larger steps and more directed movements in resource-poor pasture, and cropland habitats where anthropogenic activity is higher. We found evidence to support tortuous movement (i.e., high turning frequency) for wild pigs when their steps (i.e., GPS locations) started in forested or cropland habitats and directed movement in pasture habitat. Wild pigs are opportunistic omnivores and likely use tortuous movement behavior to cost-effectively forage in forests containing mast-producing trees and exploit agricultural croplands (Kay et al. 2017; Anderson et al. 2016; Cutini et al. 2013; Irizar et al. 2004; Hafeez et al. 2008). In addition, tortuous movements in forested habitats could be the result of cryptic predator avoidance behaviors to reduce detection or for hindrance to predators (Lone et al. 2014). Given that portions of the study sites are open pasture or old field, it is plausible that wild pigs used directed movement behaviors when traveling to other available habitat types.

Similar to other studies, we found evidence of wild pigs modifying their movements in response to thermoregulation (Clontz et al, 2021; Hartley et al. 2014; Kay et al. 2017, Dexter, 1998). For example, we observed that wild pigs reduced their movements by taking smaller steps with more directed movement during warmer temperatures consistent with other regional studies (Johann et al. 2020; Froehly et al. 2020; Hartley et al. 2014; Kay et al. 2017; Dexter, 1998). We found evidence that wild pigs on average, stayed farther from cropland during warmer temperatures, likely in response to intense heat and a lack of cover in open habitat. We found that wild pigs were less likely to step into habitat locations with warmer daily temperatures and preferred habitat locations with intermediate daily temperatures, thus avoiding locations with extremely low or high temperatures. Heat thresholds for wild pig populations have been documented for wild pigs in the southern United States (Kay et al. 2017; Froehly et al. 2020), however, their populations throughout the United States are also limited by cold temperatures and the availability of water (McClure et al. 2015). Thus, wild pigs likely fail to thrive in environments that surpass their thermoregulatory capabilities.

We found evidence that wild pigs selected for farther distances from cropland habitat during dawn hours, relative to reference class daytime. Both study sites offer hunting opportunities for wild pigs, deer, and other species. Strong evidence has shown that wild pigs adjust their diel activity patterns under anthropogenic disturbance (Johann et al. 2020; Ohashi et al. 2013; Keuling et al. 2008), and in undisturbed conditions may prefer to exhibit cathemeral activity patterns (Johann et al. 2020, Satter et al. 2022 – *PhD dissertation Ch.2*). Contradictory to our hypothesis, we found evidence that wild pigs selected for closer distances to forests during dawn and night hours, relative to reference class daytime, which may suggest that wild pigs perceived forests as a safe refuge from humans (e.g., hunters) and predators (Johann et al. 2020). Wild pigs are primarily nocturnal (Reinke et al. 2021, Gray et al. 2020; Thurfjell et al. 2014) or crepuscular (Hartley et al. 2014; Johann et al. 2020); and will spend more than half of the day resting (Johann et al. 2020). Other studies have demonstrated forests being predominately selected during the day for resting (Boitani et al. 1994). In general, diel activity patterns are closely tied to anthropogenic risk, food availability, cover, and thermoregulation (Kramer et al. 2022). Overall, we found evidence for wild pigs selecting for closer distances to wetland habitat. Preferences for wetland habitat have been documented, which wild pigs likely use for wallowing (i.e., thermoregulation) and available food sources (Johann et al. 2020; Hayes et al. 2009). We also observed wild pigs staying farther distances from wetland habitats during dusk and night hours, relative to reference class daytime, which we speculate might be the result of perceived risk in wetland habitats during darker hours, or when the benefit of thermoregulation is lower.

We acknowledge a limitation of our population-level model in that we were not able to update the selection-free movement kernel for some of the interaction terms between movement characteristics and environmental covariates. However, it is still appropriate to draw ecological inferences from coefficients estimated with the selection-free movement kernel (Fieberg et al. 2021). For example, we can quantify how likely an animal is to take large versus small steps or to turn left or right relative to moving straight by estimating the main-effect step-length and turn-angle distributions (Fieberg et al. 2021). We can also quantify the expected selection-free step lengths as a function of an environmental covariate (i.e., temperature was included in our model as an interaction with step length; Fieberg et al. 2021). However, we did update the step length and turn angle distributions for each individual separately and found the tentative and adjusted distribution estimates were very similar among individual wild pigs (Appendix – Figure A1). In addition, we reduced bias in our inference by including movement covariates (e.g., step lengths or log step lengths) into our analysis compared to a step selection function that does not (Forester et al. 2009).

In conclusion, selection for wetland habitats may have been partly due to thermoregulatory requirements, which was likely least beneficial during dawn and night hours (relative to daytime) given that they stayed farther distances away during those times of the day. Wild pigs exhibited slower and straighter movements when in locations with warmer temperatures and seemed to avoid more open habitats during warmer temperatures (e.g., cropland). Wild pigs preferred locations with intermediate temperatures and thus avoided locations with extreme temperatures. Our findings support the conclusions of Alston et al.

(2020), who found that moose (*Alces alces*), also a heat sensitive species, behaviorally thermoregulated during hot periods by reducing movement rates and selecting for more shaded, cooler habitats. Also, evidence for a greater likelihood of selection of forests during dawn and night hours (relative to daytime) in conjunction with tortuous movement suggests that forested habitat is serving an important ecological role to wild pig ecology during those times of day. A better understanding of the movement behavior and resource selection of wild pigs adds to our understanding of their behavior, life history, and ecology in Southwest Florida. We show that wild pigs are a heat-sensitive species that use their landscape in a manner that does not exceed their thermoregulatory abilities. They achieve this by adjusting the speed and directionality in which they move and by selecting habitats at optimal temperatures and times of day. Therefore, if ambient temperatures continue to increase (e.g. climate change), dependence on thermal refuge for wild pigs may also increase and thus habitat associations will increase.

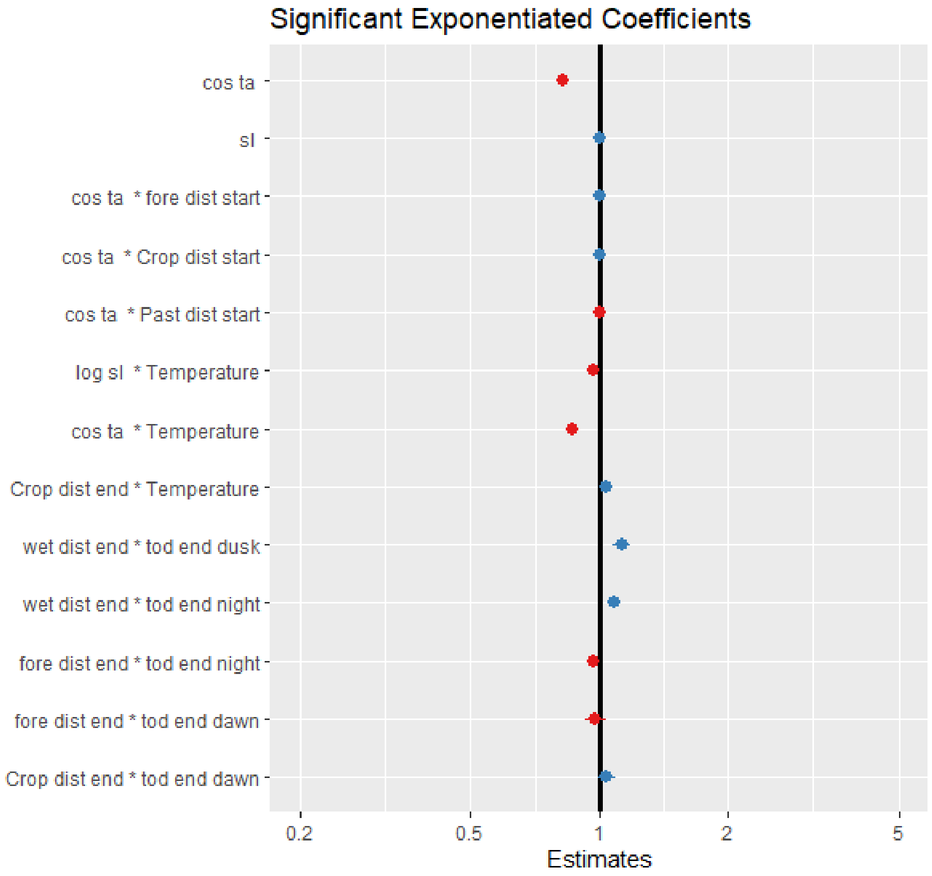

Figure 1. Plotted significant exponentiated coefficients from a population-level, fitted mixed-effect conditional logistic regression, integrated step-selection model. The thick vertical intercept indicates no effect (i.e., selection), while to either side of the vertical line indicates the direction and relative magnitude of the integrated step selection model selection. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

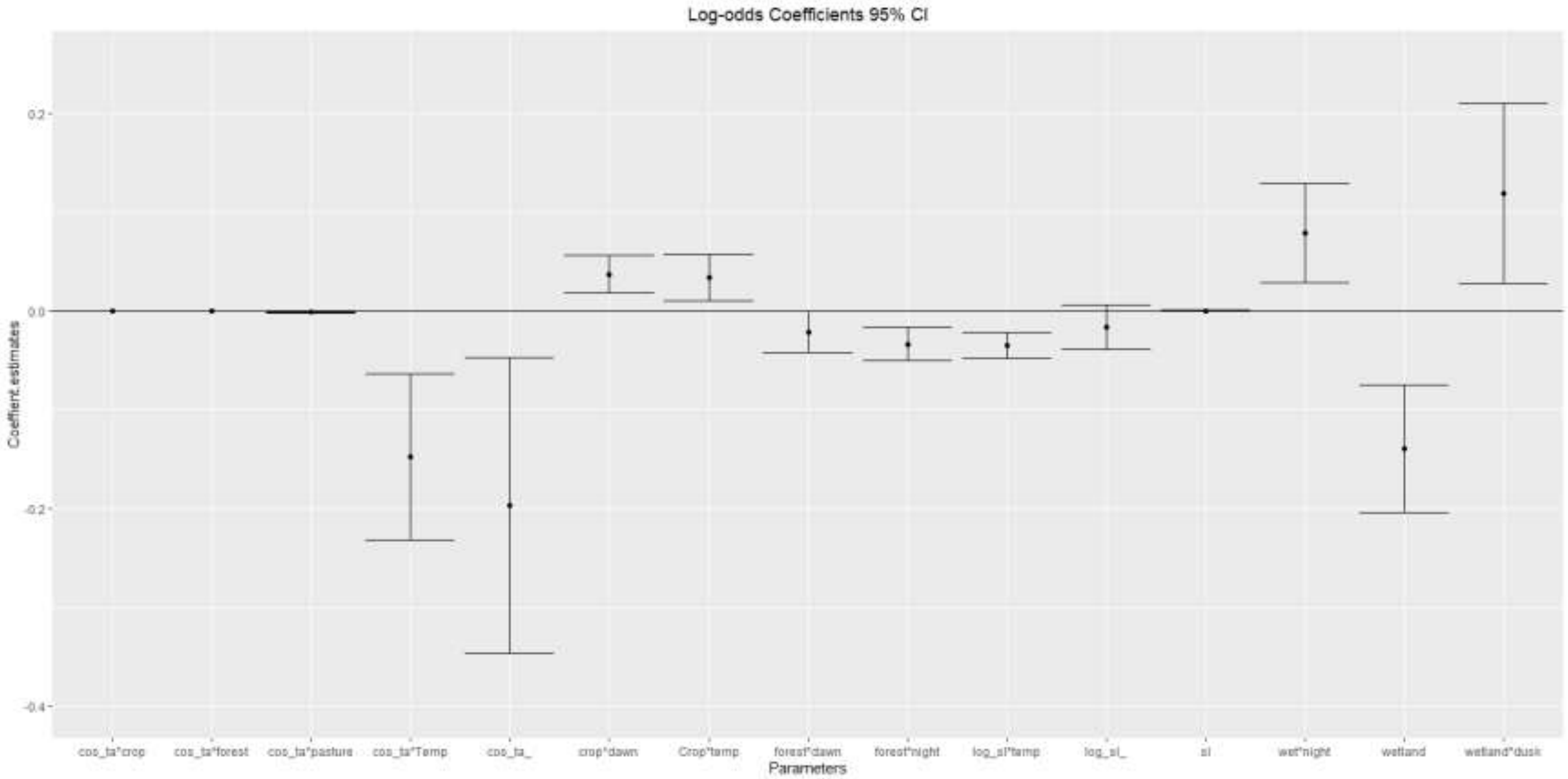

Figure 2. Plotted significant coefficients from a fitted mixed-effect conditional logistic regression model, with 95% Confidence Intervals. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

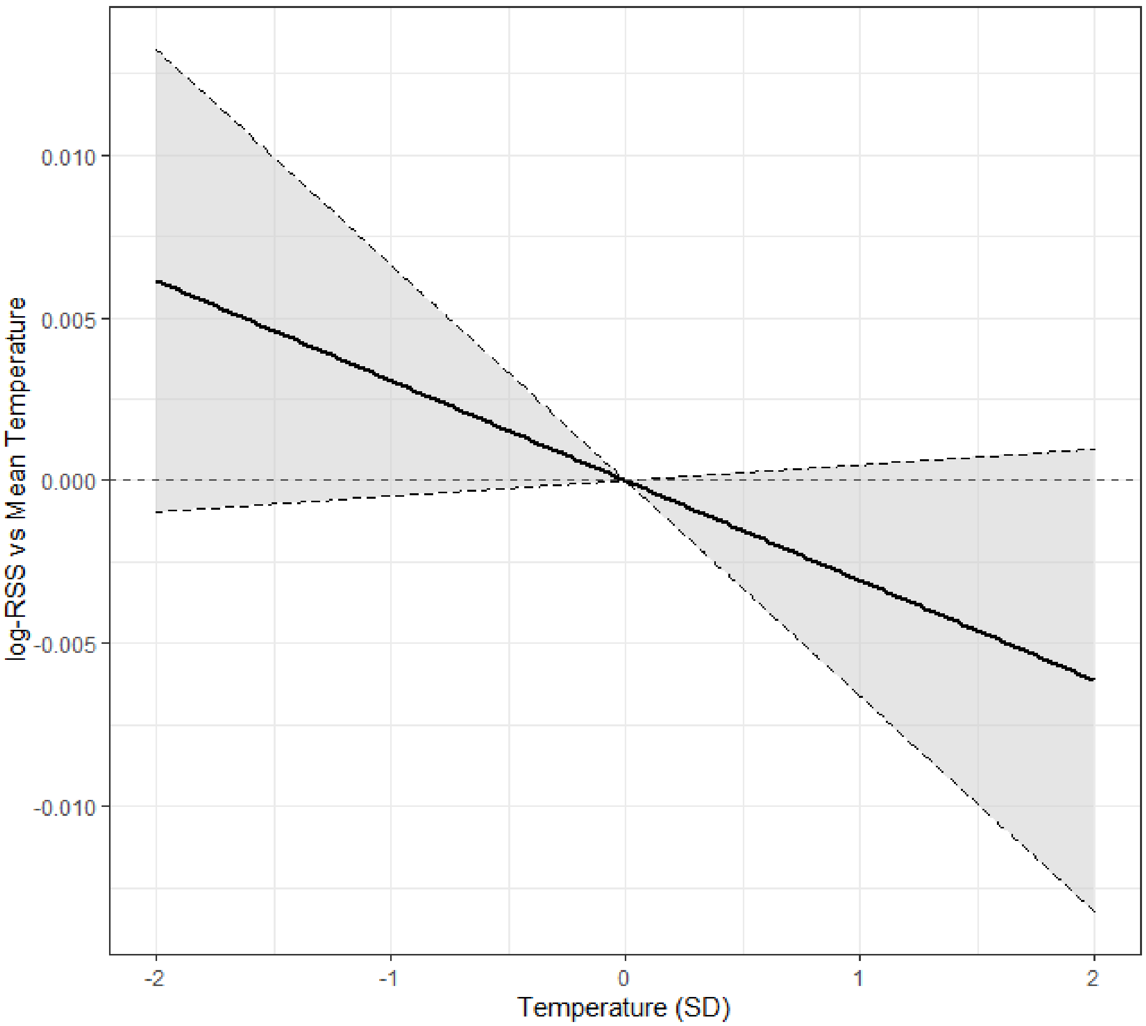

Figure 3. The log-Relative Selection Strength verse mean temperature of wild pig step lengths as a function of daily temperature. Wild pigs were 0.98 times more likely to step into a habitat with a daily-temperature of 35.7° C than 16.1° C. Daily temperature variable was centered and scaled. The log-RSS is equal to 0 when the two locations are identical (i.e.,, when temperature = 0). Shaded areas indicate the lower and upper bounds of the 95% confidence interval. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

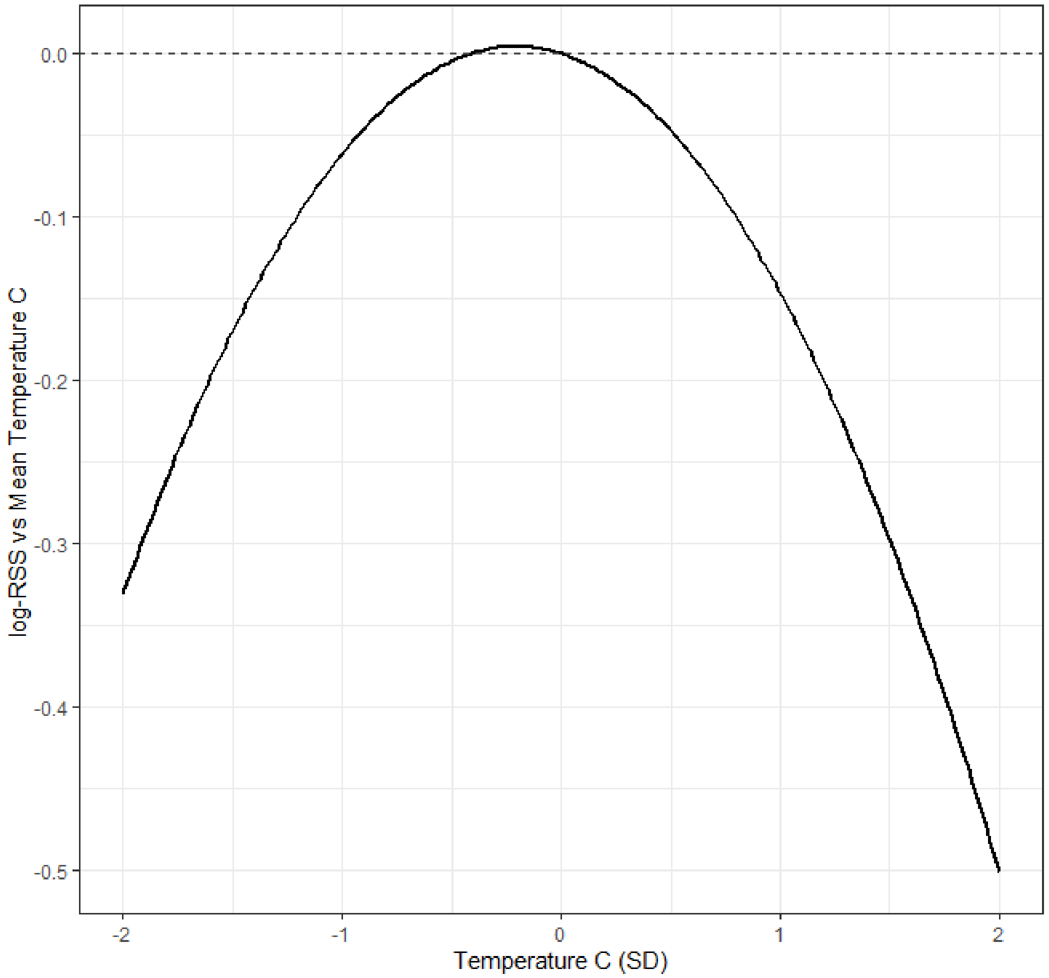

Figure 4. The log-Relative Selection Strength verse mean temperature of wild pig step lengths as a function of a quadratic daily temperature variable. We found support for wild pigs selecting for intermediate temperatures, over extreme temperatures (16.1° C to 35.7° C), given that the estimated quadradic effect is conclave in shape. The log-RSS is equal to 0 when the two locations are identical (i.e., when temperature = 0). Daily temperature variable was centered and scaled. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

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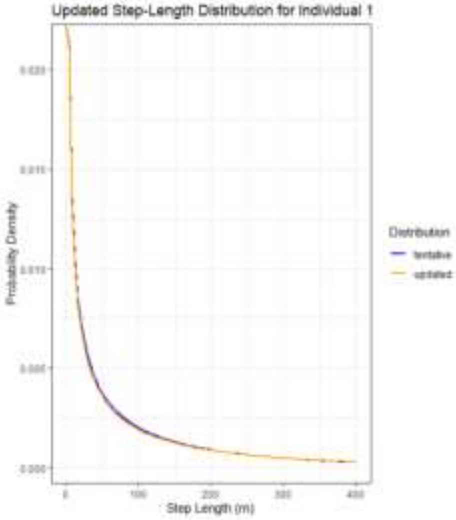
Appendix - Figures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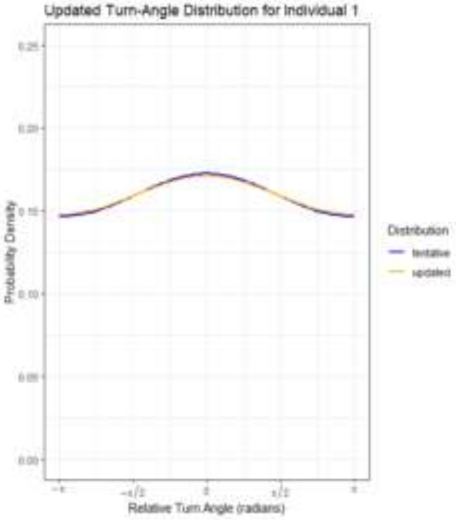
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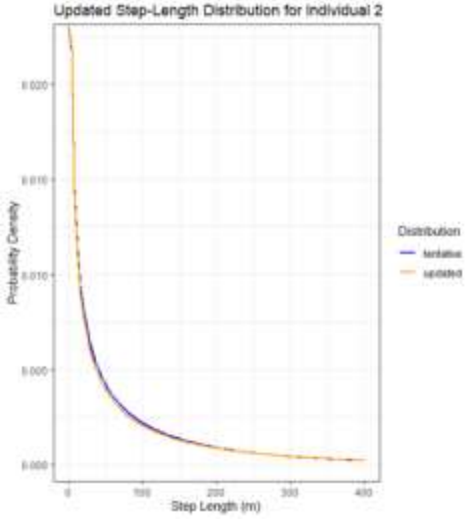
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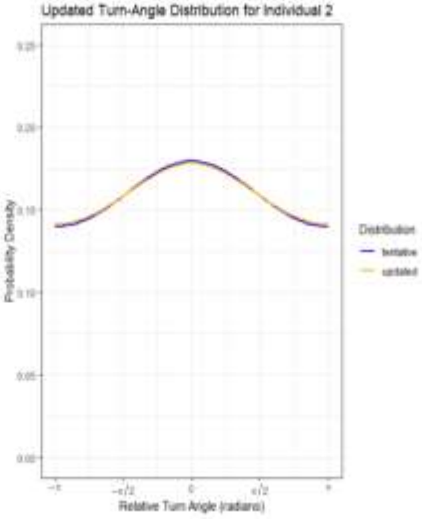
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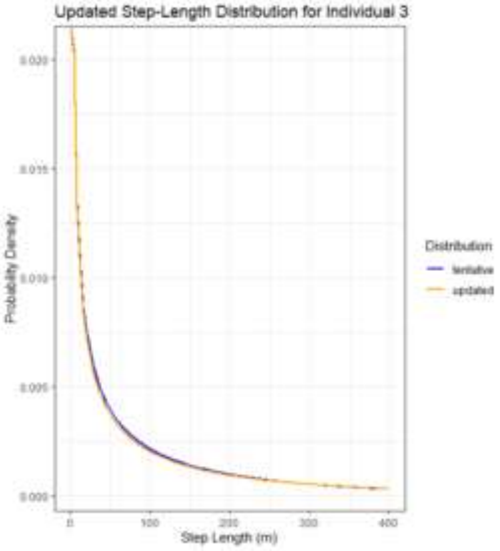
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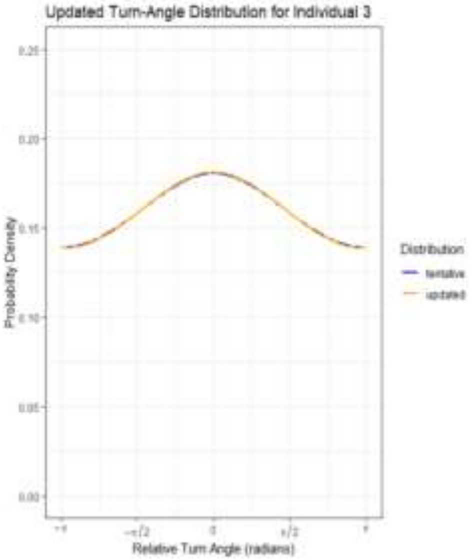
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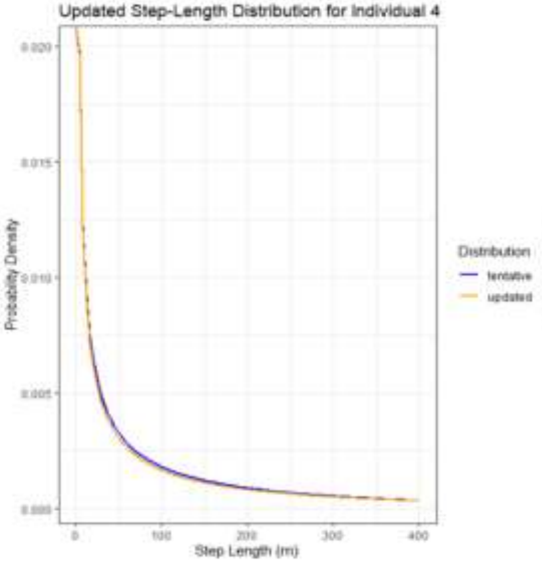
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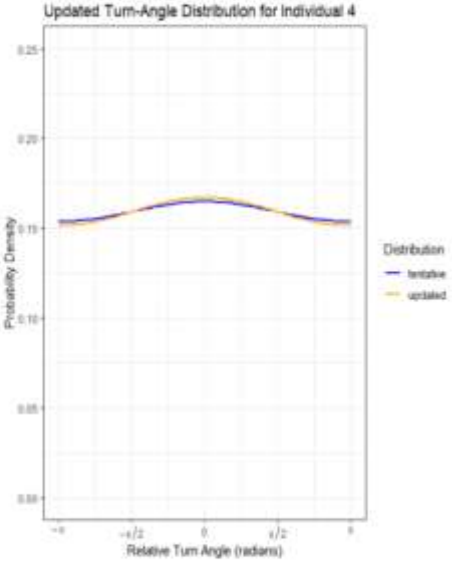
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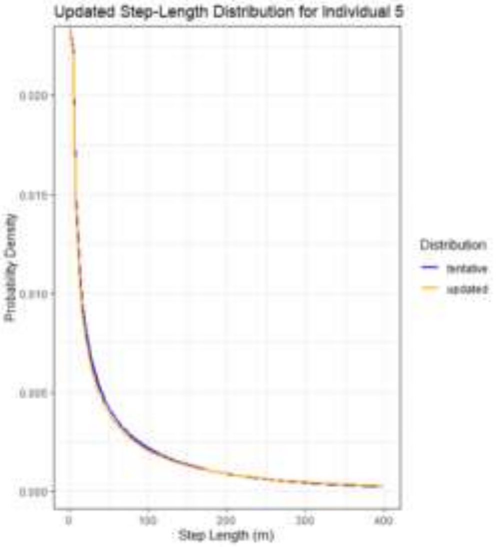
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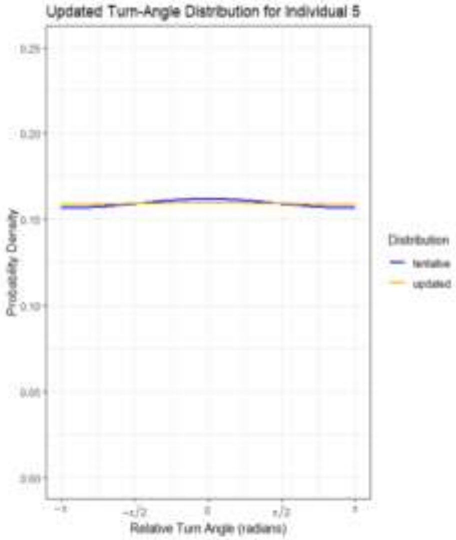
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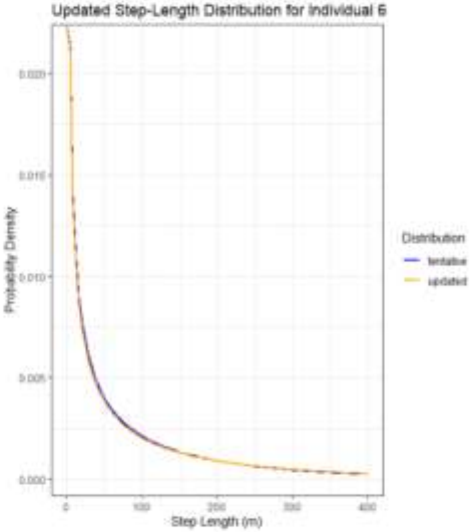
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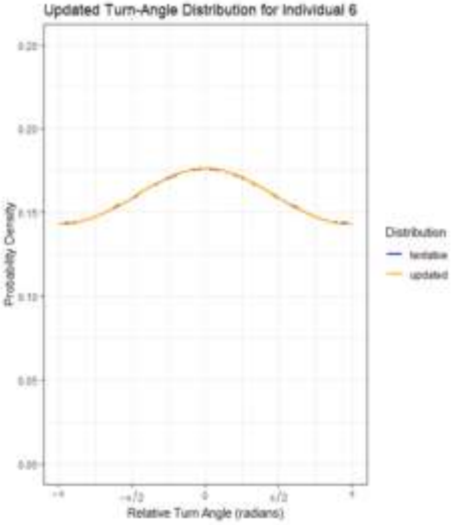
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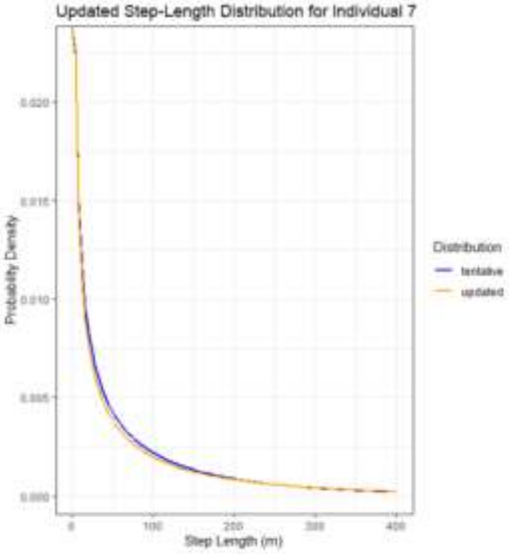
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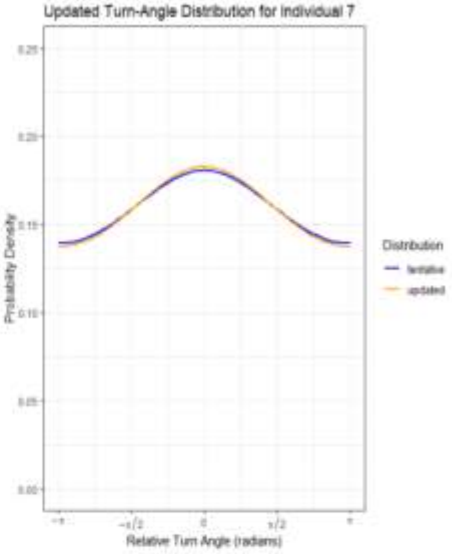
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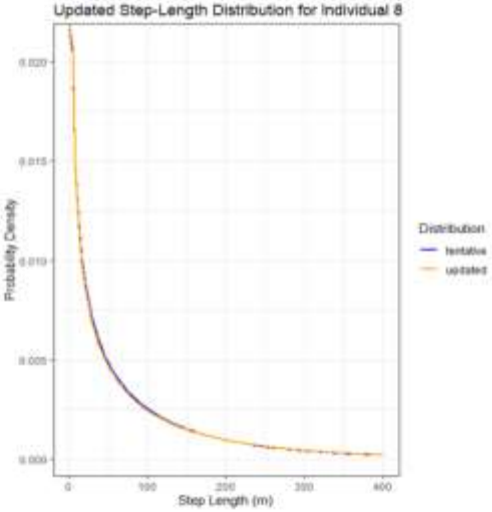
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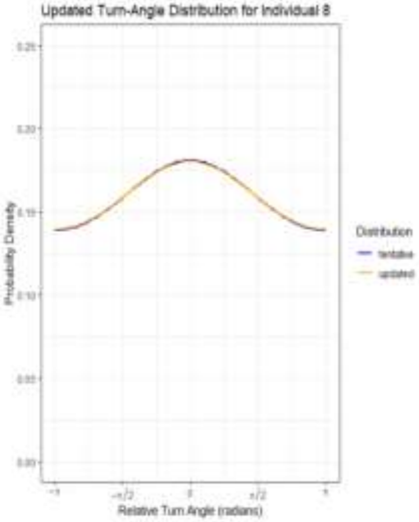
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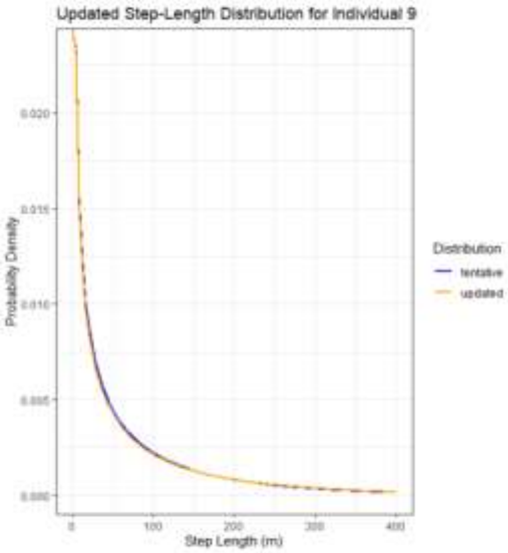
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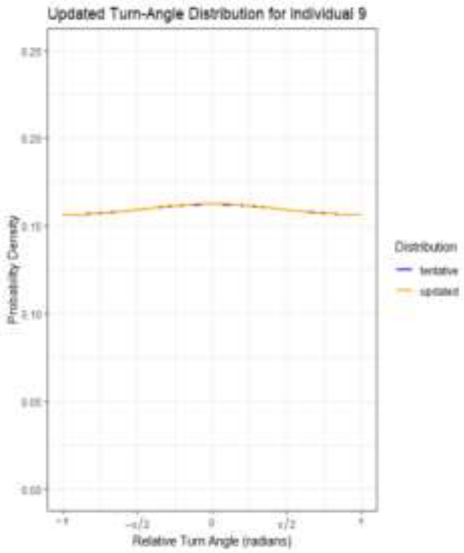
Probability Density
0.000
0.005
0.010
0.015
0.020
0
100
200
300
400
Step Length (m)
Distribution
tentative
updated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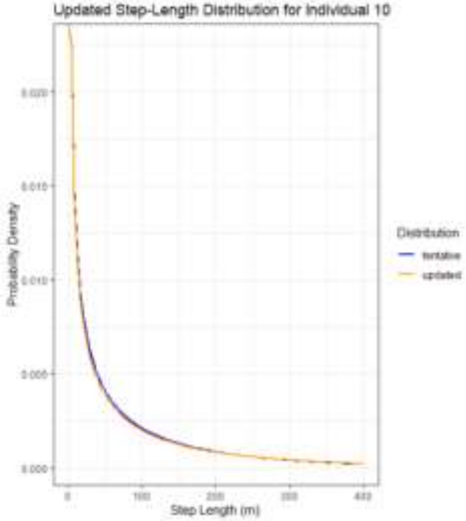
Probability Density
0.00
0.05
0.10
0.15
0.20
0.25
−π
−π/2
0
π/2
π
Relative Turn Angle (radians)
Distribution
tentative
updated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Probability Density
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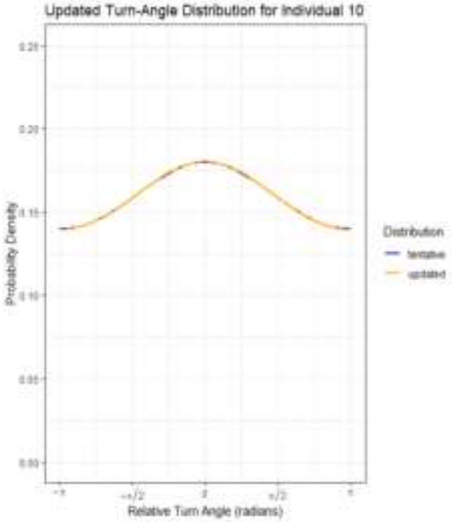
0.010
0.015
0.020
0
100
200
300
400
Step Length (m)
Distribution
tentative
updated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Probability Density
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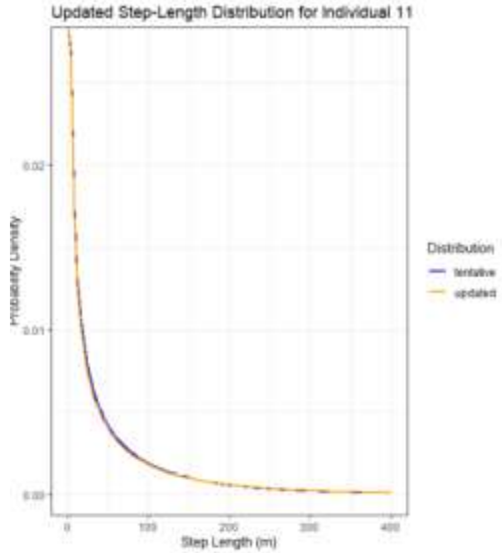
0.05
0.10
0.15
0.20
0.25
−π
−π/2
0
π/2
π
Relative Turn Angle (radians)
Distribution
tentative
updated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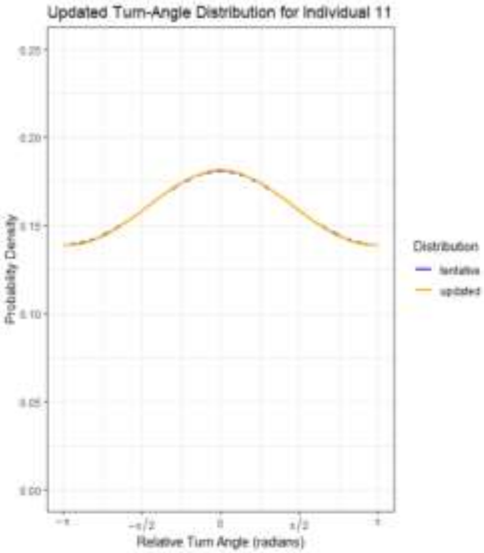
0.01
0.02
0
100
200
300
400
Step Length (m)
Distribution
tentative
updated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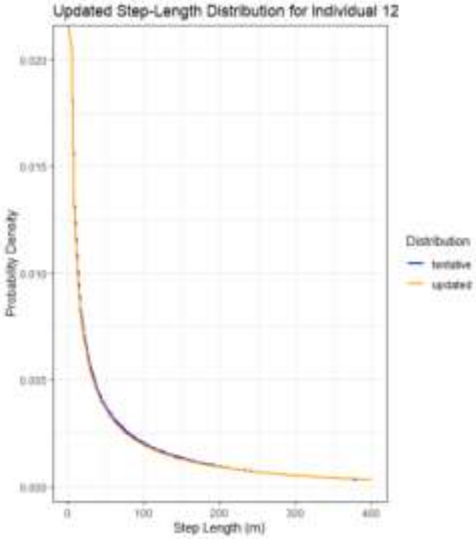
Probability Density
0.00
0.05
0.10
0.15
0.20
0.25
−π
−π/2
0
π/2
π
Relative Turn Angle (radians)
Distribution
tentative
updated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0.020
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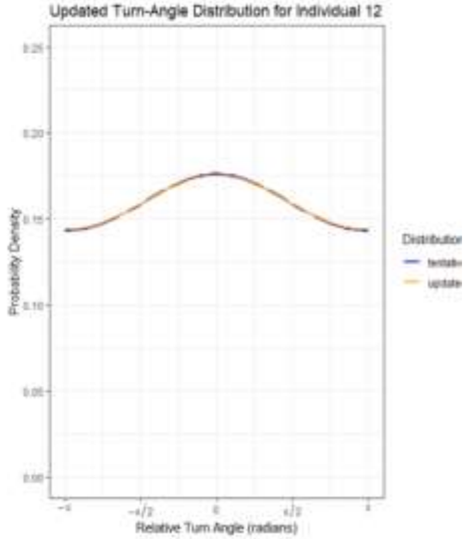
100
200
300
400
Step Length (m)
Distribution
tentative
updated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Probability Density
0.00
0.05
0.10
0.15
0.20
0.25
−π
−π/2
0
π/2
π
Relative Turn Angle (radians)

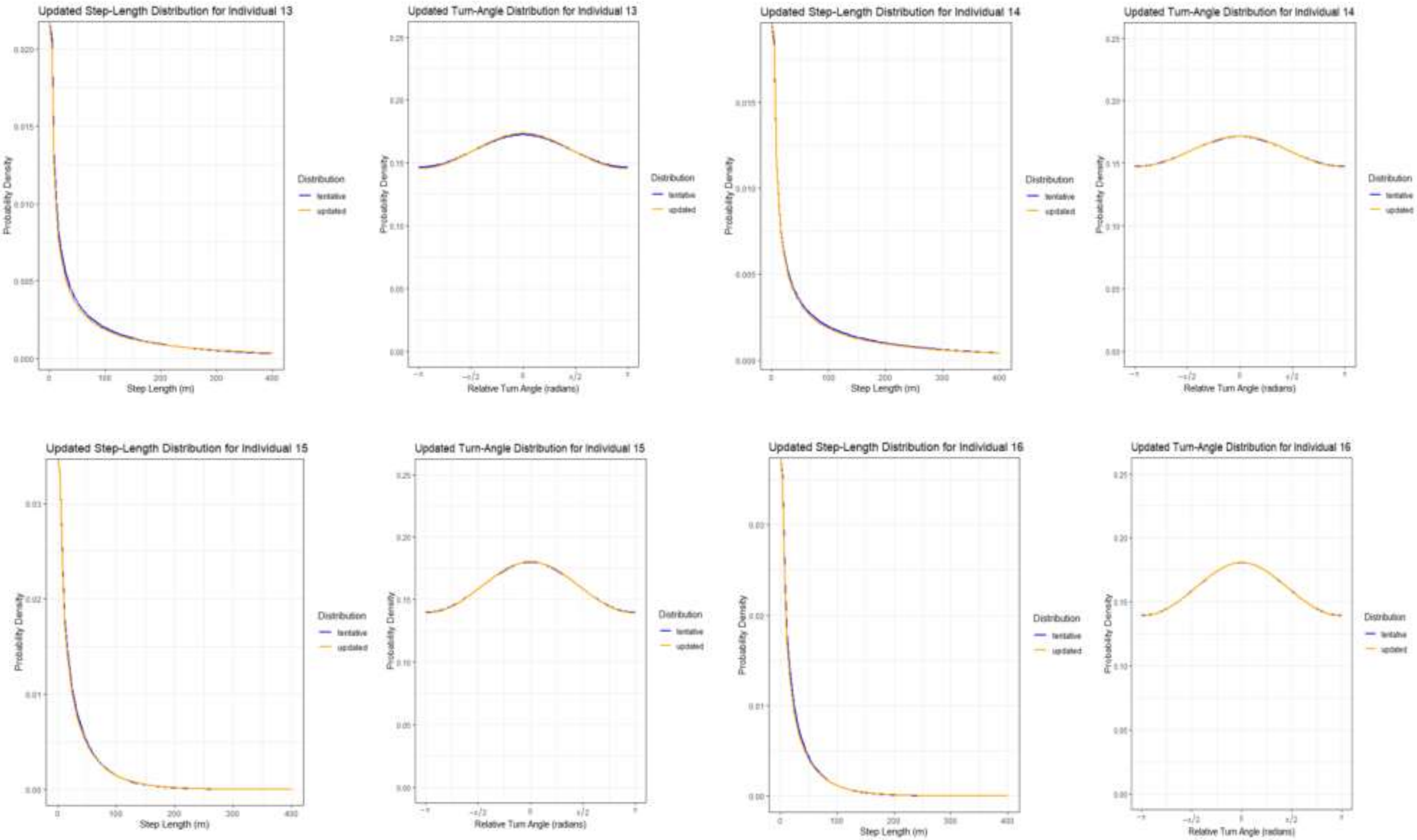

Figure A1. Tentative and updated distribution estimates very similar among individuals, despite the coefficients associated with sl_ and cos_ta_ being statistically significant in our fitted fixed-effect model. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Appendix – Tables

Table A.3.1. Log-odds coefficient estimates from a fitted mixed-effect conditional logistic regression model. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Term	Coef	Exp(coef)	SE(coef)	Robust Se	Z-score	Pr(>|z|)	Reference Class
log_sl_	-0.0163	0.9840	0.0039	0.0115	-1.4140	0.1574	
cos_ta_	-0.1971	0.8211	0.0121	0.0762	-2.5860	0.0097 *	
sl_	0.0003	1.0000	0.0000	0.0000	6.3540	0.0000 *	
wet_dist_end	-0.1397	0.8697	0.0055	0.0330	-4.2310	0.0000 *	
fore_dist_end	0.0215	1.0220	0.0059	0.0147	1.4650	0.1428	
Crop_dist_end	0.0097	1.0101	0.0053	0.0139	0.6970	0.4858	
Past_dist_end	0.0201	1.0200	0.0051	0.0214	0.9400	0.3470	
log_sl_:wet_dist_start	0.0001	1.0000	0.0000	0.0001	1.0960	0.2733	
cos_ta_:wet_dist_start	0.0003	1.0000	0.0001	0.0004	1.1500	0.2500	
log_sl_:fore_dist_start	0.0000	1.0000	0.0000	0.0000	-0.3930	0.6943	
cos_ta_:fore_dist_start	0.0001	1.0000	0.0000	0.0000	2.9120	0.0036*	
log_sl_:Crop_dist_start	0.0000	1.0000	0.0000	0.0000	-0.6050	0.5450	
cos_ta_:Crop_dist_start	0.0000	1.0000	0.0000	0.0000	2.2220	0.0263 *	
log_sl_:Past_dist_start	-0.0001	0.9999	0.0000	0.0001	-1.7490	0.0803	
cos_ta_:Past_dist_start	-0.0013	0.9987	0.0001	0.0003	-4.1500	0.0000 *	
log_sl_: Temperature	-0.0348	0.9658	0.0008	0.0067	-5.1820	0.0000 *	
cos_ta_:Temperature	-0.1480	0.8624	0.0040	0.0428	-3.4570	0.0005 *	
wet_dist_end:Temperature	0.0009	1.0010	0.0034	0.0106	0.0880	0.9302	
fore_dist_end:Temperature	-0.0093	0.9908	0.0042	0.0112	-0.8250	0.4091	
Crop_dist_end:Temperature	0.0332	1.0340	0.0041	0.0120	2.7600	0.0058 *	
Past_dist_end:Temperature	-0.0244	0.9759	0.0041	0.0150	-1.6240	0.1043	

wet_dist_end:tod_end_dusk	0.1186	1.1260	0.0260	0.0463	2.5610	0.0104 *	Daytime
wet_dist_end:tod_end_night	0.0788	1.0820	0.0075	0.0256	3.0760	0.0021 *	Daytime
wet_dist_end:tod_end_dawn	-0.0242	0.9761	0.0238	0.0266	-0.9110	0.3623	Daytime
fore_dist_end:tod_end_dusk	-0.0156	0.9845	0.0291	0.0144	-1.0880	0.2767	Daytime
fore_dist_end:tod_end_night	-0.0337	0.9668	0.0085	0.0085	-3.9530	0.0001*	Daytime
fore_dist_end:tod_end_dawn	-0.0212	0.9790	0.0282	0.0107	-1.9860	0.0471 *	Daytime
Crop_dist_end:tod_end_dusk	-0.0095	0.9905	0.0248	0.0146	-0.6540	0.5128	Daytime
Crop_dist_end:tod_end_night	0.0084	1.0080	0.0071	0.0066	1.2260	0.2201	Daytime
Crop_dist_end:tod_end_dawn	0.0372	1.0380	0.0245	0.0098	3.8040	0.0001 *	Daytime
Past_dist_end:tod_end_dusk	-0.0436	0.9573	0.0280	0.0307	-1.4200	0.1556	Daytime
Past_dist_end:tod_end_night	-0.0250	0.9753	0.0075	0.0131	-1.9130	0.0557	Daytime
Past_dist_end:tod_end_dawn	-0.0206	0.9796	0.0263	0.0172	-1.1990	0.2304	Daytime

Table A1 continued

Table A.3.2. Log-odds ratio coefficient estimates from a main-effect conditional logistic regression model incorporating a daily temperature covariate. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Term	Coef	Exp(coef)	SE(coef)	Robust Se	Z-score	Pr(>|z|	Significance
log_sl_	-0.0290	0.9714	0.0012	0.0015	-19.8570	0.0000	*
cos_ta_	-0.1008	0.9042	0.0039	0.0477	-2.1140	0.0345	*
sl_	0.0004	1.0000	0.0000	0.0000	8.7700	0.0000	*
wet_dist_end	-0.0677	0.9345	0.0032	0.0159	-4.2680	0.0000	*
fore_dist_end	0.0104	1.0100	0.0036	0.0076	1.3540	0.1757	
Crop_dist_end	0.0054	1.0050	0.0032	0.0039	1.4080	0.1592	
Past_dist_end	0.0082	1.0080	0.0035	0.0092	0.8850	0.3762	
Daily-temperature	-0.0031	0.9969	0.0030	0.0018	-1.6950	0.0902	

Table A.3.3. Log-odds coefficient estimates from a main-effect conditional logistic regression model incorporating a quadratic daily temperature covariate. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Term	Coef	Exp(coef)	SE(coef)	Z-score	Pr(>|z|	Significance
log_sl_	-0.0290	0.9714	0.0012	-23.8100	0.0000	*
cos_ta_	-0.1008	0.9042	0.0039	-25.7110	0.0000	*
sl_	0.0004	1.0000	0.0000	16.5980	0.0000	*
wet_dist_end	-0.0677	0.9345	0.0032	-20.8780	0.0000	*
fore_dist_end	0.0103	1.0100	0.0036	2.8350	0.0046	*
Crop_dist_end	0.0054	1.0050	0.0032	1.6870	0.0916	
Past_dist_end	0.0082	1.0080	0.0035	2.3610	0.0182	*
time_var_covar_end	-0.0037	0.9964	0.0042	-0.8710	0.3840	
I(Daily-temperature^2)	-0.0005	0.9995	0.0023	-0.2000	0.8418	

Chapter 4: Resource Selection of Wild Pigs in Southwest Florida

Abstract

Resource selection analysis is a valuable tool for understanding how animals interact with heterogeneously distributed resources. Wild pigs (*Sus scrofa*) are a long-lived iteroparous species that use many habitat types across their range and are associated with tremendous economic and environmental damage. Understanding which resources wild pigs depend on in Southwest Florida will help wildlife managers predict the distributions of pigs and better control populations and range expansion. We used 2nd and 3rd order resource selection models to quantify selection of landcover types over in Southwest Florida. We found wild pigs were more likely to select home ranges nearer to wetlands, forests, and pastures, while avoiding areas near cropland habitats. Within their home ranges they were more likely to select habitats farther from croplands, forests, and wetlands. Wild pigs can adapt to a wide variety of landcover types; however, our findings reinforce the importance of wetlands, forests and pastures to wild pig selection of home ranges, where they likely utilize these landcover types for thermoregulation (e.g. forests and wetlands) and for foraging resources (e.g. pastures). However, at both spatial scales of selection, wild pigs avoided cropland habitats, possibly due to a lack of cover in open habitats and anthropogenic disturbance. Within home ranges wild pigs selected for areas farther from forests and wetlands. This may be attributed to perceived predation risk being higher in those habitats, thus causing wild pigs to forgo higher quality resources to reduce risk.

Key words: Habitat, home range, second-order resource selection, *Sus scrofa*, third-order resource selection, wild pigs

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Introduction

Wild pigs are a nonnative species in the United States that cause significant environmental damage (e.g., rooting and wallowing behaviors), and pose a health risk to humans by the transmission of zoonotic diseases ((Corn and Jordan, 2017; Centner and Shuman, 2015; Krull et al. 2013). Wild pigs are among the worst invasive species in the world as ranked by the International Union for Conservation of Nature (Corn and Jordan, 2017). Still, wild pigs are culturally important in Florida and are prized by hunters. As such, they and are often transported to privately owned lands and released for hunting. This accelerates population expansion throughout the state (Grady et al. 2019). Human-mediated translocations are considered to be the key factor in long-range dispersal across the united states (McCann et al. 2018). Wild pigs now occur statewide with a population size of ~ 1 million (Florida Department of Agriculture and Consumer Services, 2016). Their populations have not only been increasing quickly, but they have thrived across the heterogeneous landscapes of Florida, partly due to their generalist attributes. For example, between 1982 and 2016, wild pig range expansion across the United States nearly tripled, with populations increasing from 18 to 35 states (Grady et al. 2019; Corn and Jordan, 2017). Expensive control policies (e.g., Farm Bill) have been implemented to mitigate ecological and economic damages (Grady et al. 2019). Investigating scale-dependent spatiotemporal variation in resource selection across heterogeneous landscapes is informative for wild pig management.

Knowledge of broad and fine-scale resource selection is informative in determining management decisions and conservation planning (Schlichting et al. 2016), and in gaining a better understanding of what resources are essential to the biological needs (reproduction and survival) of wild pigs. Abiotic and biotic environmental conditions likely influence wild pigs' distribution, movement, and spatial ecology, which ultimately shapes the spatial and temporal dynamics of home-range selection. The broad-scale distribution of wild pigs on the landscape is dictated partly by food availability and dietary shits throughout the year (Mayer and Brisbin, 2009). However, after establishing a home range they often select resource patches that maximize their biological needs (e.g., resting, mating) and energetic demands (Clontz et al.2021). Resource patches are not chosen randomly but rather to meet their immediate needs, which are different throughout different life stages and across seasons (Börger et al. 2008). However, resource availability and composition fluctuate across seasons, thus prompting animals to respond by shifting their distributions. Additionally, differences in habitat selection can occur between spatial scales as resources on the landscape (e.g., high-quality forage) fluctuate (Van Beest et al. 2011). Resource selection is a multiscale process that can reveal the mechanisms responsible for home range and within-home range selection (Johnson, 1980). Therefore, to take advantage of the conditionally nested nature across orders of selection, investigators should quantify resource selection across scales (DeCesare et al. 2012). Wild pigs are a generalist species that utilize many different habitats (Giuliano, 2010), therefore, there may be an increased likelihood of individual variation in resource use (e.g. some individuals using areas avoided by the rest). Thus, quantifying resource selection at the second (i.e., home range selection) and third order selection (i.e., within-home range) is necessary for detecting variation in resource use across spatial scales and heterogeneous habitats. It is also important to study selection at more than one scale, which will ultimately increase our understanding of long-term resource requirements of wild pig populations (Manly et al. 2002).

The Southwest Florida region is characterized by low-elevation prairies and marsh, freshwater slough, mesic pine flatwoods, oak-cabbage hammocks, cypress (Taxiodium spp.), and inactive pasture lands. Various species, such as live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*), and other mast-producing trees provide resources to wild pigs throughout the year (Cutini et al. 2013). Wild pigs are associated with forested habitats areas with abundant food sources and dense cover for bedding and protection from predators and hunters (Giuliano, 2010). Wild pigs have poor thermoregulation (Johann et al. 2020) and therefore are range limited by areas without available water sources, which wild pigs need for wallowing and rooting (Giuliano, 2010). Therefore, wild pigs will modify their movement patterns in response to physiological needs and alter their selection strength for different resources depending on their immediate biological needs (Clontz et al. 2021; Paolini et al. 2018). Selection of home range attributes (e.g. distance to landcover type) will depend on resource quality and animals will expand their range to increase high quality resources at the second order of selection (van Beest et al. 2010, Johnson, 1980). Therefore, it can be beneficial to sample home range selection at a large enough landscape scale to identify species-specific habitat use in areas where habitat is different from the study site (DeCesare et al. 2012; Jesmer et al. 2018). We quantified home range selection at the second order (home range) and third order (within home range) in two adjacent wildlife management areas in Southwest Florida. We hypothesized that at the second order scale wild pigs would select for areas closer to habitats that provide thermal refuge (e,g., forests and wetlands), while avoiding more open, hotter areas such as croplands and pasture habitats. However, at the within home range scale, we predicted that wild pigs would still select for areas containing thermal protection (e.g., forests and wetlands) but also habitats that provide essential food sources, such as pasture and croplands (Froehly et al. 2020) to meet nutritional requirements.

Methods

We worked on a study area (~ 262.87 km^2) located south of the Caloosahatchee River in Clewiston, Southwest Florida, and comprised of two adjacent sites: Okaloacoochee Slough Wildlife Management Area (WMA) and Dinner Island Ranch WMA (See Figure 1 – Chapter 2). The landcover composition consisted of inactive pasture lands, various types of wetland habitats (e.g., sloughs, wet prairie, mesic flatwoods), cypress dome (Taxiodium spp.), pine flatwoods, and hammocks consisting of various hardwood and palm species, such as live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*). General Management techniques for the sites included: active cattle grazing, citrus production, habitat restoration projects, prescribed fires, and chemical or mechanical treatments of exotic vegetation (See chapter 2 for site-specific details; Figure 1 – chapter 2).

We captured and collared adult and subadult pigs (≥ 23.0 kg) with GPS collars (Advanced Telemetry Systems, Isanti, Minnesota, USA), using open-topped corral and welded steel box traps with a trigger mechanism attached to a guillotine door. We chemically immobilized wild pigs with a mixture of Xylazine (4.4 mg/kg), Telazol (4.4 mg/kg), and Ketamine (2.2 mg/kg) intramuscularly (e.g., shoulder, rump), and used Tolazoline (2.0 mg/kg) as a reversal agent. We administered sedatives with a .22 caliber cartridge-fired rifle with a 5cc slow-inject disposable dart (Model 389, Pneu-Dart Inc., Williamsport, PA, USA). We recorded sex, weight, and morphological measurements for all captured individuals. We fitted each individual with a G5-2D Iridium GPS collar, weighing 0.7 kg, and programmed with a GPS fix rate at half-hour intervals recording 48 locations/day. The satellite transmission interval and mortality rate schedule were programmed at 4 hours intervals. We trapped wild pigs with equal effort across a variety of habitat types representative of the greater the region. A Special Purpose Permit was issued by the Florida Fish and Wildlife Conservation Commission Division of Hunting and

Game Management (permit numbers: SPGS-19-24; SPGS-19-63; SPGS-19-63-A1), and all procedures were permitted by Virginia Tech Institutional Animal Care and Use Committee Protocol number: 18-248. We conducted animal handling in accordance with the American Society of Mammologists (ASM) guideline (Sikes et al. 2016).

We generated individual raster layers for four landcover categories from the 2019 National Landcover Database (NLCD). We chose cover types representative of the vast majority of the study area. Raster layer categories included: (1) wetlands (i.e., woody wetlands, emergent herbaceous wetlands), (2) pasture/hay, (3) cultivated crops, and (4) forest (i.e., deciduous forest, evergreen forest, mixed forest). We used a Euclidian distance-based approach to determine selection or avoidance of each habitat type by measuring the distance from each raster cell to the nearest cell with a value. A distance-based approach reduces edge effect and telemetry error biases (Thurfjell et al.2014; Conner et al. 2003). We transformed and projected the coordinate reference system of our GPS movement data to match that of the NLCD raster data. We then cropped the NLCD raster layers to a bounding box with a 30,000 m^2 buffer containing GPS movement data within our study area, to account for long-distance movements across a much larger landscape encompassing agricultural and private areas to infer more broad-scale resource selection associated with the placement of the home range (e.g., Figure 1; Jesmer et al. 2018; Fattebert et al. 2015; Manly et al. 2007). Within the landscape scale polygon, we quantified second-order selection by treating population home ranges as available which we characterized by generating 10 random locations per observed animal for comparison with GPS telemetry-based used locations. To test *a priori* resource selection hypotheses at a fine scale, we used a third order resource selection function to quantify habitat availability for individuals within their estimated home ranges by generating 10 random points per observed animal location within the

95% home range polygon or each individual wild pig. To directly account for the inherent autocorrelation structure of movement data, and to reduce negative bias in home range size, we produced individual home ranges for wild pigs using the autocorrelated kernel density estimator (AKDE) in the continuous-time movement modeling (ctmm) R package (Fleming et al. 2015; Fleming and Calabrese, 2021-R package version 0.6.1). To implement an appropriate autocorrelation structure within the ctmm framework, we visually assessed individual based empirical variograms to provide an unbiased means of visualizing the autocorrelation structure (Calabrese et al. 2016). We then selected initial autocorrelation parameter estimates and chose the best-supported maximum likelihood-based movement model using Akaike's Information Criterion (AICc) to select the most parsimonious model estimating 95% AKDE home range contours and confidence intervals for each individual wild pig.

We extracted covariate values to both used and available locations and scaled (*SD* =1) and centered (mean = 0) all habitat covariates prior to fitting generalized mixed-effect models (GLMM; Schielzeth, 2010). We converted the response variable from a categorical (i.e., True or False) to a numeric variable (i.e., 1 = used or 0 = available points). We then used a Chi-Squared forward stepwise model selection procedure to determine variables that explained the most variation in our response variable, and AICc was used to identify the most parsimonious resource selection function (Burnham and Anderson, 2002). We inspected for collinearity ($r \leq |0.5|$; Pearson's correlation) among independent variables using the cor function in R (R package stats, version 3.6.2). The models for second and third order selection were fit with a maximum likelihood binomial response distribution (logistic regression), containing a logit link to the used-available data. All GLM models were computed using the glmer function in R package Lme4

(Bates et al. 2006). To further evaluate model fit, we performed a k-fold cross-validation test repeated 100 times to evaluate prediction success (Boyce et al. 2002).

Results

We used a sample of 16 wild pigs (13 M, 3 F) tracked between June 2019 and February 2021, with GPS collars programmed to record 48 locations/day at half-hour fix rates, resulting in 203,352 validated and cleaned locations. Collared pigs on Dinner Island Ranch WMA had an average functioning collar retainment rate of 6.85 months and 5.83 months in Okaloacoochee Slough WMA. The longest length of time an individual retained a functioning collar was 17.22 months, and the shortest was 0.60 months. Wild pig body weight ranged from 24.2 kg to 102.9 kg across our study site (See Table A1. – Chapter 2).

For second order selection the most parsimonious AICc selected model was a population-level generalized linear model (GLM) containing all four habitat covariate categories. We included individual-specific random intercepts to account for variation in sampling duration among individuals (Gillies et al. 2006). Wild pigs selected home ranges in habitats that were closer distances to wetlands, forests and pasture habitats, while avoiding areas nearer to cropland habitat (Figure 2, Table 1). More specifically, the probability of use decreased approximately 8% for every 100 m increase from wetland habitats (β = -2.42258, SE = 0.03107, *p* = > 0.0001). Next, the probability of use decreased approximately 37% for every 100 m increase from forested habitats (β =-0.53729, SE = -0.53729, *p* = > 0.0001). Third, the probability of use decreased approximately 3% for every 100 m increase from pasture habitats (β =-8.19562, SE = 0.06135, *p* = > 0.0001). Finally, the probability of use increased approximately 89% for every 100 m increase from croplands (β =2.12236, SE = 0.01066, *p* = > 0.0001). Cross-validation values for the mean coefficient of variation of the population-level second order selection model was 0.99, with values close to one indicating good model fit. We generated a predicted raster layer based on the top second order RSF model (Figure 3).

For third order selection the initial most parsimonious AICc selected model was a population-level GLM containing an individual-specific random intercept and all four habitat covariate categories. However, further evaluation of the top model revealed poor model fit (i.e. Pseudo $R^2 = 0.17$; k-fold cross validation = -0.7). Therefore, to account for individual-level random variation we included a population-level GLM containing individual-specific random intercepts and slopes (i.e. Pseudo $R^2 = 0.85$; k-fold cross validation = 0.98). The fixed-effect coefficient estimates demonstrated significance in wild pigs selecting areas farther from croplands (β = 0.41704, SE = 0.16474, *p* = 0.0114), forests (β = 0.89013, SE = 0.17167, *p* = > 0.0001) and wetlands (β = 0.40629, SE = 0.06329, *p* = > 0.0001). For every 100 m increase from croplands, forests, and wetlands, probability of use increased approximately 60%, 71% and 60% respectively (Figure 4, Table 2). Population-level random effect parameter estimates demonstrated evidence that the variance in the change in one unit (m) increases in distance from landcover types contained some variation among intercepts (i.e. individual pigs) and groups (i.e. landcover types; Table 3). In addition, individual-level coefficient estimates demonstrated evidence of both inter and intra-individual variation among direction and relative magnitude of slopes (Table 4)

Discussion

Understanding relationships between habitat composition and home range (e.g. of and within home range) selection can provide valuable insight into resource requirements for nonnative invasive species. Often, these processes can influence spatiotemporal distributions of species. Our study demonstrated that wild pigs in Southwest Florida largely depended on different landscape characteristics across spatial scales and orders of selection. For example, our results showed evidence that home range selection was largely dependent on selecting habitats nearer to wetlands, forests and pastures, and farther from croplands, at the larger landscape scale. However, at the within home range scale, we found evidence that wild pigs were more likely to avoid wetlands, forests, and croplands, and insufficient evidence for the selection or avoidance of pasture habitat. Our finding that wild pigs selected for pasture habitats at the home range scale is congruent with a large body of evidence demonstrating wild pigs' use of pasture habitat (e.g., Froehly et al. 2020; Mersinger and Silvy, 2007), which provides essential food sources (Froehly et al. 2020). However, as wild pigs root in the soil for food resources they often do extensive damage to pastures which can have negative economic impacts for both cattle and sod production (Ellington, 2022).

In agreeance with our prediction, wild pigs selected for home ranges nearer to forested habitats which may be a strategy to keep their core body temperatures lower, especially during resting, and to seek perceived safety from predators (Johann et al. 2020). Wild pigs have poor thermoregulation (Johann et al. 2020; VerCauteren et al. 2019; Bracke et al. 2011), and likely selected for areas nearer to forests as a direct response to hot temperatures (Clontz et al, 2021; Hartley et al. 2014; Kay et al. 2017, Dexter, 1998). Wild pigs are diet generalist that consume nutritional food sources such as forbs, foliage of woody plants, and hard or soft mast (Froehly et al. 2020), which occur in forested habitats in Florida (Guiliano, 2010). Therefore, forested habitats likely maximize the fitness of wild pigs by acting as a means of providing thermal insulation and to meet nutritional requirements.

As predicted, wild pigs selected for home ranges nearer to wetland habitats, which provide wet conditions that are likely necessary to wild pigs given their poor physiological cooling abilities (Guiliano, 2010). Wet conditions are ideal areas for wallowing in wet mud which is a beneficial behavior for wild pigs because it provides thermoregulation and the removal of parasites (Gray et al. 2019). In addition, the saturated areas in wetlands are optimal for rooting behavior (Welander, 2000), which is a known foraging strategy (Sandom et al.2013). Wetland habitats provide the necessary components (e.g., water, food, and sometimes cover) that have been shown to dictate the spatial distributions of wild pigs (Gray et al. 2019; McIlroy, 1989), as well as suitable habitat for farrowing (e.g., central Alabama, Gatson et al. 2008). Wild pigs are diet generalists that feed on the vegetation types commonly found in riparian areas, marshes, and swamps (Gray et al. 2019). Across their North American range, the relationship between water and temperature has been thoroughly documented (e.g., Thurfjell et al. 2009; Cooper and Sieckenius, 2016; Mersinger and Silvy, 2007).

Finally, as predicted, wild pigs selected home ranges farther from cropland, which may be in direct response to a lack of cover in open habitats and anthropogenic disturbance. This would make sense give that across their geographic distributions evidence demonstrates wild pigs modifying their movements and habitat selection to avoid extreme temperatures (Satter et al. 2022 – *PhD Dissertation, Ch.3*; Clontz et al, 2021; Hartley et al. 2014; Kay et al. 2017, Dexter, 1998). Portions of our study site are used for citrus production and adjacent to private farmlands and ranches where agricultural production occurs. Evidence has shown that wild pig occurrence is negatively related to humans (O'Brien et al. 2019) and anthropogenic activity has been shown to affect the diel activity patterns of wild pigs (Johann et al. 2020).

We found evidence that within home ranges wild pigs were selecting for areas farther from cropland habitats which is likely explained by a lack of thermal protection and anthropogenic activities. However, we also found evidence that wild pigs were selecting for areas farther from forests and wetlands within their home ranges. We speculate that this could be due to stress-induced predator-prey interactions where wild pigs may perceive predation risk to be higher in those habitats. For example, according to the optimal foraging theory, animals should select resources that maximize benefits, while minimizing cost. However, sometimes the highest quality resources (i.e. most energetically profitable) are accompanied by a high risk of predation. Thus, prey may choose lower quality habitats in order to reduce risk (Preisser and Bolnick, 2008). In our study system, wild pigs shared the landscape with a large carnivore guild [e.g. Florida black bear (*Ursus americanus floridanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and the American alligator (*Alligator mississippiensis*)] that could induce trait-mediated effects on wild pigs, including the Florida panther (*Puma concolor coryi*) which have been documented to prey on wild pigs (Maehr et al. 1990, Dalrymple and Bass, 1996). In addition, anthropogenic disturbance (e.g. hunting) within or adjacent to WMA's may impact habitat selection (Johann et al. 2020; O'Brien et al. 2019; Ohashi et al. 2013; Keuling et al. 2008). However, the lack of evidence for selection at the within home range scale may be attributed to a more stable climate given that wild pigs often display stronger selection in harsher climates (Gray et al. 2019). In addition, wild pigs are a highly adaptive generalist species, which make quantifying trends over heterogeneous habitat challenging to detect. Therefore, the generalist nature of wild pigs may partially explain the lack of performance of our initial population-level generalized linear model. We speculate that this may be due to a fair degree of individual variation (e.g., some individuals preferring areas avoided by the rest), given the generalist nature of wild pigs across their geographic range.

Wild pigs are highly destructive to ecosystems in Florida, where they inflict irreparable damage to agriculture and the ecosystem (Krull et al. 2013), and expanding populations may pose a direct health risk to livestock, wildlife, and humans (Centner and Shuman, 2015). Therefore, using fine-scale GPS data to quantify scale-dependent resource selection is necessary for understanding species spatial ecology (Johnson 1980; Manly 2002). As with most species, wild pigs rely on water, food, and cover (McIlroy, 1989) and select areas that satisfy these ecological requirements (Gray et al. 2019). On the larger landscape scale, our findings are consistent with the scientific literature regarding resource selection of home ranges nearer to wetlands, forests, and pastures, while avoiding areas nearer to croplands (e.g. Kramer et al. 2022; Giuliano, 2010; Gatson et al. 2008). However, our findings at the within home range scale are novel and warrants further investigation incorporating additional environmental covariates (e.g. food availability, crop harvest, season, etc.) to account for individual variation in resource selection of a generalist species. However, other studies have demonstrated that inter-individual resource selection for wild pigs showed minimal preference of any particular habitat type, which was attributed to their generalist nature (Adkins and Harveson, 2007).

Overall, our work highlights the habitat associations of wild pigs in Southwest Florida across two orders of selection on a landscape surrounded by agricultural and private ranch lands. Our findings reinforce both the roles of habitat types on resource selection and the high inter-individual variation of wild pigs on resource selection. Additional research in Southwest Florida is needed to reveal trends in resource selection of wild pigs across spatial and temporal scales.

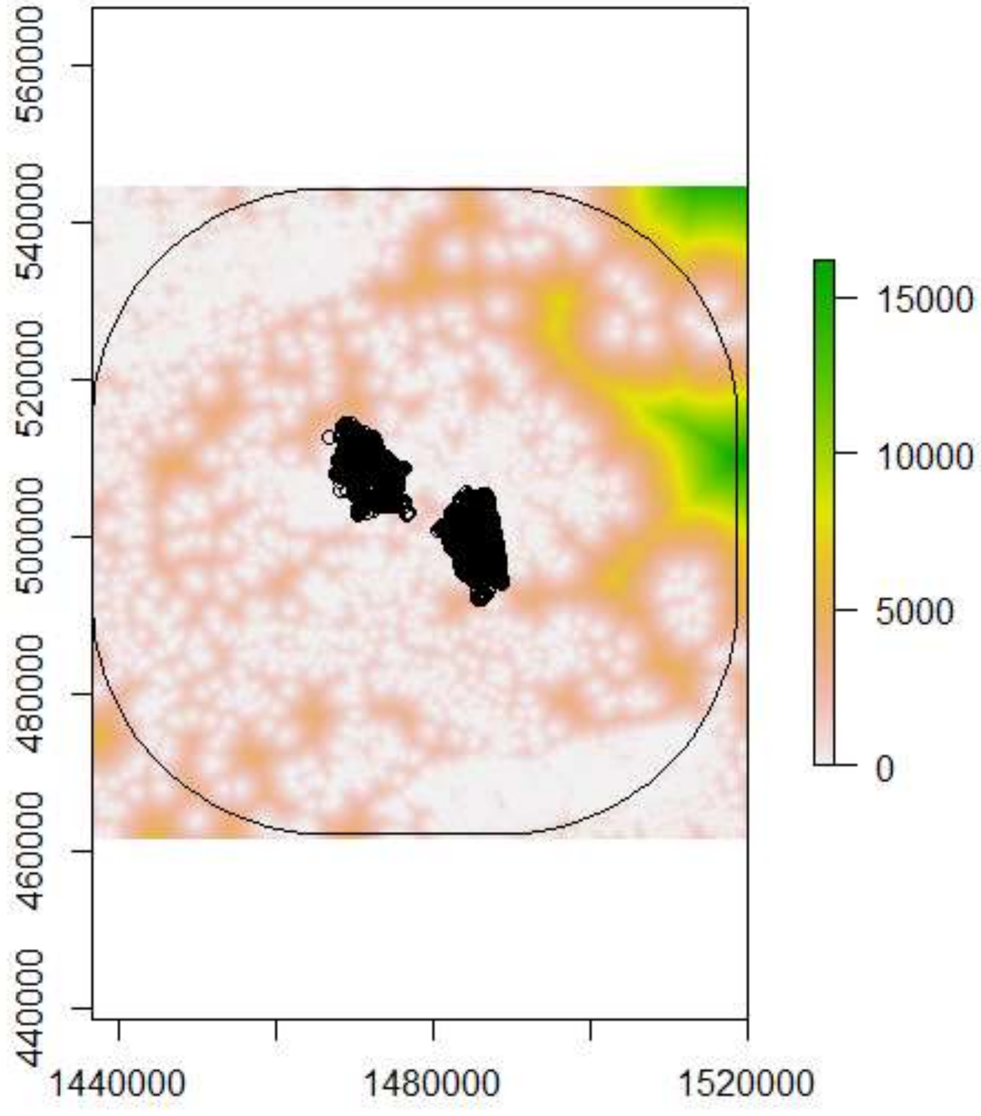

Figure 1. Example of a 30,000 m^2 buffer used for broad-scale 2^{nd} order resource selection model plotted against a forest raster. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

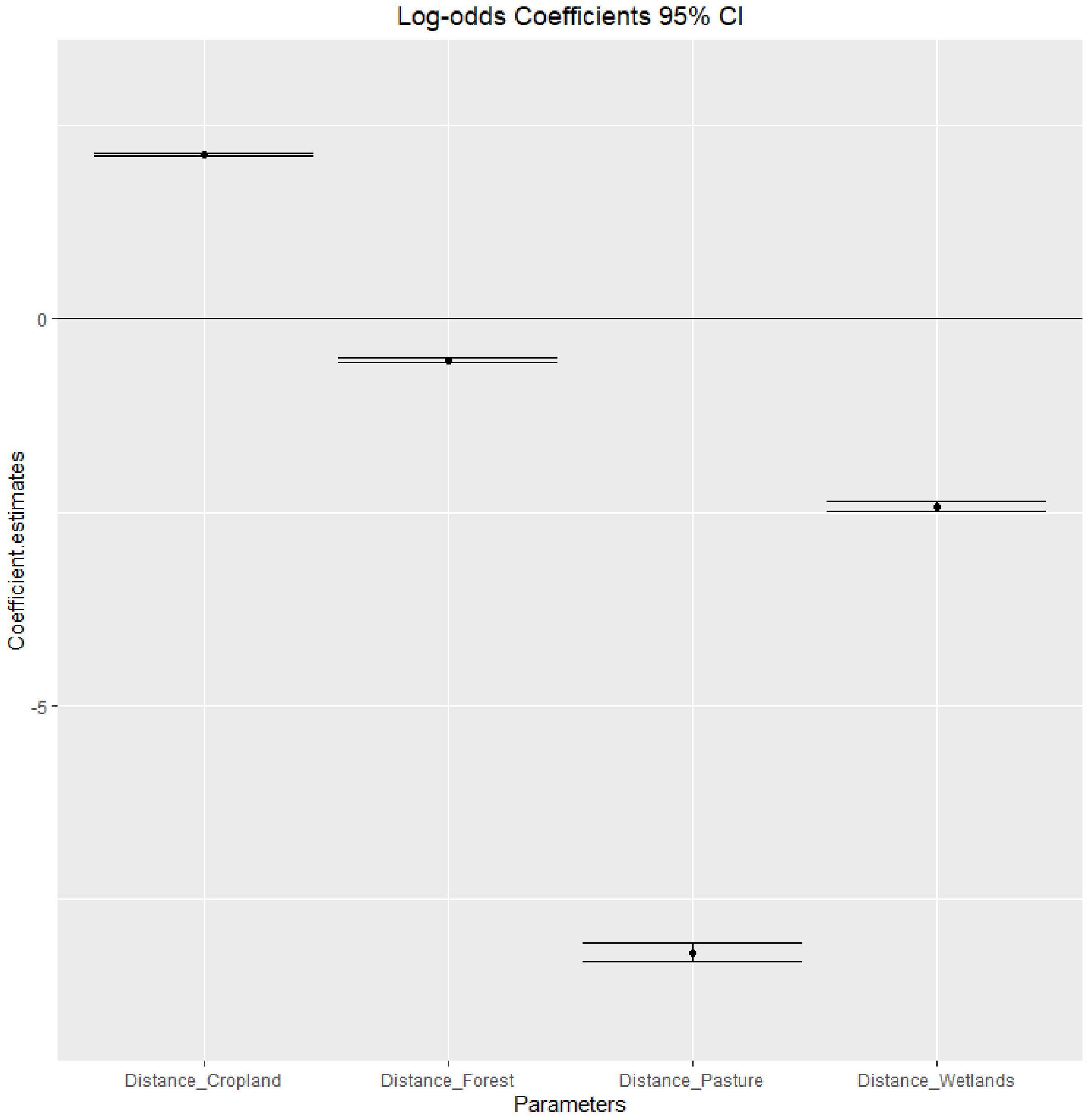

Figure 2. Plotted significant log-odds coefficients from a second order population-level generalized linear model (GLM), fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link for second-order resource selection. Error bars represent 95% Confidence Intervals. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

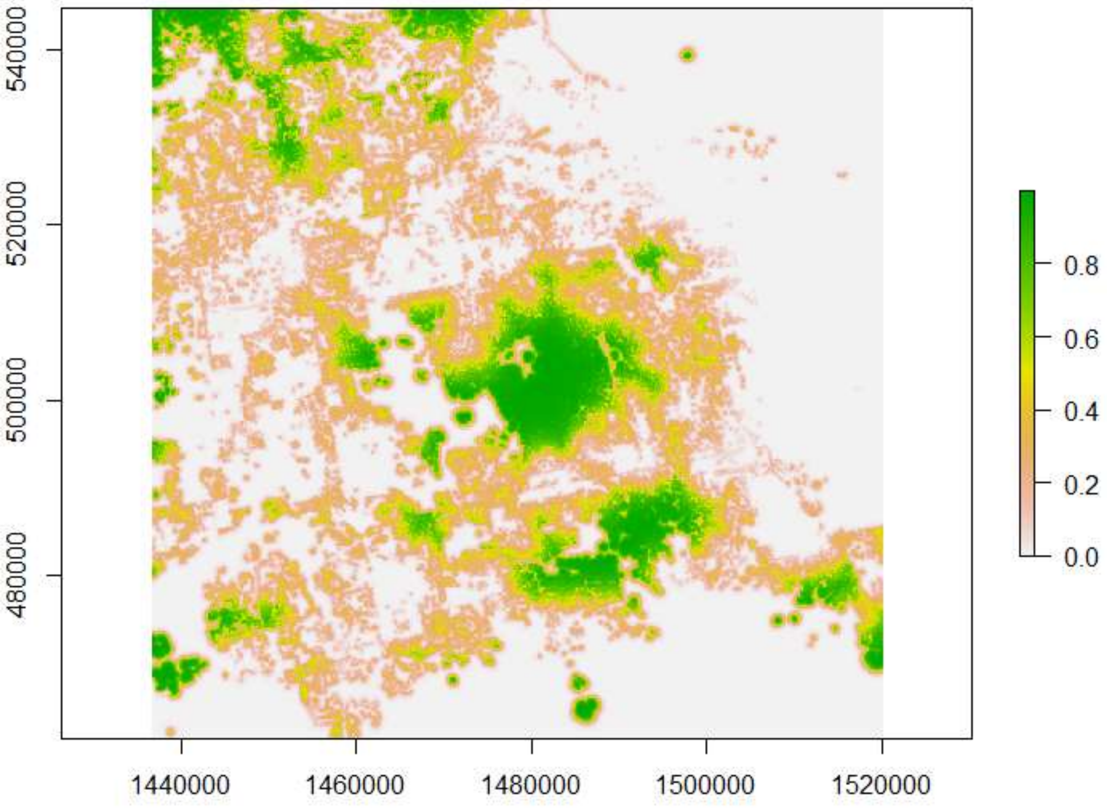

Figure 3. Predictor raster layer plot containing all habitat covariates, based on top 2nd and 3rd order resource selection model coefficient estimates. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

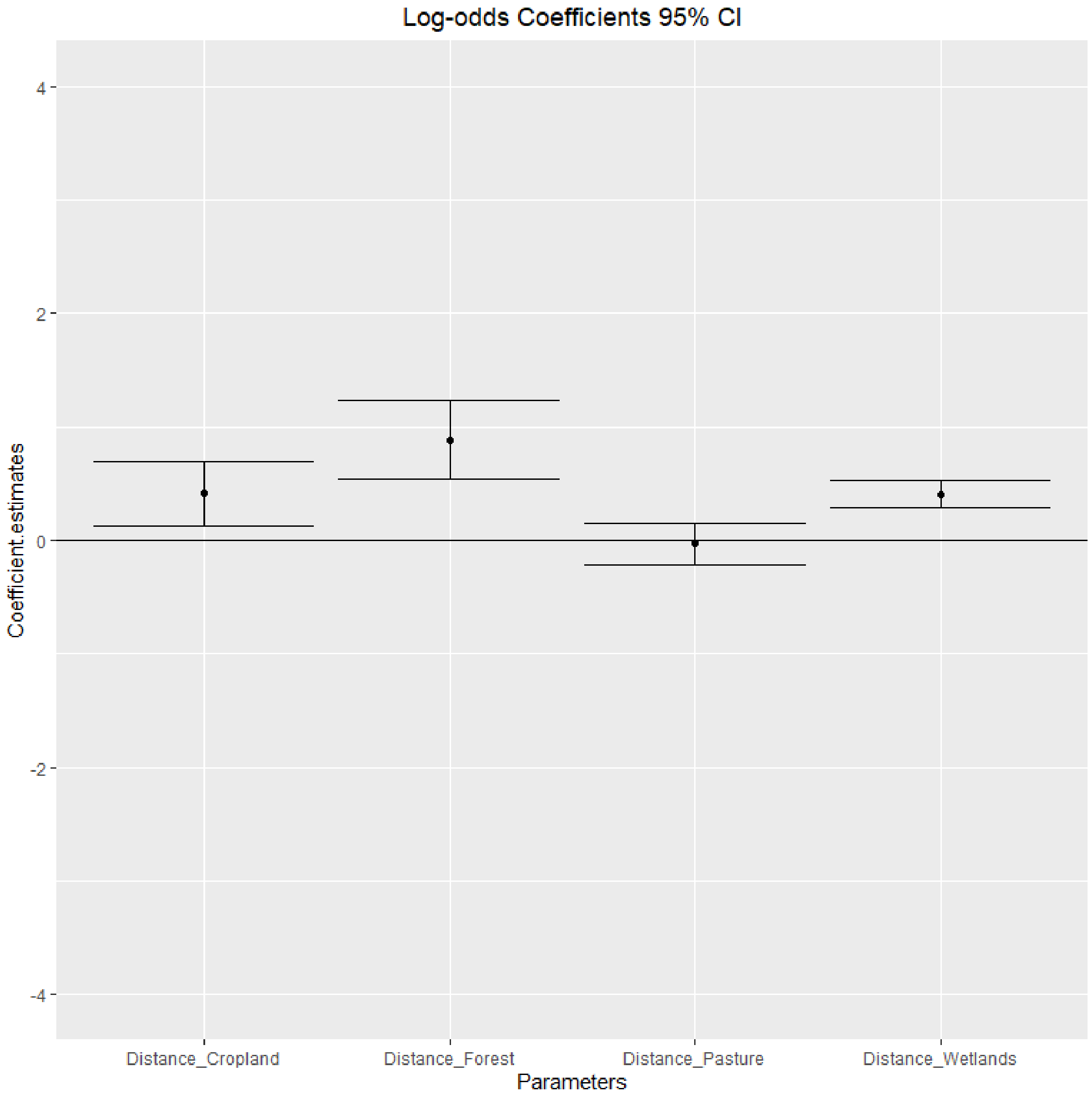

Figure 4. Fixed effect significant logs-odds coefficients from a third-order population-level generalized linear model (GLM), fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link. Error bars represent 95% Confidence Intervals. The thick vertical intercept indicates no effect (i.e., selection), while to either side of the vertical line indicates the direction and relative magnitude of the resource selection model. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

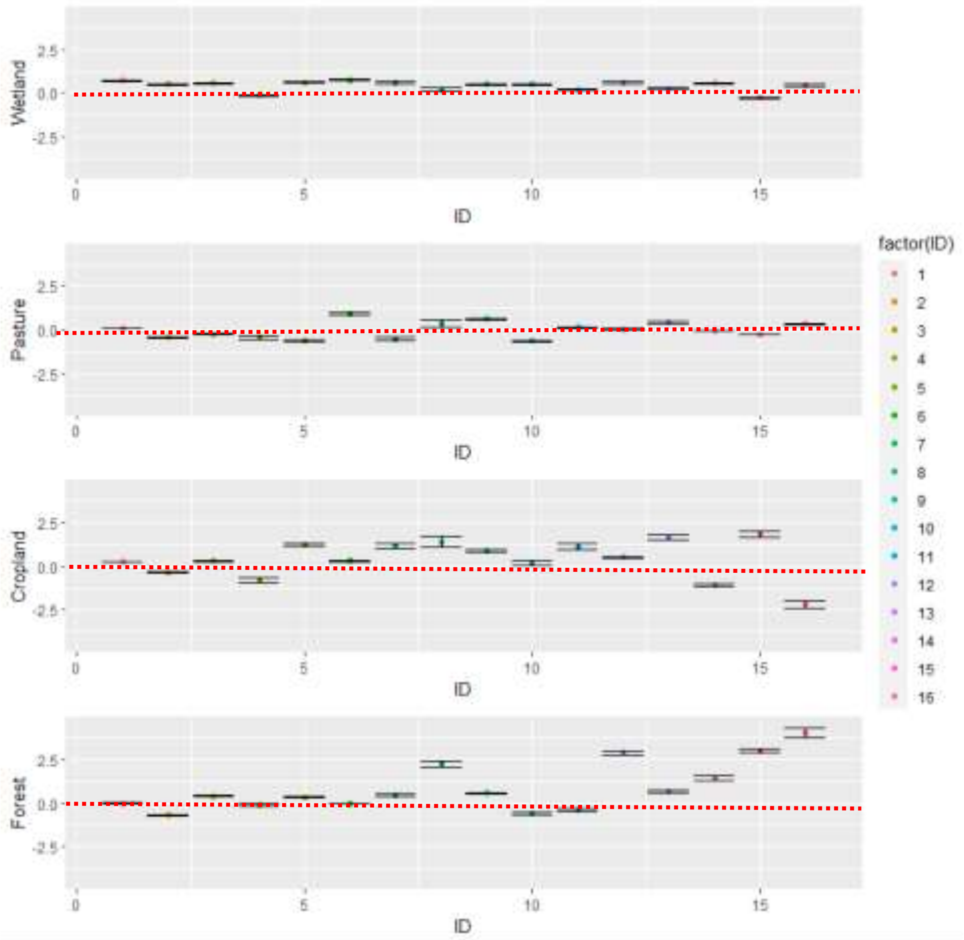

Figure 5. Individual-level logs-odds coefficients from a third-order generalized linear model (GLM) containing individual-specific random intercepts and slopes, fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Table 1. Population-level generalized linear model (GLM) fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link for second-order resource selection. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Term	β (95% CI)	SE	Z	Pr(>|z|)
Intercept| ID	-2.921 (3.628 - 2.213)	0.310	-9.427	<0.001
Distance_Cropland	2.122 (2.10 -2.14)	0.011	199.065	<0.001
Distance_Pasture	-8.196 (-8.317 - -8.07)	0.061	-133.581	<0.001
Distance_Forest	-0.537 (-0.565 - -0.509)	0.014	-37.725	<0.001
Distance_Wetlands	-2.423(-2.484 - -2.362)	0.031	-77.978	<0.001

Table 2. Fixed effect logs-odds coefficients from a third-order population-level generalized linear model (GLM), fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Term	β (95% CI)	SE	Z	Pr(>|z|)
Intercept| ID	3.331 (3.036 – 3.627)	0.169	19.787	<0.001
Distance_Cropland	0.412 (0.131 – 0.698)	0.165	2.532	0.011
Distance_Pasture	-0.020 (-0.211 – 0.157)	0.101	-0.296	0.767
Distance_Forest	0.889 (0.548 – 1.233)	0.172	5.185	<0.001
Distance_Wetlands	0.405 (0.285 – 0.531)	0.063	6.419	<0.001

Table 3. Random effect logs-odds coefficients from a third-order population-level generalized linear model (GLM), fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

Random Effects:

Groups	Name	Variance	Std. Dev	Corr
ID	Intercept	0.196	0.443	
	Cropland_distance	1.08	1.039	0.16
ID.1	Intercept	0.105	0.325	
	Pasture_distance	0.205	0.453	-0.42
ID.2	Intercept	2.227	1.492	
	Forest_distance	1.873	1.369	0.69
ID.3	Intercept	0.337	0.581	
	Wetland_distance	0.081	0.284	-0.99

Table 4. Individual-level slope logs-odds coefficients from a third-order population-level generalized linear model (GLM), fit by a maximum likelihood binomial response distribution (logistic regression), containing a logit link. Study was conducted on Dinner Island Ranch Wildlife Management Area and Okaloacoochee Slough Wildlife Management Area in Southwest Florida, USA, 2019-2020.

ID	Intercept	Cropland_ distance	Pasture_ distance	forest_ distance	Wetland_ distance	Intercept SE	Cropland SE	Pasture SE	Forest SE	Wetlands SE
1	2.451	0.281	0.074	-0.001	0.703	0.009	0.010	0.011	0.006	0.010
2	2.638	-0.341	-0.442	-0.690	0.482	0.019	0.022	0.020	0.016	0.015
3	2.145	0.322	-0.254	0.409	0.560	0.018	0.014	0.016	0.016	0.016
4	2.980	-0.779	-0.434	-0.127	-0.143	0.064	0.059	0.046	0.034	0.021
5	2.029	1.257	-0.628	0.331	0.609	0.014	0.033	0.025	0.014	0.016
6	2.446	0.310	0.905	-0.036	0.731	0.022	0.021	0.033	0.013	0.015
7	1.899	1.204	-0.537	0.451	0.618	0.030	0.074	0.050	0.032	0.035
8	1.284	1.417	0.368	2.262	0.198	0.219	0.160	0.097	0.089	0.054
9	1.449	0.876	0.605	0.577	0.482	0.051	0.038	0.027	0.021	0.016
10	2.542	0.210	-0.650	-0.577	0.489	0.045	0.081	0.029	0.041	0.029
11	3.796	1.140	0.124	-0.383	0.175	0.125	0.085	0.010	0.021	0.013
12	5.836	0.527	0.021	2.913	0.574	0.070	0.029	0.010	0.055	0.026
13	4.836	1.688	0.416	0.679	0.260	0.095	0.067	0.024	0.030	0.019
14	3.552	-1.070	-0.051	1.470	0.562	0.082	0.042	0.007	0.070	0.026
15	7.942	1.863	-0.281	2.992	-0.276	0.156	0.094	0.012	0.055	0.024
16	5.444	-2.196	0.340	4.037	0.459	0.159	0.096	0.015	0.146	0.038

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Chapter 5. A Brief Synopsis of Wild Pig Ecology in Southwest Florida

In Southwest Florida, wild pigs (*Sus scrofa*) are a nonnative species that are responsible for major economic and ecological damage, ranging in 10's of millions of dollars annually in Florida alone (Wisely, 2021), as well as across the United States (Timmons et al. 2012). Our study sites, Dinner Island Ranch Wildlife Management Area (WMA) and Okaloacoochee Slough WMA, are surrounded by agricultural production (e.g., various crops and cattle), with portions under active cattle grazing and citrus production contracts. In Southwest Florida, the agricultural and natural resource industry generates billions of dollars annually for the economy (Florida Department of Agriculture and Consumer Services, 2022), which underlines the importance of restricting wild pig population growth and range expansion. In addition, wild pigs carry numerous zoonotic diseases and parasites that pose an immediate health risk to cattle, domestic swine, wildlife, and humans (Centner and Shuman, 2015; Leiser et al. 2013). Therefore, investigating wild pig space use (i.e., home range size), movement behavior (i.e., speed and directionality), and various scales of resource selection (i.e., integrated step selection, 2nd and 3rd orders of selection) is critical for land managers to stem the expansion of wild pigs. For example, by better understanding aspects of their ecology, such as: (1) how diel activity patterns influence movement behaviors (e.g., time of day for resting, foraging, or traveling), (2) space use requirements (home range size), and (3) resource selection modeled simultaneously with movement and environmental covariates (e.g., ISSF models), and (4) resource selection of and within home ranges, land managers will be quipped to better predict movement patterns in heterogeneous landscapes. Wild pigs are highly intelligent animals that will adapt to human pressure by learning avoidance behaviors (e.g., becoming nocturnal or seeking new areas with less perceived risk); therefore, it is essential to collect fine-scale GPS data to predict these trends. The primary ways to control wild pig populations are typically through lethal removal (e.g., trapping, chasing with dogs, shooting, poisoning) and exclusion (e.g., fencing).

The goal of our study was to better understand the spatiotemporal ecology of an anecdotal low-density wild pig population by first studying wild pig movement behavior and space use. First, we tested hypotheses regarding diel activity patterns and used hidden Markov models to infer movement path characteristics (resting, foraging, rooting, traveling). We also investigated home range size and how it varied seasonally across individuals. We used generalized linear models to assess landcover's effects on home range size variation. We found low support for precipitation and sex affecting movement characteristics but did find evidence that high temperature resulted in decreased traveling behavior and increased foraging behavior. We found wild pigs primarily foraged between 8:00 and 17:00 and traveled farther distances between 18:00 and 7:00, indicating that wild pigs are cathemeral in Southwest Florida. Finally, home range size increased as the proportion of pastures increased and decreased as herbaceous wetlands increased, and the average home range size was 13.0 km^2 (n=16). Our results highlighted broad inter-individual variation in home range size, cathemeral diel activity, and that resources in agricultural areas were more diffuse than in natural habitats, which resulted in more extensive home ranges.

Next, we used an integrated step selection process (i.e., simultaneous estimation of movement and resource selection) to investigate the effects of temperature on resource selection and how that selection changed during different times of day. We also investigated how movement patterns changed in different landcover types. We found that wild pigs tended to make slower straighter movements on the landscape during warmer temperatures, and in particular, avoided cropland habitats when temperatures were warmer. We found that wild pigs were less likely to step into locations with hotter daily temperatures and preferred locations with intermediate temperatures. Wild pig movements were tortuous (i.e., more turning) in forested and cropland habitats, indicating potential foraging behaviors. Additionally, wild pig movement was more directed in pasture habitats, indicating that wild pigs may use pasture as corridors to ther habitat types. Wild pigs avoided wetland habitats during dusk and night hours and cropland habitats during dawn hours. However, wild pigs selected for forested habitats during night and dawn hours, possibly as a human avoidance behavior.

Finally, to better understand how wild pigs interact with the heterogeneously distributed resources in their environment and which of those resources (i.e., landcover types) they depend on the most in Southwest Florida, we used 2nd and 3rd order resource selection to quantify habitat selection over broad and fine-scale geographic regions of Southwest Florida. We found that wild pigs selected home ranges nearer to wetlands, forests, and pastures while avoiding areas near croplands. However, within their home ranges they were more likely to select habitats farther from croplands, forests, and wetlands. Although, wild pigs can adapt to a wide variety of landcover types, our findings reinforce the importance of wetlands, forests and pastures to wild pig selection of home ranges, where they likely utilize these landcover types for thermoregulation (e.g. forests and wetlands) and for foraging resources (e.g. pastures).

Wild pig space use and movement behavior vary widely across their geographic range, mainly due to their generalist ecology. Our study sites undergo active cattle grazing, pasture restoration, and agriculture, and are adjacent to numerous agricultural farms and private ranches. Therefore, the high proportion of landcover types, pastures, croplands, and wetlands within wild pig home ranges are a reason of concern due to the spread of zoonotic diseases to cattle, domestic swine, hunting dogs, and native wildlife (Carr et al. 2018; Hernández et al. 2018). In addition, wild pigs are responsible for substantial economic loss to the agricultural industry in Florida (Wisely, 2021). Wild pig populations are likely hampering habitat restoration, food production, native habitat ecology, and endangered plant and animal species due to rooting, trampling, and compaction of sensitive lands (West et al.2009).

Throughout each chapter, we found strong evidence for the importance of wetland habitats for both space use (e.g., home range size) and resource selection at the home range scale. We attribute this evidence to the physiological need for wild pigs to seek environments that meet their thermoregulatory requirements. Temperature was the one predictor that had the most influence on wild pig spatial ecology compared to precipitation and sex and adds to the large body of evidence demonstrating that wild pigs are a heat-sensitive species that need to behaviorally thermoregulate during hot periods by reducing movement rates and selecting for shadier habitats. Also, we found crepuscular use of forested habitats, which is informative for wildlife managers implementing site-specific control measures. Studying the spatial ecology of highly generalist species like wild pigs is imperative to understand how these animals change their spatial ecology in heterogeneous habitats to adapt to anthropogenic pressures from agriculture and hunting pressure. We did not find any evidence of predator/prey interactions between wild pigs and Florida panthers, or any other predators, given that we had zero mortality events. However, our sample size was likely too small to uncover evidence of predation events. In addition, with our results, wildlife managers can better predict which landcover types are providing refuge (e.g., wetlands and forests) and which landcover types are providing potential movement corridors (e.g., pasture and cropland habitats).

Fine-scale GPS data to quantify scale-dependent resource selection is necessary for making complex and expensive management decisions (e.g., Clontz et al. 2021). Our findings were consistent with the scientific literature regarding space use, movement behavior, and resource selection in other tropical and sub-tropical regions with similar vegetative communities. However, we have filled a critical knowledge gap by highlighting that wild pigs in Southwest Florida have broad inter-individual variation in home range size, are strongly regulated by temperature, and are largely dependent on wetlands and forests to meet their energetic demands. To the best of our knowledge, we produced the first estimates of home range, movement behavior, and resource selection of wild pigs in Florida. Our findings will better equip wildlife managers to make informed management decisions regarding scale-dependent conservation planning to mitigate farther range expansion of wild pigs throughout Southwest Florida.

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