

29 Nov 2021
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RH: Gray et al. • Wild pig behavioral states

**BEHAVIORAL STATES IN SPACE AND TIME: UNDERSTANDING LANDSCAPE
USE BY AN INVASIVE MAMMAL**

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ABSTRACT Animal movement models can be used to understand species behavior and inform implementation of management activities. We explored behavioral states of an invasive wild pig (*Sus scrofa*) population that recently colonized central Michigan, USA. To quantify environmental factors related to wild pig movement ecology and spatio-temporal landscape use, we predicted wild pig behavioral states relative to land cover type, landscape structure (i.e., edge and patch cohesion), and weather conditions. We GPS-collared and monitored 8 wild pigs over a four-year period. We fit local convex hulls and calculated movement metrics revealing three wild pig behavioral states (resting, exploratory, and relocating) and constructed a three-level model to predict behavioral state probabilities relative to biotic and abiotic conditions. Probabilities of exploratory and resting behaviors were higher nearer to riparian and open herbaceous cover types (oftentimes emergent marsh), indicating that these cover types provided security cover during activity and bedding. Hard mast cover types had a strong positive association with relocating behaviors. More cohesive patches of agriculture and shrub cover types were associated with higher probabilities of exploratory behaviors while resting was more likely in continuous patches of agriculture (mostly mid-summer corn). We also found the probability of exploratory behaviors increased exponentially with warming ambient temperature. We note that our study was based on a relatively small sample of wild pigs ($n = 8$) comprised primarily of females and both should be considered when interpreting our findings. Our results may be used by managers to develop control strategies conducive to landscape and environmental conditions where the likelihood of encountering wild pigs is highest or targeting wild pigs when in a behavioral state most vulnerable to a particular removal technique.

KEY WORDS feral swine, internal state, movement, movement states, *Sus scrofa* Linnaeus, wild pig

Animal movements are a complex expression of behaviors, related to immediate (e.g., disturbance, temperature) and longer-term (e.g., learned) spatio-temporal environmental factors. Animals move in pursuit of forage (Mårell et al. 2002, Brooks and Harris 2008, Fryxell et al. 2008), to decrease probability of encountering predators (Frair et al. 2005, Moriarty et al. 2016, Weterings et al. 2016), to select resting sites (Maillard and Fournier 1995, Brown et al. 2014, Larroque et al. 2015, Wittemyer et al. 2017), and to avoid sources of disturbance (Pruett et al. 2009, Leblond et al. 2013, Stillfried et al. 2015), among other reasons. In addition to external factors, there are also a variety of internal drivers that may influence animal movements, including sex, reproductive status, age (e.g., experience), and motivation (e.g., hunger, shelter; Martin et al. 2013). Given these ecological and fitness implications, movement is critical to the structure and function of populations, animal communities, and trophic systems, more broadly (Swingland and Greenwood 1983, Dingle 1996, Hanski 1999, Bullock et al. 2002, Greenberg and Marra 2005). Thus, research into animal movements and space use serves as a cornerstone of many ecological inquiries.

Recent growth in animal movement research followed advances in animal tracking technology capable of yielding increasingly resolute spatio-temporal data (Millsbaugh and Marzluff 2001, Cagnacci et al. 2010, Tomkiewicz et al. 2010). Furthermore, concurrent progress in analytical tools and conceptual frameworks built to quantify animal movement processes has led to novel ways of understanding animal ecology and behavior (Morales et al. 2004, Nathan et al. 2008, Long and Nelson 2013). For example, animal movements can be extrapolated from global positioning system (GPS) telemetry locations and subsequently linked to specific behaviors, often referred to as behavioral states (e.g., resting, foraging; Morales et al. 2004, Patterson et al. 2008, Van Moorter et al. 2010). As behavioral states are largely determined by

prevailing biotic and abiotic conditions (Zhirovsky et al. 1996, Forester et al. 2007, Nathan et al. 2008, Revilla and Wiegand 2008), exploration of external factors affecting shifts among these states are ecologically important. A broader understanding of the spatio-temporal conditions that coincide with behavioral states can be used to inform conservation and management practices.

Linking movements and behaviors of non-native invasive species to potential biotic and abiotic conditions within recently colonized landscapes may be particularly important to inform management. For example, wild pigs (*Sus scrofa*) are relatively new to landscapes in the northern United States of America (USA; e.g., established in the last 20 years), often facilitated by inadvertent or unlawful introduction or escapees from private hunting reserves (Etter et al. 2020, Mayer et al. 2020). Unlike wild pig populations found in the southeastern USA, which principally consist of feral domestics and hybrids (i.e., typically the offspring of domestic pigs or Eurasian wild boar hybrids), wild pig populations in landscapes of the northern USA are primarily comprised of individuals that are morphologically and genetically similar to Eurasian wild boars (Etter et al. 2020, Smyser et al. 2020), perhaps exhibiting unique movement and behavioral states. Non-native and invasive wild pigs are destructive and economically harmful, posing important disease risks to livestock (Pimentel et al. 2005, Gortázar et al. 2007, Ruiz-Fons et al. 2008), damaging crops (Frederick 1998, Anderson et al. 2016), and threatening native flora and fauna (Singer et al. 1984, Gabor and Hellgren 2000, Siemann et al. 2009, Jolley et al. 2010, Gray et al. 2020a). Therefore, for the purposes of ecological knowledge and population management, examinations of movements and behaviors of wild pigs in newly colonized landscapes of the northern USA are needed.

Wild pigs are a highly adaptable generalist capable of proliferating in a wide range of environments. Wild pigs often utilize cover types relative to their availability (Ilse and Hellgren

1995, Gabor et al. 2001), but this can vary seasonally based on pulses in resources or access to other life history requirements (McIlroy 1989, Baber and Coblentz 1986, Keuling et al. 2009). For example, in both California and Tennessee, wild pigs used oak (*Quercus* spp.) thickets and oak-pine (*Pinus* spp.) slopes when acorns were abundant (Singer et al. 1981, Barrett 1982). Similarly, wild pigs will also use agricultural crops extensively when available (Sparklin et al. 2009, Schlichting et al. 2015), as these areas can offer ample cover and forage. Additionally, access to thermoregulatory refuge is a strong determinant of wild pig use, especially during periods of high temperatures when animals reduce activity (Kay et al. 2017) and favor water saturated cover types (e.g., wetlands, riparian zones; Baber and Coblentz 1986, Mersinger and Silvy 2007). Structure and configuration of cover types may also influence wild pig movements and behaviors, as use of narrow landscape elements (e.g., streams, tree rows, ditches) and proclivity for forest edge have been documented in agricultural landscapes (Thurfjell et al. 2009). Given the wide diversity of land cover, structure, and vegetation used by wild pigs throughout their range, a detailed understanding of biotic and abiotic associations relative to wild pig behaviors may offer insights into effective management strategies that can be implemented in newly colonized environments.

We explored movement and behavioral ecology of a low-density, emergent wild pig population in the state of Michigan, USA. Specifically, we: *i*) assigned behavioral states to wild pig locations derived from GPS telemetry-tracking, *ii*) examined correlations between wild pig behavioral states and landscape composition and structure, temporal attributes, and weather variables, and *iii*) predicted likelihood of behavioral states given a range of biotic and abiotic conditions. We hypothesized that wild pigs would show an affinity for riparian cover types that offer thermoregulatory refuge for resting and concealment during prolonged movements. We

also expected wild pigs to exhibit foraging/exploratory behaviors in land cover types that were resource rich (e.g., hard mast), move rapidly through areas with high edge density, and reduce exploratory behaviors and movements during weather extremes. To our knowledge, this is the first study to examine movements of invasive wild pigs, largely of Eurasian boar ancestry, in recently colonized landscapes of the northern USA.

STUDY AREA

Our study was conducted between 2014 and 2018 in six counties (Arenac, Bay, Gladwin, Midland, Ogemaw, and Roscommon; 9,090 km²) in the central Lower Peninsula of Michigan, USA (Fig. 1). We selected these counties based on wild pig reports received by the Michigan Department of Natural Resources (MDNR) and United States Department of Agriculture - Wildlife Services. Wild pig populations in Michigan have broadly been classified as emerging to transitional (Mayer 2009, Corn and Jordan 2017), with all populations characterized as low-density and of Eurasian wild boar lineage (Etter et al. 2020, Smyser et al. 2020). The climate in our study area is characterized by humid summers and cold winters. Average monthly temperatures range from -6.5 (January) to 20.8 °C (July), with average monthly precipitation highest in September (8.9 cm) and lowest in February (3.9 cm; Michigan State Climatologist's Office 2019). Study area counties occur along a forest transitional zone, comprised primarily of deciduous hardwoods in the south and conifer, mixed conifer, and hardwoods in the north (Barnes and Wagner 1981, Albert 1995). Land cover in this region is primarily agriculture and forestlands with interspersed woody and emergent wetlands throughout. Elevation ranges from 170-481 m in study area counties (1/3 arc-second; U. S. Geological Survey 2019).

METHODS

Capture and Handling

From 2014 to 2017, we live-captured 8 wild pigs in our study area and 2 additional animals were captured in Marquette County of the Upper Peninsula, Michigan, USA. All animals were captured using neck snares and corral traps (1.5 m tall metal fencing with a guillotine door) baited with soured corn (Ditchkoff and Bodenchuk 2020). We immobilized captured pigs using a combination of xylazine (Rompun®, Miles Inc., Shawnee Mission, Kansas, USA) and Telazol (Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA). We fit each pig with an IridiumTrackM GPS collar (Lotek Wireless Inc., Newmarket, Ontario, Canada) programmed to record a GPS-fix every 30 minutes. Due to the unique morphology of wild pigs (e.g., neck that is thicker than the head), we fashioned a harness that fit around the forelegs to secure the collar to the animal (Etter et al. 2020). All capture and handling protocols were approved by the Michigan State University Institutional Animal Care and Use Committee (01/14-013-00). All collared animals were actively monitored via remote trail cameras and were humanely dispatched at the end of study.

During our study, some collared animals were harvested unexpectedly and some collars malfunctioned, leading to variation in the duration of collar data. For our analyses we used GPS data from individuals that carried active collars for at least three months. Additionally, we removed GPS locations of poor quality (i.e., having a dilution of precision (DOP) >5; Edenius 1997, Moen et al. 1997). We also removed the first seven days of tracking data following collaring of each animal to remove any biased movements associated with post-capture stress (Dechen Quinn et al. 2012).

Behavioral States

To quantify wild pig behavioral states, we used data collected from all 10 captured pigs (i.e., from the Lower and Upper Peninsulas) totaling 39,915 locations. We considered movement trajectories and time-use in local convex hulls to delineate behavioral states because they incorporate aspects of movement and space use and can be readily linked to species behavior and ecology (Lyons et al. 2013, Thiebault and Tremblay 2013). We used the *adehabitatLT* package (Calenge 2011) in R (version 3.5.0; R Core Team 2018) to calculate movement metrics for each trajectory by an individual wild pig. A trajectory was defined as multiple discrete steps that connected sequential relocations of an animal (Turchin 1998). From trajectories, we extracted step-lengths depicting the distance between successive locations, which is a common metric used in assigning behavioral states (Franke et al. 2004, Morales et al. 2004). Trajectories are time-sensitive, thus, we specified a new trajectory *post-hoc* if successive locations were >32 or <28 minutes apart, as all collars were programmed to record fixes at 30-min intervals. This prevented calculation of abnormally large or small step-lengths in a trajectory due to irregular GPS-fixes.

Next, we delineated local hulls using the T-LoCoH package (Lyons 2014) in R to create home ranges for each individual animal. The T-LoCoH method is unique in that it incorporates time stamps to calculate time-scaled distances used in local convex hull estimation (Lyons et al. 2013). This method provides a temporally explicit estimate of a home range and allows for calculation of time-use metrics in local hulls, such as revisitation rate (number of separate visits to a location over time) and duration of visit (mean number of locations per visit; Lyons et al. 2013). In calculating hulls, we selected the *a*-method, via nearest neighbor analyses, which uses a cumulative distance and is optimal for estimating conservative hulls robust to overestimation (Lyons 2014). Calculation of these time-use metrics are contingent upon an inter-visit gap, which specifies the amount of time an animal would need to be away from a hull for calculations of

time-use metrics to be re-initiated (Lyons 2014). We selected a temporally resolute inter-visit gap (i.e., one hour) given our interest to assess movement and behavior at fine temporal scales. Though wild pigs are assumed to be primarily nocturnal in our study area (S. M. Gray, personal observation) variation in this behavioral pattern has been documented (Ohashi et al. 2013, Podgórski et al. 2013). Therefore, we investigated relationships between behavioral states and time of day to provide further insights into wild pig ecology and activity in our study area.

We conducted k-means clustering on three metrics (step-length, revisitation rate, duration of visit) using the optimal number of clusters (i.e., behavioral states) specified by the gap statistic (Tibshirani et al. 2001), which has been effectively used to depict large mammal behavioral states (Van Moorter et al. 2010). We used the gap statistic method to estimate optimal number of clusters (k) via comparison of variation within clusters for different values of k (Tibshirani et al. 2001). Using the `clusGap` function in the `cluster` R package (Maechler et al. 2019), we specified a maximum of 10 potential clusters (see Van Moorter et al. 2010) with 1000 bootstrap replicates. Finally, we identified the optimal number of clusters as the instance where the gap statistic was maximized and did not overlap the standard error of previous observations (Maechler et al. 2019).

Our analysis revealed three clusters (behavioral states; Fig. S1), which we characterized using descriptive statistics for step-length, revisitation rate, and duration of visit (Table 1). We classified the relocating behavioral state as the cluster with the largest step-lengths, moderate revisitation (instances where individuals used similar travel routes), and low visit duration (Table 1). This state represents rapid movement and low spatial fidelity, which may correspond to directed travel (e.g., fleeing or dispersal behaviors) in wild pigs. The exploratory behavioral state was identified in the second cluster given intermediate step lengths, low revisitation, and high

visit duration (Table 1). This state indicates a moderate level of movement and high spatial fidelity, aligning with exploratory behaviors such as foraging or use of an energy rich resource. We identified the resting behavioral state in the third cluster, characterized by small step lengths and high revisitation rates, along with intermediate duration of visit (Table 1).

Biotic and Abiotic Conditions

We compiled habitat and weather covariates known to influence wild pig movements, behaviors, and ecology (see Table 2). We sought to test associations between wild pig behavioral states and proportions of land cover types sufficiently tall to provide overhead cover or those that offered forage, so we extracted variables from existing vegetation type and height rasters (30-m resolution) provided by the 2014 LANDFIRE Program (LANDFIRE EVT, LANDFIRE EVH; LANDFIRE 2014). We reclassified the LANDFIRE EVH vegetation height raster into two classes: open areas and high vegetation (>5 m), as this permitted delineation of edge between open and closed cover types (Table 2). Additionally, we reclassified the LANDFIRE EVT raster for agriculture and high shrub cover (>3 m in height) to calculate a patch cohesion index (Table 2), where higher values correspond to greater connectedness and lower values represent heterogeneity in a cover type (Evans 2015). We overlaid a 100 m grid across our study area, corresponding to the average distance moved between subsequent GPS locations by individuals in this study ($\bar{x} = 100$ m, $SE = 1.37$). Within each grid cell, we calculated the proportion of area that was classified as: *i*) human development (e.g., urban, suburban), *ii*) riparian, *iii*) open herbaceous, or *iv*) hard mast (Table 2). We used the spatialEco package (Evans 2015) in R to calculate open-forest edge density and patch cohesion indices for reclassified agriculture and shrub layers within each grid cell (Table 2).

We obtained local weather data from the National Oceanic and Atmospheric Administration (NOAA) online portal. We extracted hourly data from two local weather stations (Saginaw and Roscommon), matching the temporal extent of our GPS telemetry data. We appended data from the closest weather station to each GPS location ($\bar{x} = 44.62$ km, range: 21.33 – 58.16 km) at a temporal resolution of the nearest hour. Here, we considered surface pressure (Pa) and ambient temperature ($^{\circ}\text{C}$; Table 2).

Statistical Modeling

Because we telemetered wild pigs from two geographically distinct populations (i.e., Upper and Lower Peninsulas), we had difficulty fitting robust, spatially explicit models from data acquired from individual wild pigs in both study areas simultaneously. Therefore, we proceeded to focus solely on data collected from wild pigs in the Lower Peninsula ($n = 8$). Based on USDA culling records, camera traps, and public reports during and after our study, we estimated that this sample represented 20-25% of the wild pig population in this study area. To model all behavioral states concurrently (three states identified by the gap statistic method for optimal clustering), we used the stochastic partial differential equation (SPDE) method (Lindgren et al. 2011, Krainski et al. 2018) and constructed a three-level joint model with shared spatial components as described by Humphreys et al. (2021). This approach enabled each behavioral state to be evaluated within a dedicated model level while also accounting for spatial relationships. We tested for multi-collinearity by calculating variance inflation factors for all covariates within the model, where any covariate with a value > 3.0 was removed (Zuur et al. 2010). In addition, we standardized each predictor variable to have a mean of 0 and standard deviation of 1. The three-level, jointly fit model to estimate behavioral states took the form:

$$y_1(s) = \alpha_1 + \beta_1 X + z_1(s) \quad (1)$$

$$y_2(s)|y_1(s) = \alpha_2 + \beta_2 X + \lambda_1 * z_1(s) + z_2(s) \quad (2)$$

$$y_3(s)|y_1(s), y_2(s) = \alpha_3 + \beta_3 X + \lambda_2 * z_1(s) + \lambda_3 * z_2(s) + z_3(s) \quad (3)$$

where each level is a spatially explicit binomial regression used to estimate a particular behavioral state: exploratory (y_1 [Eqn 1]), resting (y_2 [Eqn 2]), relocating (y_3 [Eqn 3]). As given, the α_j are model intercepts and $\beta_j X$ are level-specific regression coefficients for fixed and random effects, which accounted for individual wild pig, hour, day, year, and cohort group. Here, cohort represents an identifier attached to individuals captured together and considered to be in the same social group. Although all three model levels are fit jointly, covariates are specified and estimated separately for each behavioral state. The $\beta_j X$ term captures fine-scale spatial structure and temporal correlation within individual wild pig GPS records. Although we included spatial effects in our model to account for spatial autocorrelation across the study area ($z_j(s)$ discussed below), we also fit nearest neighbor distances between point locations to a two-dimensional spline to capture fine-scale spatial structure occurring below the resolution of the spatial fields (Illian et al. 2012, Humphreys et al. 2017, 2020). We then modeled temporal correlation using an order-1 autoregression on GPS time-steps by individual wild pig. The λ_j term estimated scaling parameters for shared components (Blangiardo and Cameletti 2015, Krainski et al. 2018), and $z_j(s)$ give zero mean spatial fields for $j = 1; 2; 3$ at GPS locations s ($s = 1, 2, 3, \dots, n$). All model spatial fields were specified as continuous Gaussian random fields with Matérn covariance following the SPDE approach (Lindgren et al. 2011). Importantly, Eqn 2 includes a shared copy of the spatial field from $y_1(s)$ and Eqn 3 contains copies of the spatial fields from both $y_1(s)$ and $y_2(s)$. By modifying these shared spatial fields, the λ_j provide scaling coefficients that control for spatial correlation between model levels (Jones-Todd et al. 2018). In this instance, the λ_1 quantifies spatial interaction between the exploratory and resting behavioral states, while λ_2 and λ_3 respectively represent the spatial similarity between exploratory and resting with the

relocating behavioral state modeled in the third level. Non-informative priors were specified for all terms and the INLA method (Rue et al. 2009) was used as a fast and accurate alternative to Markov Chain Monte Carlo for latent Gaussian models.

In total, we fit and compared seven models. First, we fit three single level models to estimate the exploratory (Model 1), resting (Model 2), and relocating (Model 3) behavioral states individually and in the absence of shared model components. Before fitting the full joint model with all predictor variables, we created a model (Model 4) using only the spatial, temporal, year, and individual wild pig random effects to gauge the ability of the model to account for data structure and sampling bias in absence of other variables. We then fit the full model (Model 5), followed by a model that exchanged the temporal autoregressive term for an Ornstein-Uhlenbeck process (Model 6), and a non-spatial and non-temporal model (Model 7) to determine the importance of the spatial and temporal random effects. We considered a parameter significant if 95% credible intervals did not overlap 0. Predictions were generated for each significant parameter and estimated across the range of an isolated variable while holding all other predictors at their mean.

We tested the predictive performance of our top-ranked model by subsetting GPS data into training and testing sets. We trained the model using 80% of GPS locations, randomly selected from each individual pig. The remaining 20% of data were applied to test the model and estimate classification accuracy using the area under the receiver operating characteristic curve (AUC; McNeil et al. 1983). Values of AUC range from 0.0 to 1.00 where those closer to 1.00 indicate near perfect predictive performance.

RESULTS

From 2014 to 2018, we collared 8 wild pigs (2-M, 6-F) in our study area. Overall, these wild pigs represented four cohorts, most being lone or single-sex female groups primarily comprised of sub-adults or a mixture of adults and sub-adults (group size range = 1 – 4). Fix rates for collars were relatively high at ~93% across all collars with mean DOP of 2.94 (SE = 0.01). In total, we used 23,473 locations to model changes in wild pigs exhibiting different behavioral states. Mean number of locations per individual was 2,934 (SE = 823.76) with seasonal representation being highest in fall (September – November) and lowest in summer (June – August; Table 3). Subsequent monitoring and removal of study animals did not reveal evidence of piglets or pregnancy, which can potentially influence movements and behaviors.

We found associations between time of day and wild pig behavioral states, where exploratory and resting behaviors were more likely during the morning and daylight hours and relocating tended to occur during the evening (i.e., 18:00 – 22:00; Fig. 2). We also noted variability in behavioral states by wild pig cohort, particularly in resting and exploratory behaviors (Fig. S2). Cohort 2 exhibited less resting and more exploratory behaviors while cohort 4 displayed more resting than others (Fig. S2), substantiating the importance of accounting for wild pig cohort in our analysis.

We found that the joint model incorporating all three behavioral states, random effects, and spatiotemporal effects outperformed simpler models in both DIC and WAIC, except for the exploratory state (Table 4). Model validation indicated that our Joint (Full) model performed better than random (i.e., AUC's >0.5), but varied depending on behavioral state and model performance metric (Table S1). The model predicting resting performed best (AUC = 0.71) followed by relocating (AUC = 0.70) and exploratory (AUC = 0.68; Table S1). Conversely, the proportion correctly classified (PCC) indicated our model was best suited for predicting the

relocating behavioral state (PCC = 0.71), followed by resting (PCC = 0.66), and exploratory states (PCC = 0.60; Table S1).

We found wild pig exploratory and resting behavioral states significantly and positively correlated with increasing proportions of riparian cover, while relocating behavior was negatively associated with this cover type (Table 5; Fig. 3a). We also found a higher probability of exploratory behaviors in open herbaceous cover types and relocating behaviors in hard mast cover types (Table 5). Probability of the exploratory behavioral state increased linearly with increasing proportions of open herbaceous cover and coincided with a decrease in probability of relocating (Fig. 3b). Conversely, we found a linear increase in relocating behaviors and decrease in exploratory behaviors with increasing proportions of the hard mast cover type (Fig. 3c).

We found that both agriculture and shrub patch cohesion indices aided in predicting wild pig behavioral states, however, we did not find an important edge density effect (Table 5). For increasing patch cohesion of agriculture, we noted a strong increase in resting and exploratory behaviors and decrease in relocating (Fig. 4a). Effects were less pronounced for shrub patch cohesion, which had a significant and increasing linear relationship with exploratory behavior in wild pigs (Fig. 4b).

We found temperature to be the lone weather variable that significantly influenced wild pig behavioral states (Table 5). The exploratory behavioral state had the strongest correlation with temperature, where the probability of exploratory behaviors displayed an s-curve relationship (Fig. 5). Probability of exploratory behaviors was near 0.0 at cold temperatures (i.e., $\sim -30^{\circ}\text{C}$) but increased rapidly once temperatures reached $\sim -10^{\circ}\text{C}$, but then tapered off at $\sim 30^{\circ}\text{C}$ (Fig. 5).

DISCUSSION

We believe this research offers two main contributions on the topic of wild pig ecology. First, as indicated by Morelle et al. (2014), wild pig movement is an understudied topic and there is a need to relate movements and behaviors to better understand the ecology of this species. We found methods using k-means clustering along with attributes from movement trajectories and local convex hull time-use metrics to be an intuitive approach for delineating behavioral states in wild pigs from GPS data. Along with semi-hidden Markov models and other state-space modeling techniques, these methods offer another approach for examining animal movements and behaviors in tandem. Second, this study is one of the first to explore movements of wild pigs, largely of Eurasian wild boar ancestry (see Smyser et al. 2020), within northern systems of the USA where pigs occur at low densities, likely contributing to the behaviors, movement patterns, and ecological associations quantified herein. Our results provide insights on the ecology of wild pigs in these newly colonized systems while also identifying conditions when the probability of encountering wild pigs is higher to facilitate population control activities.

We hypothesized that wild pigs in this region would rely on riparian areas and open herbaceous cover types for cover and concealment when resting. Our findings revealed that increasing proportions of both riparian and open herbaceous cover types more strongly associated with exploratory behavior, and to a lesser degree, resting. This highlights the importance of riparian areas for wild pigs, as these areas offer relatively unbroken vegetation cover that extend across landscapes for relatively concealed activity (Caley 1997, Thurfjell et al. 2009) and resting sites that may be preferred over other cover types (Kurz and Marchinton 1972, Baber and Coblenz 1986, Mersinger and Silvy 2007, Friebe and Jodice 2009, Beasley et al. 2014). Similarly, we found a strong, positive effect of open herbaceous areas on exploratory

behavior, likely due to abundant vegetation and productivity of these cover types. Research on wild pigs in other regions indicated that open herbaceous cover types are important for foraging and thermoregulation via wallowing (Mitchell and Mayer 1997, Arrington et al. 1999, Welander 2000, Sharp and Angelini 2019). Our findings are largely in alignment, suggesting that open herbaceous cover types serve a similar purpose for wild pigs in northern landscapes of the USA.

We found hard mast cover types had a strong association with wild pig behavioral states. Increasing proportions of hard mast cover types corresponded with an increased probability of relocating, sharp decline in exploratory, and moderate decrease in resting behavior. The negative association between hard mast and the exploratory behavioral state was unexpected, as we anticipated this cover type to provide essential wild pig forage. Hard mast is an important dietary component throughout native and invasive ranges of this species (Sjarmidi et al. 1996, Schley and Roper 2003, Elston and Hewitt 2010) and has also been linked to higher densities of wild pigs (Geisser and Reyer 2005). Moreover, we expected this cover type to play a larger role in northern systems given the necessity of hard mast in building fat reserves for cold weather months and serving as a primary dietary item in fall and winter when aboveground forage is scarce (Wood and Roark 1980, Herrero et al. 2005, Schlichting et al. 2015). We note that our hard mast cover type only served as a coarse proxy for hard mast availability and perhaps incorporating variables reflective of hard mast production would better describe patterns in wild pig use. In terms of relocating, our finding of higher probabilities of this behavior with increasing proportions of hard mast cover is likely related to reduced understory vegetation, especially in mature and closed canopy forests, necessitating more directed movements given lack of concealment.

Most investigations of landscape structure on wild pig movements describe agricultural damage juxtaposed to forest edge, where proximity to forest edge increases the likelihood of use and damage by wild pigs (Gerard et al. 1991, Meriggi and Sacchi 2001, Thurfjell et al. 2009). As such, we anticipated wild pigs to display an affinity for forest edge and to exhibit foraging and resting behaviors in certain agricultural cover types (i.e., corn). We found open to forest edge density to be of relatively minor importance in predicting wild pig movements and behavior in our study area. Rather, patch cohesion of agriculture and shrub cover types were better predictors of behavioral state. Given that most agriculture fields in our study area were >1 ha, the positive association between agricultural patch cohesion and probability of resting and exploratory behavioral states suggests that these behaviors are more likely to occur in the interior of contiguous agricultural fields. A primary crop in our study area was corn, and mature corn provides both thermal and visual cover as well as forage. We repeatedly documented wild pigs resting in mature corn, even during winter in extremely cold temperatures (see Etter et al. 2020). However, a higher likelihood of interior field foraging contrasts with findings from Sweden, where wild pig damage occurred along the periphery of fields near forest edges; though, this effect was reduced when crops were mature (Thurfjell et al. 2009). The stronger, positive relationship between exploratory behaviors and agricultural patch cohesion in comparison to the reduced response between this behavioral state and hard mast cover types suggests that agriculture may be a more important source of forage in northern landscapes of the USA. Indeed, agriculture has been identified as a cover type facilitating range expansion of wild pigs into the Midwest, however, it is likely that a heterogeneous agriculture-forest matrix is most conducive to wild pig habitation (Snow et al. 2017). For patch cohesion of shrub cover types, increased probability of exploratory behavior in more cohesive patches of shrub is in alignment with other

studies, which documented seasonal use of these areas for cover and refuge but also for forage (Dexter 1998, Gaston et al. 2008).

The influence of abiotic conditions on wild pigs have been explored in the southern USA, broadly indicating that increasing temperature and barometric pressure lead to a corresponding decrease in movements at multiple scales, though this relationship is not always linear (Kay et al. 2017). Others also noted reductions in wild pig activity coinciding with increasing temperature (Blasetti et al. 1988, Lemel et al. 2003, Wyckoff et al. 2006). We found temperature to have the most profound effect on probability of the exploratory behavioral state, where the likelihood of an individual exhibiting this state increased exponentially at -15 °C before gradually declining near the observed maximum temperature (i.e., 32.8 °C). While this result contradicts some of the patterns previously reported in wild pig populations in the USA, it more closely aligns with observations on wild boar populations in their native range. In Sweden, wild boar were less active during colder weather and increased movement speed and activity with increasing temperature during the late summer, potentially to find ample foraging areas (Thurfjell et al. 2014).

In our study, we observed that time of day and social group affected wild pig behavioral states. Proclivity for exploratory-type activities (e.g., foraging) during the daylight hours was somewhat unexpected, though the exploratory behavioral state featured low movement potentially allowing individuals to remain active and undetected. Other studies reported diurnal activity in wild pigs, particularly in areas where animals are less likely to experience disturbance (Keuling et al. 2008a, Podgórski et al. 2013, Cremonesi et al. 2021). Our study area was primarily forested with substantial understory cover, potentially limiting human disturbances and

435 providing enough concealment to facilitate modest diurnal activity. Our finding that relocating
436 behavior was most likely to occur at dusk and the early nighttime hours conformed with
437 observations from other regions, where sunset serves as a cue to initiate activity and movement
438 (Lemel et al. 2003, Silveira de Oliveira et al. 2020). For social group, it is unsurprising to see
439 differences in the proportion of behavioral states exhibited by separate groups, as wild pigs are a
440 highly adaptable species that readily respond to their environment (Gray et al. 2020b). While
441 research exploring differences in movements among wild pig social groups is limited, there is
442 some evidence that wild pig social groups employ different strategies in movement and space use
443 in response to local pressures, age structure, and the environment (Keuling et al. 2008b, 2009,
444 Podgórski et al. 2013). To a degree, our results may indicate similar plasticity in movement and
445 behavior among wild pig social groups.

446 We caution that the environmental relationships to behavioral states in this study were
447 based on a limited sample (i.e., 8 individuals), therefore, we encourage further exploration of
448 wild pig movements to elucidate potential geographic similarities and differences. Our sample
449 was largely comprised of female wild pigs, which are highly social and exhibit site fidelity
450 (Gabor et al. 1999, Kaminski et al. 2005, Keuling et al. 2008b, Lavelle et al. 2018). Given that
451 females primarily reside in social groups (i.e., sounders), knowledge on the ecology and behavior
452 of females is beneficial to managers in potentially facilitating whole group removal (Ditchkoff
453 and Bodenchuk 2020). Control strategies prioritizing whole group removal are desirable in wild
454 pig management, as failure to do so may scatter individuals from known locations, hampering
455 future management efforts and potentially facilitating disease transmission, which tends to be
456 constrained spatially and within social groups (Podgórski et al. 2018). Considering male wild
457 pigs were underrepresented in our sample, continued examination of movement and behavior of

males in this region is warranted, as adult males may present more challenges to removal given their capability to travel greater distances, occupy larger home ranges (Kay et al. 2017), and sometimes differ in their response to control (Lavelle et al. 2018). We suspect that adult males in our study area show less site fidelity and frequently relocate to access multiple sounders, therefore, frequency of behavioral states and the biotic and abiotic associations observed here may have differed if our sample consisted of more adult males. Additionally, we focused on cover type, landscape structure, and weather associations at fine spatio-temporal scales and thus our findings are inherently linked to scales we examined. We believe the scales used in this analysis are relevant to practitioners and managers, especially those faced with controlling localized and emerging populations of invasive wild pigs. However, quantification of wild pig movements, much like any other animal, is scale-dependent and patterns that we observed may change if evaluated at different spatio-temporal scales (Kay et al. 2017).

MANAGEMENT IMPLICATIONS

Our study is the first to correlate wild pig behavioral states at northern latitudes in North America to fine-scale biotic and abiotic conditions, while providing further insights into the ecology, function, and potential management of this species in northern systems of the USA. Our methods and results provide a means for managers to predict locations and abiotic conditions that correspond with wild pig use and behavior. In doing so, managers can cater control strategies to landscape and environmental conditions where likelihood of encountering wild pigs is highest, or target wild pigs when exhibiting a behavioral state most vulnerable to a particular removal technique (e.g., aerial gunning and resting). Moreover, these predictions allow managers to tactically deploy bait sites and camera traps in areas modeled as high use to help pattern wild pig movements and facilitate targeted trapping and shooting efforts. Additionally, predicting

behavioral states in cover types that offer minimal overhead cover may improve effectiveness of aerial monitoring and control efforts. In our study area for example, we found low movement behavioral states corresponded with shrub-scrub and open herbaceous cover types, potentially indicating areas to prioritize when conducting aerial surveys or removals. Regardless of removal strategy, practitioners should strive for whole group removal to ensure individuals do not disperse into previously unoccupied areas and to maximize effectiveness of future control efforts. We observed expansive and prolonged movements in multiple individuals following a shooting event, stressing the need to remove entire groups in regions with low density wild pig populations.

ACKNOWLEDGMENTS

The authors declare no conflict of interest. Funding for this research was provided by the Michigan Department of Natural Resources – Wildlife Division with funds from the Federal Pittman – Robertson Wildlife Restoration Act grant administered by the US Fish and Wildlife Service (W-155-R: Michigan’s Statewide Wildlife Research, Surveys, and Monitoring Program), the Michigan State University College of Agriculture and Natural Resources, College of Agriculture and Natural Resources Alumni Association, Michigan Pork Producers Association, Safari Club International – Michigan Involvement Committee, and the Vera M. Wallach scholarship awarded by the Michigan State University Department of Fisheries and Wildlife. Thanks to USDA – Wildlife Services for their trapping efforts and field support. We thank E. Raifsnider, A. Hauger and A. Dutcher for their assistance in data collection. We acknowledge that our work was conducted on the ancestral, traditional, and contemporary Lands of the Anishinaabeg – Three Fires Confederacy of Ojibwe, Odawa, and Potawatomi peoples. The findings and conclusions of this publication are those of the authors and should not be construed

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505 products or companies does not represent an endorsement by the US government.

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FIGURE LEGENDS

Figure 1. Four county (Arenac, Bay, Gladwin, Midland) study area in Michigan, USA used for studying wild pig movement ecology, 2014–2018.

Figure 2. Hourly movement probabilities on the logit scale for each behavioral state of wild pigs in Michigan, USA, 2014–2018.

Figure 3. Probability of behavioral state and proportion of A) riparian, B) open herbaceous, and C) hard mast cover types in 1 ha cells for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimates.

Figure 4. Probability of behavioral state and A) agriculture and B) shrub patch cohesion indices in 1 ha cells for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimates.

Figure 5. Probability of behavioral state and temperature for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimate.

859 Table 1. Descriptive statistics for step-length (m), revisitation rate, and duration of visit for each
 860 behavioral state estimated for 8 wild pigs GPS telemetry-tracked in Michigan, USA, 2014–2018.

861 Term \bar{x} represents mean and SE is standard error.

Behavioral State	Metric					
	Step-length		Revisitation rate		Duration of visit	
	\bar{x} (SE)	Range	\bar{x} (SE)	Range	\bar{x} (SE)	Range
Exploratory	27.5 (1.3)	0.1 – 1504.3	14.7 (0.1)	1.0 – 38.0	8.9 (0.0)	2.2 – 39.0
Resting	8.9 (0.1)	0.1 – 96.8	77.9 (0.3)	14.0 – 216.0	6.2 (0.0)	1.9 – 12.9
Relocating	218.6 (3.2)	7.5 – 2950.1	46.8 (0.4)	1.0 – 214.0	4.4 (0.0)	1.1 – 11.7

862

863 Table 2. Description, data source, mean, range, and references for covariates used in modeling behavioral states of 8 wild pigs GPS
 864 telemetry-tracked in Michigan, USA, 2014–2018. Term \bar{x} represents mean and SE is standard error.

Name	Description	Source ^a	\bar{x} (SE)	Range	Reference(s)
Proportion Cover Type					
Developed	Proportion of developed cover types in 1 ha cells	LANDFIRE	1.23 (0.03)	0.00 – 100.00	Ohashi et al. (2013), Podgórski et al. (2013), Gantchoff and Belant (2015)
Riparian	Proportion of eastern floodplain forest and Atlantic swamp forest cover types in 1 ha cells	LANDFIRE	39.79 (0.19)	0.00 – 100.00	Mersinger and Silvy (2007), Beasley et al. (2014), Cooper and Sieckenius (2016)
Open Herbaceous	Proportion of open (i.e., transitional herbaceous, barren, quarries) and emergent marsh (i.e., inland marshes and prairies) cover types in 1 ha cells. Areas dominated by herbaceous vegetation, potentially used for resting cover or foraging.	LANDFIRE	8.46 (0.10)	0.00 – 100.00	Wood and Brenneman (1980), Dardaillon (1987)
Hard Mast	Proportion of cover types dominated by mast producing tree species (i.e., white oak-red oak-hickory, black oak and savanna, beech-maple-basswood) in 1 ha cells	LANDFIRE	0.32 (0.02)	0.00 – 100.00	Singer et al. (1981), Bieber and Ruf (2005), Elston and Hewitt (2010)

Landscape Metrics

Agriculture patch cohesion index	Patch cohesion index for row crop and close grown crop cover types	spatialEco/ LANDFIRE	0.39 (0.01)	0.00 – 4.44	Dardaillon (1987), Herrero et al. (2006), Morelle and Lejeune (2015)
Shrub patch cohesion index	Patch cohesion index for shrub cover types > 3 m	spatialEco/ LANDFIRE	0.26 (0.00)	0.00 – 4.31	Dexter (1998), Gaston et al. (2008)
Open-Forest Edge	Density of hard edge between open area and forest > 5 m	spatialEco/ LANDFIRE	2.10 (0.03)	0.00 – 26.00	Thurfjell et al. (2009), Morelle and Lejeune (2015)

Weather Metrics

Temperature	Hourly temperature (° C)	NOAA	5.26 (0.06)	-33.30 – 32.80	Dexter (1998), Schlichting et al. (2016), Kay et al. (2017)
Pressure	Hourly pressure (Pa)	NOAA	97,324.81 (3.89)	94,006.15 – 99,830.74	Kay et al. (2017)
Julian Date	Numeric representation of date to account for seasonality	-	199.40 (0.52)	1 – 365	Singer et al. (1981), Keuling et al. (2009), Podgórski et al. (2013)

^a Source and/or method used to acquire data: spatialEco – landscape metrics calculated using the spatialEco package in program R (version 3.5.0); LANDFIRE – land cover and vegetation data from existing vegetation type and height rasters (30-m resolution) provided by the LANDFIRE Program (LANDFIRE EVT, LANDFIRE EHT; <http://www.landfire.gov/>); NOAA – hourly weather data obtained from the National Oceanic and Atmospheric Administration.

869 Table 3. Sex, cohort, weight, age, and number of GPS locations, by season, for 8 wild pigs tracked in Michigan, USA, 2014–2018.

ID	Cohort ID	Sex	Weight (kg)	Age	Fall ^a	Winter ^a	Spring ^a	Summer ^a	Total
F1	1	Female	54.88	Adult	2,565	2,234	165	661	5,625
F2	2	Female	44.23	Adult	1,957	0	0	0	1,957
F3	3	Female	25.85	Sub-adult	0	79	40	0	119
F4	4	Female	29.94	Sub-adult	0	1,054	38	0	1,092
F5	3	Female	23.60	Sub-adult	0	1,371	3,327	2,441	7,139
F6	2	Female	47.17	Adult	1,080	0	1,007	0	2,087
M1	2	Male	46.31	Adult	2,762	0	0	0	2,762
M2	2	Male	49.44	Adult	2,692	0	0	0	2,692
Total					11,056	4,738	4,577	3,102	23,473

870 ^a Fall = September – November; Winter = December – February; Spring = March – May; Summer = June - August

871 Table 4. Deviance information criterion (DIC) and widely-applicable information criterion (WAIC) comparison for each model
872 estimating wild pig behavioral state probabilities in Michigan, USA, 2014–2018. Lower values indicate improved parsimony. Note
873 that Base models only estimate a single behavioral state while joint models estimate all three states concurrently. Relocating, resting,
874 and exploratory represent wild pig behavioral states.

Model	Exploratory		Resting		Relocating		Effects
	DIC	WAIC	DIC	WAIC	DIC	WAIC	
Model 1	6272.12	6263.31	—	—	—	—	Base Model (Exploratory)
Model 2	—	—	11600.40	11036.49	—	—	Base Model (Resting)
Model 3	—	—	—	—	13369.35	12915.51	Base Model (Relocating)
Model 4	5106.56	4857.62	10077.37	9723.60	21235.58	27294.45	Joint Random Effects
Model 5	5077.18	4766.05	10019.93	9687.76	18299.66	19876.19	Joint (Full)
Model 6	4881.74	4827.58	10318.47	10253.80	21952.87	27375.40	Joint (Ornstein-Uhlenbeck)
Model 7	9073.67	8904.25	17470.98	17447.30	17625.67	17630.07	Joint (Non Spatiotemporal)

875

876 Table 5. Fixed effects of joint (full) model estimating wild pig behavioral state probabilities in
877 Michigan, USA, 2014–2018. States shown in bold text indicate that the covariate was important
878 as judged by 95% credible intervals (Q025, Q975). Effects are as estimated by the selected
879 spatiotemporal model (Model 5). Relocating, resting, and exploratory represent wild pig
880 behavioral states. SD = Standard deviation.

Covariate	State	Mean	SD	Q025	Q975
Intercept	Exploratory	-4.47	2.42	-9.22	0.28
	Resting	-6.85	2.99	-12.72	-0.99
	Relocating	0.64	2.37	-4.02	5.30
Developed	Exploratory	0.01	0.07	-0.12	0.15
	Resting	0.00	0.05	-0.09	0.09
	Relocating	0.02	0.04	-0.05	0.09
Riparian	Exploratory	0.35	0.14	0.07	0.63
	Resting	0.24	0.10	0.04	0.44
	Relocating	-0.45	0.08	-0.61	-0.30
Open Herbaceous	Exploratory	0.46	0.10	0.27	0.65
	Resting	-0.04	0.09	-0.22	0.15
	Relocating	-0.35	0.06	-0.47	-0.23
Hard Mast	Exploratory	-0.17	0.08	-0.32	-0.02
	Resting	-0.06	0.05	-0.15	0.03
	Relocating	0.08	0.04	0.01	0.16
Agriculture patch cohesion index	Exploratory	0.34	0.19	-0.04	0.72
	Resting	0.41	0.10	0.22	0.60
	Relocating	-0.41	0.08	-0.58	-0.25
Shrub patch cohesion index	Exploratory	0.20	0.10	0.01	0.40
	Resting	-0.02	0.08	-0.18	0.13
	Relocating	-0.11	0.06	-0.22	0.00
Open-Forest Edge	Exploratory	-0.13	0.08	-0.28	0.02
	Resting	0.04	0.05	-0.07	0.14
	Relocating	0.06	0.04	-0.02	0.14
Temperature	Exploratory	0.85	0.31	0.23	1.46
	Resting	0.08	0.14	-0.19	0.35
	Relocating	-0.15	0.10	-0.34	0.04
Pressure	Exploratory	0.16	0.25	-0.33	0.66
	Resting	0.10	0.11	-0.12	0.32
	Relocating	-0.10	0.07	-0.23	0.04

881