2022

Behavioral states in space and time: Understanding landscape use by an invasive mammal

Steven M. Gray
Michigan State University, stevenmgray4@gmail.com

John M. Humphreys
USDA ARS, john.humphreys@usda.gov

Robert A. Montgomery
University of Oxford, robert.montgomery@zoo.ox.ac.uk

Dwayne R. Etter
Michigan Department of Natural Resources–Wildlife Division, etterd@michigan.gov

Kurt C. VerCauteren
USDA NWRC, kurt.c.vercauteren@usda.gov

Gray, Steven M.; Humphreys, John M.; Montgomery, Robert A.; Etter, Dwayne R.; VerCauteren, Kurt C.; Kramer, Daniel B.; and Roloff, Gary J., "Behavioral states in space and time: Understanding landscape use by an invasive mammal" (2022). *USDA Wildlife Services - Staff Publications*. 2563.
https://digitalcommons.unl.edu/icwdm_usdanwrc/2563

Authors

Steven M. Gray, John M. Humphreys, Robert A. Montgomery, Dwayne R. Etter, Kurt C. VerCauteren, Daniel B. Kramer, and Gary J. Roloff

Received: 30 March 2021 | Revised: 1 December 2021 | Accepted: 30 December 2021

DOI: 10.1002/jwmg.22211

NOTE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Behavioral states in space and time: understanding landscape use by an invasive mammal

Steven M. Gray[1] | **John M. Humphreys**[2] | **Robert A. Montgomery**[3] | **Dwayne R. Etter**[4] | **Kurt C. VerCauteren**[5] | **Daniel B. Kramer**[1,6] | **Gary J. Roloff**[1]

[1]Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA

[2]Pest Management Research Unit, United States Department of Agriculture, Agricultural Research Service, Sidney, MT 59270, USA

[3]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL, United Kingdom

[4]Michigan Department of Natural Resources–Wildlife Division, Lansing, MI 48911, USA

[5]National Wildlife Research Center, United States Department of Agriculture, Wildlife Services, Fort Collins, CO 80521, USA

[6]James Madison College, Michigan State University, East Lansing, MI 48824, USA

Correspondence

Steven M. Gray, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA.
Email: stevenmgray4@gmail.com

Funding information

Michigan State University Department of Fisheries and Wildlife-Vera M Wallach Scholarship; Safari Club International-Michigan Involvement Committee; Michigan Pork Producers Association; Michigan's Statewide Wildlife Research, Surveys, and Monitoring Program, Grant/Award Number: W-155-R; Michigan State University College

Abstract

Animal movement models can be used to understand species behavior and assist with implementation of management activities. We explored behavioral states of an invasive wild pig (*Sus scrofa*) population that recently colonized central Michigan, USA, 2014–2018. 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 used global positioning system (GPS)-collars and monitored 8 wild pigs from 2014–2018. We fit local convex hulls and calculated movement metrics revealing 3 wild pig behavioral states (resting, exploratory, and relocating) and constructed a 3-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). The probability of exploratory behaviors increased

of Agriculture and Natural Resources Alumni Association

exponentially with warming ambient temperature. 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.

KEYWORDS

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

Animal movements are a complex expression of behaviors, related to immediate (e.g., disturbance, temp) 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, Hanski 1999, Bullock et al. 2002, Greenberg and Marra 2005, Dingle 2014). 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 (Millspaugh 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). Because behavioral states are largely determined by prevailing biotic and abiotic conditions (Zhivotovsky 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 in 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 in developing effective control strategies in a given system. For example, wild pigs (*Sus scrofa*) are relatively new to landscapes in the northern United States (e.g., established since ~2000), and their introduction is often facilitated by inadvertent or unlawful releases or escapees from private hunting reserves (Etter et al. 2020, Mayer et al. 2020). Unlike wild pig populations found in the southeastern United States, 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 United States are primarily composed 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. 2020*a*). 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 United States are needed.

Wild pigs are a highly adaptable generalist capable of proliferating in a wide range of environments. Wild pigs often use 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 (Baber and Coblentz 1986, McIlroy 1989, Keuling et al. 2009). For example, in California and Tennessee, USA, 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) because 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 Michigan, USA. Specifically, we assigned behavioral states to wild pig locations derived from GPS telemetry-tracking; examined correlations between wild pig behavioral states and landscape composition and structure, temporal attributes, and weather variables; and 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 and 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.

STUDY AREA

We conducted our study between 2014 and 2018 in 6 counties (Arenac, Bay, Gladwin, Midland, Ogemaw, and Roscommon; 9,090 km^2) in the central Lower Peninsula of Michigan (Figure 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). Approximated annual seasons in our study area are fall (Sep–Nov), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug). The climate is characterized by humid summers and cold winters. Average monthly temperatures range from −6.5 (Jan) to 20.8°C (Jul), 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, composed primarily of deciduous hardwoods in the south and conifer, mixed conifer, and hardwoods in the north (Barnes and Wagner 1981, Albert 1995). Deciduous hardwood forests in the southern portion of our study area consisted of maple (*Acer* spp.), poplar (*Populus* spp.), and oak, where conifer forests in northern counties included pine, fir (*Abies* spp.), and spruce (*Picea* spp.; 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).

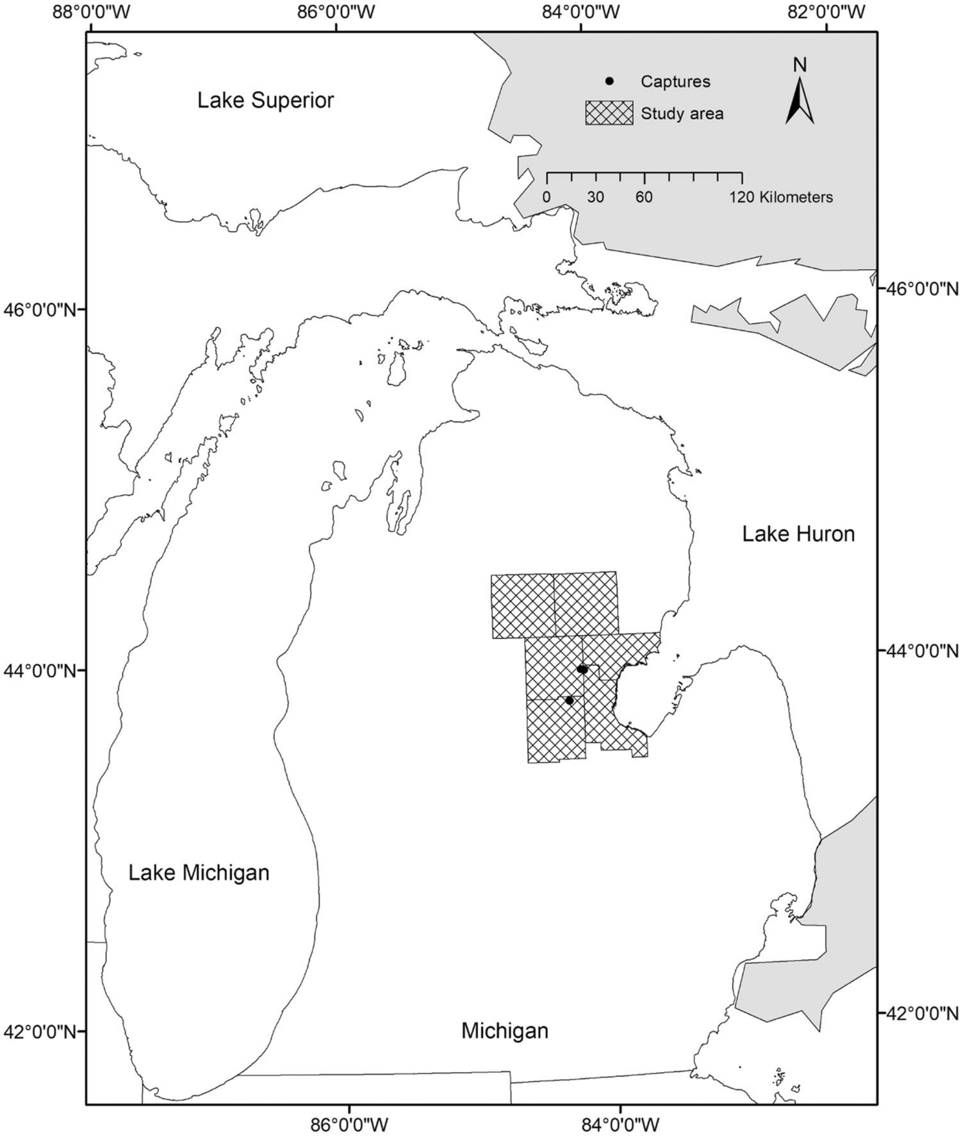

FIGURE 1 Six county (Arenac, Bay, Gladwin, Midland, Ogemaw, and Roscommon) study area in Michigan, USA, used for studying wild pig movement ecology, 2014–2018.

METHODS

Capture and handling

From 2014 to 2017, we live-captured 8 wild pigs in our study area and 2 additional animals in Marquette County of the Upper Peninsula, Michigan. We captured all animals 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, Shawnee Mission, KS, USA) and Telazol (Fort Dodge Laboratories, Fort Dodge, IA, USA). We fit each pig with an IridiumTrackM GPS-collar (Lotek Wireless, Newmarket, Ontario, Canada) programmed to record a GPS-fix every 30 minutes. Because of 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). We actively monitored all collared animals via remote trail cameras and humanely dispatched them 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 ≥3 months. Additionally, we removed GPS locations of poor quality (i.e., having a dilution of precision >5; Edenius 1997, Moen et al. 1997). We also removed the first 7 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. We defined a trajectory 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 because all collars were programmed to record fixes at 30-minute 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., 1 hr) given our interest in assessing movement and behavior at fine temporal scales. Though wild pigs are assumed to be primarily nocturnal in our study area (S. M. Gray, Michigan State University, 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 3 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 the 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 (Van Moorter et al. 2010) with 1,000 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 3 clusters (behavioral states; Figure S1, available in Supporting Information), which we characterized using descriptive statistics for step length, revisitation rate, and duration of visit (Table 1). We classified the

TABLE 1 Descriptive statistics for step length (m), revisitation rate, and duration of visit (number of locations) for each behavioral state estimated for 8 wild pigs telemetry-tracked with global positioning system-collars, Michigan, USA, 2014–2018.

	Metric								
	Step length			Revisitation rate			Duration of visit		
Behavioral state	x̄	SE	Range	x̄	SE	Range	x̄	SE	Range
Exploratory	27.5	1.3	0.1–1,504.3	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	7.5–2,950.1	46.8	0.4	1.0–214.0	4.4	0.0	1.1–11.7

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. We identified the exploratory behavioral state 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 (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 2 classes: open areas and high vegetation (>5 m) because 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 ($\bar{x} = 100\,\text{m} \pm 1.37\,\text{m}$ [SE]). Within each grid cell, we calculated the proportion of area that was classified as human development (e.g., urban, suburban), riparian, open herbaceous, or 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 online portal. We extracted hourly data from 2 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. We considered surface pressure (Pa) and ambient temperature (°C; Table 2).

Statistical modeling

Because we telemetered wild pigs from 2 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

TABLE 2 Description, data source, mean, range, and references for covariates used in modeling behavioral states of 8 wild pigs telemetry-tracked with global positioning system collars, Michigan, USA, 2014–2018.

Name	Description	Source[a]	$\bar{x}$	SE	Range	Reference(s)
Proportion cover type						
Developed	Percent 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	Percent 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	Percent 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	Percent of cover types dominated by mast-producing tree species (i.e., white oak [*Quercus alba*]-red oak [*Quercus rubra*]-hickory [*Carya* spp.], black oak [*Quercus velutina*] and savanna, beech [*Fagus* spp.]-maple [*Acer* spp.]-basswood [*Tilia* spp.) 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)

(Continues)

TABLE 2 (Continued)

Name	Description	Source[a]	$\bar{x}$	SE	Range	Reference(s)
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 (m/m^2) 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)

[a] Source 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 (LANFIRE EVT, LANDFIRE EHT; http://www.landfire.gov/); NOAA–hourly weather data obtained from the National Oceanic and Atmospheric Administration.

simultaneously. Therefore, we proceeded to focus solely on data collected from wild pigs in the Lower Peninsula (n = 8). Based on United States Department of Agriculture culling records, remote-sensing camera photographs, 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 (3 states identified by the gap statistic method for optimal clustering), we used the stochastic partial differential equation method (Lindgren et al. 2011, Krainski et al. 2018) and constructed a 3-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 we removed any covariate with a value >3.0 (Zuur et al. 2010). In addition, we standardized each predictor variable to have a mean of zero and standard deviation of 1. The 3-level, jointly fit model to estimate behavioral states took the form:

$$y_1(s) = \alpha_1 + \beta_1 X + z_1(s) \tag{1}$$

$$y_2(s) \mid y_1(s) = \alpha_2 + \beta_2 X + \lambda_1 \times z_1(s) + z_2(s) \tag{2}$$

$$y_3(s) \mid y_1(s), y_2(s) = \alpha_3 + \beta_3 X + \lambda_2 \times z_1(s) + \lambda_3 \times z_2(s) + z_3(s), \tag{3}$$

where each level is a spatially explicit binomial regression used to estimate a particular behavioral state: exploratory (y_1 [Equation 1]), resting (y_2 [Equation 2]), relocating (y_3 [Equation 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. Cohort represents an identifier attached to individuals captured together and considered to be in the same social group. Although all 3 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 2-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), where z_1, z_2, and z_3 are zero mean spatial fields for j = 1, 2, and 3 based on GPS locations s (s = 1, 2, 3,..., n). We specified all model spatial fields as continuous Gaussian random fields with Matèrn covariance following the stochastic partial differential equation approach (Lindgren et al. 2011). Equation 2 includes a shared copy of the spatial field from $y_1(s)$ and Equation 3 contains copies of the spatial fields from $y_1(s)$ and $y_2(s)$. By modifying these shared spatial fields, the λ_j terms 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. We specified non-informative priors for all terms and used the integrated nested Laplace approximation method (Rue et al. 2009) as a fast and accurate alternative to Markov chain Monte Carlo for latent Gaussian models.

We fit and compared 7 models. First, we fit 3 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 (i.e., ordinal time steps used to account for temporal correlation), 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 zero. We generated predictions for each significant parameter and estimated predictions 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. We applied the remaining 20% of data to test the model and estimate classification accuracy using the area under the receiver operating characteristic curve (area under 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 males, 6 females) in our study area. Overall, these wild pigs represented 4 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 dilution of precision of 2.94 ± 0.01 (SE). We used 23,473 locations to model changes in wild pigs exhibiting different behavioral states. Mean number of locations per individual was 2,934 ± 823.76 with seasonal representation being highest in fall (Sep–Nov) and lowest in summer (Jun–Aug; Table 3). Subsequent monitoring and removal of study animals did not reveal evidence of piglets or pregnancy, which can potentially influence movements and behaviors.

Time of day was associated with 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; Figure 2). We also noted variability in behavioral states by wild pig cohort, particularly in resting and exploratory behaviors (Figure S2, available in Supporting Information). Cohort 2 exhibited less resting and more exploratory behaviors, while cohort 4 displayed more resting than others (Figure S2), substantiating the importance of accounting for wild pig cohort in our analysis.

The joint model incorporating all 3 behavioral states, random effects, and spatiotemporal effects tended to outperform simpler models in widely applicable information criterion and often deviance information criterion, except for the relocating state (Table 4). Model validation indicated that our joint (full) model performed better than random (i.e., AUCs > 0.5) but varied depending on behavioral state and model performance metric (Table S1,

TABLE 3 Sex and identification (ID), cohort, mass, age, and number of global positioning system locations, by season, for 8 wild pigs tracked in Michigan, USA, 2014–2018.

ID	Cohort ID	Sex	Mass (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

[a] Fall = September–November; Winter = December–February; Spring = March–May; Summer = June–August.

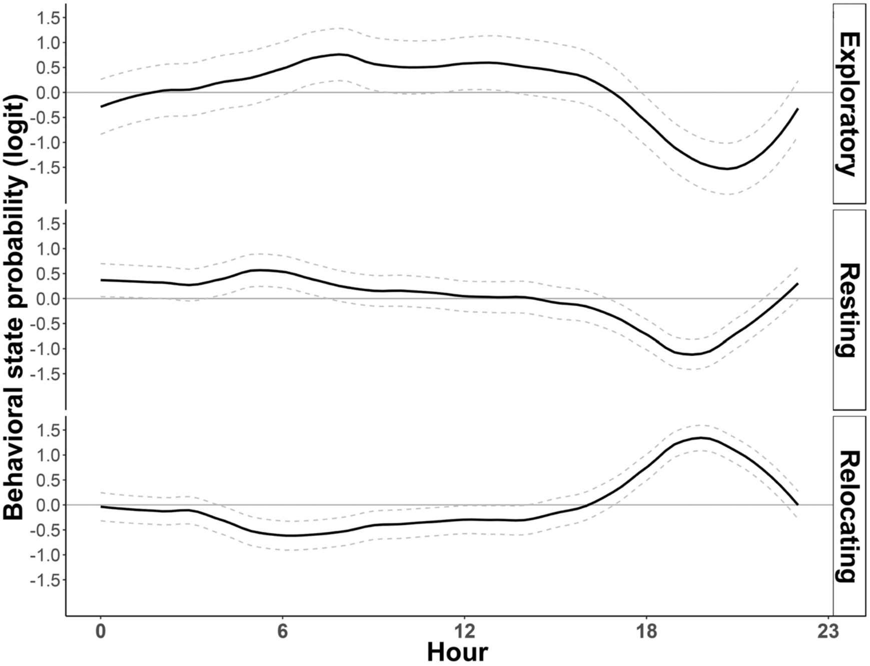

FIGURE 2 Hourly movement probabilities on the logit scale for each behavioral state of wild pigs in Michigan, USA, 2014–2018. Dashed lines represent the standard error of prediction estimates.

TABLE 4 Deviance information criterion (DIC) and widely applicable information criterion (WAIC) comparison for each model estimating wild pig behavioral state probabilities in Michigan, USA, 2014–2018. Lower values indicate improved parsimony. Base models only estimate a single behavioral state, while joint models estimate all 3 states concurrently. Relocating, resting, and exploratory represent wild pig behavioral states.

	Exploratory		Resting		Relocating		
Model	**DIC**	**WAIC**	**DIC**	**WAIC**	**DIC**	**WAIC**	**Effects**
Model 1	6,272.12	6,263.31					Base model (exploratory)
Model 2			11,600.40	11,036.49			Base model (resting)
Model 3					13,369.35	12,915.51	Base model (relocating)
Model 4	5,106.56	4,857.62	10,077.37	9,723.60	21,235.58	27,294.45	Joint random effects
Model 5	5,077.18	4,766.05	10,019.93	9,687.76	18,299.66	19,876.19	Joint (full)
Model 6	4,881.74	4,827.58	10,318.47	10,253.80	21,952.87	27,375.40	Joint (Ornstein-Uhlenbeck)
Model 7	9,073.67	8,904.25	17,470.98	17,447.30	17,625.67	17,630.07	Joint (non-spatiotemporal)

available in Supporting Information). 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).

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; Figure 3A). We also predicted a higher probability of exploratory behaviors in open herbaceous cover types and

TABLE 5 Fixed effects of the joint (full) model estimating wild pig behavioral state probabilities in Michigan, USA, 2014–2018. States with an asterisk (*) indicate that the covariate was important as judged by 95% credible intervals (Q025, Q975). Effects are as estimated by the selected spatiotemporal model (model 5). Relocating, resting, and exploratory represent wild pig behavioral states.

Covariate	State	x̄	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

relocating behaviors in hard mast cover types (Table 5). Open herbaceous cover was associated with an increased probability of the exploratory behavioral state and a decrease in probability of relocating (Figure 3B). Conversely, increasing proportions of the hard mast cover type predicted a nearly linear increase in relocating behaviors and decrease in exploratory behaviors (Figure 3C).

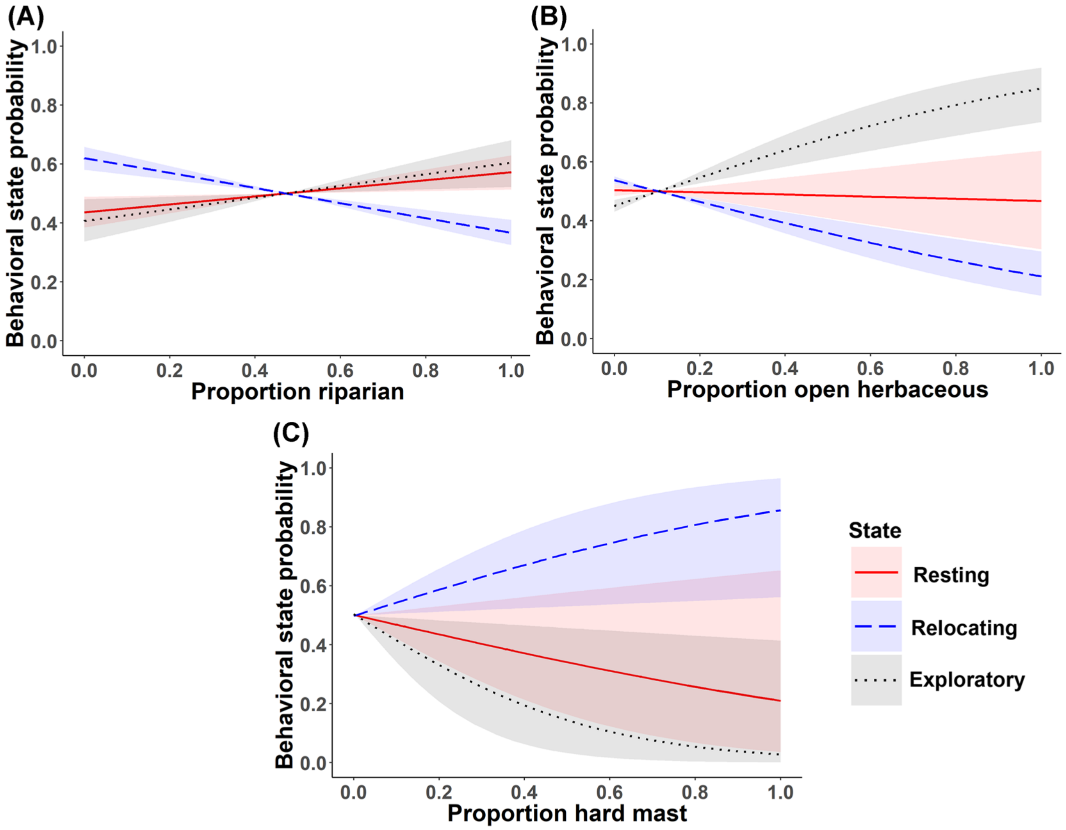

FIGURE 3 Probability of behavioral state and proportion of riparian (A), open herbaceous (B), and hard mast (C) cover types in 1-ha cells for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimates.

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 moderate increase in exploratory behaviors, while relocating behaviors decreased (Figure 4A). Effects were less pronounced for shrub patch cohesion, which had a significant and increasing linear relationship with exploratory behavior in wild pigs (Figure 4B).

Temperature was 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 (Figure 5). Probability of exploratory behaviors was near zero at cold temperatures (i.e., ~−30°C), increased rapidly once temperatures reached −10°C, and then tapered off at 30°C (Figure 5).

DISCUSSION

Our research offers 2 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. Methods using k-means clustering with attributes from movement trajectories and local convex hull time-use metrics are an intuitive approach for delineating behavioral states in wild

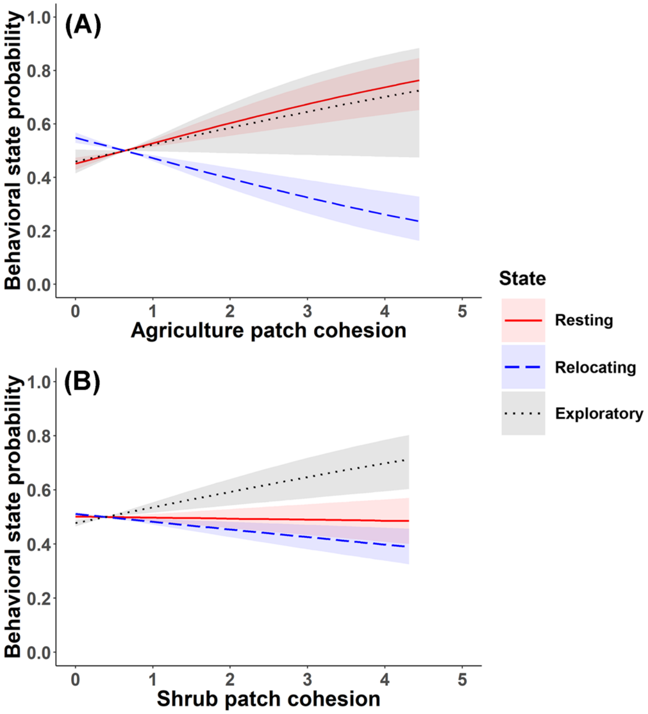

FIGURE 4 Probability of behavioral state and agriculture (A) and shrub patch cohesion (B) indices in 1-ha cells for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimates.

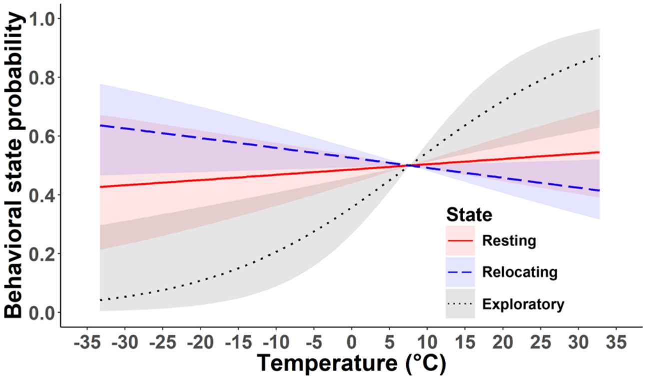

FIGURE 5 Probability of behavioral state and temperature for 8 wild pigs in Michigan, USA, 2014–2018. Shaded area represents the standard error of prediction estimate.

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 (Smyser et al. 2020), within northern systems of the United States 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 data revealed that increasing proportions of 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 and may be preferred over other cover types (Kurz and Marchinton 1972, Baber and Coblentz 1986, Mersinger and Silvy 2007, Friebel and Jodice 2009, Beasley et al. 2014). Similarly, we noted 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 results are largely in alignment, suggesting that open herbaceous cover types serve a similar purpose for wild pigs in northern landscapes of the United States.

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 because 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). Our hard mast cover type served only 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). Open to forest edge density was 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 (Etter et al. 2020). 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 United States. 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 United States, 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). Temperature had the most profound effect on probability of the exploratory behavioral state in our study, 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 United States, 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).

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. 2008*a*, Podgórski et al. 2013, Cremonesi et al. 2021). Our study area was primarily forested with substantial understory cover, potentially limiting human disturbances and providing enough concealment to facilitate modest diurnal activity. Our conclusion that relocating behavior was most likely to occur at dusk and the early nighttime hours conformed with observations from other regions, where sunset serves as a cue to initiate activity and movement (Lemel et al. 2003, Silveira de Oliveira et al. 2020). For social animals, it is unsurprising to see differences in the proportion of behavioral states exhibited by separate groups and wild pigs are a highly adaptable species that readily respond to their environment (Gray et al. 2020*b*). While research exploring differences in movements among wild pig socials groups is limited, there is some evidence that wild pig social groups employ different strategies in movement and space use in response to local pressures, age structure, and the environment (Keuling et al. 2008*b*, 2009; Podgórski et al. 2013). To a degree, our results may indicate similar plasticity in movement and behavior among wild pig social groups.

We caution that the environmental relationships to behavioral states in this study were based on a limited sample (i.e., 8 individuals); therefore, we encourage further exploration of wild pig movements to elucidate potential geographic similarities and differences. Our sample was largely composed of female wild pigs, which are highly social and exhibit site fidelity (Gabor et al. 1999, Kaminski et al. 2005, Keuling et al. 2008*b*, Lavelle et al. 2018). Given that females primarily reside in social groups (i.e., sounders), knowledge on the ecology and behavior of females is beneficial to managers in potentially facilitating whole group removal (Ditchkoff and Bodenchuk 2020). Control strategies prioritizing whole group removal are desirable in wild pig management, as failure to do so may scatter individuals from known locations, hampering future management efforts and potentially facilitating disease transmission, which tends to be constrained spatially and within social groups (Podgórski et al. 2018). Considering male wild 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; thus, our results 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. 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 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 motion-sensitive cameras 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. 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 findings and conclusions of this publication are those of the authors and should not be construed to represent any official United States Government determination or policy. Mention of commercial products or companies does not represent an endorsement by the United States Government. We thank individuals from the United States Department of Agriculture—Wildlife Services for their trapping efforts and field support. We thank E. Raifsnider, A. N. 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. 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 United States 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.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All capture and handling protocols were approved by the Michigan State University Institutional Animal Care and Use Committee (01/14-013-00).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Steven M. Gray http://orcid.org/0000-0003-2731-4416

REFERENCES

Albert, D. A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. USDA Forest Service General Technical Report NC-178, St. Paul, Minnesota, USA.

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

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

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

Barnes, B. V., and W. H. Wagner. 1981. Michigan trees. University of Michigan Press, Ann Arbor, USA.

Barrett, R. H. 1982. Habitat preferences of feral hogs, deer, and cattle on a Sierra foothill range. Journal of Range Management 35:342–346.

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

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

Blangiardo, M., and M. Cameletti. 2015. Spatial and spatio-temporal Bayesian models with R-INLA. John Wiley & Sons, Hoboken, New Jersey, USA.

Blasetti, A., L. Boitani, M. C. Riviello, and E. Visalberghi. 1988. Activity budgets and use of enclosed space by wild boars (*Sus scrofa*) in captivity. Zoo Biology 7:69–79.

Brooks, C. J., and S. Harris. 2008. Directed movement and orientation across a large natural landscape by zebras, *Equus burchelli antiquorum*. Animal Behaviour 76:277–285.

Brown, D. D., R. A. Montgomery, J. J. Millspaugh, P. A. Jansen, C. X. Garzon-Lopez, and R. Kays. 2014. Selection and spatial arrangement of rest sites within northern tamandua home ranges. Journal of Zoology 293:160–170.

Bullock, J. M., R. E. Kenward, and R. S. Hails. 2002. Dispersal ecology: 42nd symposium of the British Ecological Society. Cambridge University Press, Cambridge, United Kingdom.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society of London B Biological Sciences 365:2157–2162.

Calenge, C. 2011. Analysis of animal movements in R: the adehabitatLT package. R Foundation for Statistical Computing, Vienna, Austria.

Caley, P. 1997. Movements, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. Wildlife Research 24:77–87.

Cooper, S. M., and S. S. Sieckenius. 2016. Habitat selection of wild pigs and northern bobwhites in shrub-dominated rangeland. Southeastern Naturalist 15:382–393.

Corn, J. L., and T. R. Jordan. 2017. Development of the national feral swine map, 1982–2016. Wildlife Society Bulletin 41:758–763.

Cremonesi, G., F. Bisi, L. Gaffi, T. Zaw, H. Naing, K. Moe, Z. Aung, A. Gagliardi, L. A. Wauters, D. G. Preatoni, and A. Martinoli. 2021. Evaluation of human disturbance on the activity of medium–large mammals in Myanmar tropical forests. Forests 12:290.

Dardaillon, M. 1987. Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (Southern France). Acta Theriologica 32:389–401.

Dechen Quinn, A. C., D. M. Williams, and W. F. Porter. 2012. Postcapture movement rates can inform data-censoring protocols for GPS-collared animals. Journal of Mammalogy 93:456–463.

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

Dingle, H. 2014. Migration: the biology of life on the move. Oxford University Press, Oxford, United Kingdom.

Ditchkoff, S. S., and M. J. Bodenchuk. 2020. Management of wild pigs. Pages 175–198 *in* K. C. VerCauteren, J. C. Beasley, S. S. Ditchkoff, J. J. Mayer, G. J. Roloff, and B. K. Strickland, editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Edenius, L. 1997. Field test of a GPS location system for moose *Alces alces* under Scandinavian boreal conditions. Wildlife Biology 3:39–43.

Elston, J. J., and D. G. Hewitt. 2010. Intake of mast by wildlife in Texas and the potential for competition with wild boars. Southwestern Naturalist 55:57–66.

Etter, D. R., M. Nichols, and K. M. Hollis-Etter. 2020. Wild pigs in northeastern North America. 2020. Pages 319–345 *in* K. C. VerCauteren, J. C. Beasley, S. S. Ditchkoff, J. J. Mayer, G. J. Roloff, and B. K. Strickland, editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

Evans, J. 2015. spatialEco. R package version 2.0-0. https://github.com/jeffreyevans/spatialEco

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

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20: 273–287.

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

Frederick, J. M. 1998. Overview of wild pig damage in California. Proceedings of the Vertebrate Pest Conference 18:82–86.

Friebel, B. A., and P. G. R. Jodice. 2009. Home range and habitat use of feral hogs in Congaree National Park, South Carolina. Human-Wildlife Conflicts 3:49–63.

Fryxell, J. M., M. Hazell, L. Börger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences 105:19114–19119.

Gabor, T. M., and E. C. Hellgren. 2000. Variation in peccary populations: landscape composition or competition by an invader? Ecology 81:2509–2524.

Gabor, T. M., E. C. Hellgren, and N. J. Silvy. 2001. Multi-scale habitat partitioning in sympatric suiforms. Journal of Wildlife Management 65:99–110.

Gabor, T. M., E. C. Hellgren, R. A. Van Den Bussche, and N. J. Silvy. 1999. Demography, sociospatial behaviour and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. Journal of Zoology 247:311–322.

Gantchoff, M. G., and J. L. Belant. 2015. Anthropogenic and environmental effects on invasive mammal distribution in northern Patagonia, Argentina. Mammalian Biology 80:54–58.

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

Geisser, H., and H.-U. Reyer. 2005. The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). Journal of Zoology 267:89–96.

Gerard, J.-F., B. Cargnelutti, F. Spitz, G. Valet, and T. Sardin. 1991. Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriologica 36:119–129.

Gortázar, C., E. Ferroglio, U. Höfle, K. Frölich, and J. Vicente. 2007. Diseases shared between wildlife and livestock: a European perspective. European Journal of Wildlife Research 53:241–256.

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

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

Greenberg, R., and P. P. Marra. 2005. Birds of two worlds: the ecology and evolution of migration. Johns Hopkin University Press, Baltimore, Maryland, USA.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, United Kingdom.

Herrero, J., A. García-Serrano, S. Couto, V. M. Ortuño, and R. García-González. 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. European Journal of Wildlife Research 52:245–250.

Herrero, J., I. Irizar, N. A. Laskurain, A. García-Serrano, and R. García-González. 2005. Fruits and roots: wild boar foods during the cold season in the southwestern Pyrenees. Italian Journal of Zoology 72:49–52.

Humphreys, J. M., D. C. Douglas, A. M. Ramey, J. M. Mullinax, C. Soos, P. Link, P. Walther, and D. J. Prosser. 2021. The spatial-temporal relationship of blue-winged teal to domestic poultry: movement state modeling of a highly mobile avian influenza host. Journal of Applied Ecology 58:2040–2052.

Humphreys, J. M., J. B. Elsner, T. H. Jagger, and S. Pau. 2017. A Bayesian geostatistical approach to modeling global distributions of *Lygodium microphyllum* under projected climate warming. Ecological Modelling 363:192–206.

Humphreys, J. M., A. M. Ramey, D. C. Douglas, J. M. Mullinax, C. Soos, P. Link, P. Walther, and D. J. Prosser. 2020. Waterfowl occurrence and residence time as indicators of H5 and H7 avian influenza in North American Poultry. Scientific Reports 10:1–16.

Illian, J. B., S. H. Sørbye, and H. Rue. 2012. A toolbox for fitting complex spatial point process models using integrated nested Laplace approximation (INLA). Annals of Applied Statistics 6:1499–1530.

Ilse, L. M., and E. C. Hellgren. 1995. Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76:784–799.

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

Jones-Todd, C. M., B. Swallow, J. B. Illian, and M. Toms. 2018. A spatiotemporal multispecies model of a semicontinuous response. Journal of the Royal Statistical Society: Series C (Applied Statistics) 67:705–722.

Kay, S. L., J. W. Fischer, A. J. Monaghan, J. C. Beasley, R. Boughton, T. A. Campbell, S. M. Cooper, S. S. Ditchkoff, S. B. Hartley, J. C. Kilgo, et al. 2017. Quantifying drivers of wild pig movement across multiple spatial and temporal scales. Movement Ecology 5:14.

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

Keuling, O., N. Stier, and M. Roth. 2008*a*. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? European Journal of Wildlife Research 54:729–737.

Keuling, O., N. Stier, and M. Roth. 2008*b*. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. European Journal of Wildlife Research 54:403–412.

Keuling, O., N. Stier, and M. Roth. 2009. Commuting, shifting or remaining? different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mammalian Biology 74:145–152.

Krainski, E. T., V. Gómez-Rubio, H. Bakka, A. Lenzi, D. Castro-Camilo, D. Simpson, F. Lindgren, and H. Rue. 2018. Advanced spatial modeling with stochastic partial differential equations using R and INLA. CRC Press, New York, New York, USA.

Kurz, J. C., and R. L. Marchinton. 1972. Radiotelemetry studies of feral hogs in South Carolina. Journal of Wildlife Management 36:1240–1248.

LANDFIRE. 2014. US Department of Interior, geological survey. http://www.landfire.gov/. Accessed 3 Sep 2017.

Larroque, J., S. Ruette, J. M. Vandel, and S. Devillard. 2015. Where to sleep in a rural landscape? a comparative study of resting sites pattern in two syntopic *Martes* species. Ecography 38:1129–1140.

Lavelle, M. J., N. P. Snow, J. M. Halseth, E. H. VanNatta, H. N. Sanders, and K. C. VerCauteren. 2018. Evaluation of movement behaviors to inform toxic baiting strategies for invasive wild pigs (*Sus scrofa*). Pest Management Science 74:2504–2510.

Leblond, M., C. Dussault, and J.-P. Ouellet. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. Journal of Zoology 289:32–40.

Lemel, J., J. Truvé, and B. Söderberg. 2003. Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. Wildlife Biology 9:29–36.

Lindgren, F., H. Rue, and J. Lindström. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 73:423–498.

Long, J. A., and T. A. Nelson. 2013. A review of quantitative methods for movement data. International Journal of Geographical Information Science 27:292–318.

Lyons, A. 2014. T-LoCoH for R: tutorial and users guide. https://tlocoh.r-forge.r-project.org/tlocoh_tutorial_2014-08-17.pdf

Lyons, A. J., W. C. Turner, and W. M. Getz. 2013. Home range plus: a space-time characterization of movement over real landscapes. Movement Ecology 1:2.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2019. cluster: cluster analysis basics and extensions. R package version 2.1.0. https://CRAN.R-project.org/package=cluster

Maillard, D., and P. Fournier. 1995. Effects of shooting with hounds on size of resting range of wild boar (*Sus scrofa* L.) groups in Mediterranean habitat. Ibex Journal of Mountain Ecology 3:102–107.

Mårell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. Canadian Journal of Zoology 80:854–865.

Martin, J., B. van Moorter, E. Revilla, P. Blanchard, S. Dray, P. Y. Quenette, D. Allainé, and J. E. Swenson. 2013. Reciprocal modulation of internal and external factors determines individual movements. Journal of Animal Ecology 82:290–300.

Mayer, J. J. 2009. Taxonomy and history of wild pigs in the United States. Pages 5–24 *in* J. J. Mayer and I. L. Brisbin, Jr., editors. Wild pigs: biology, damage, control techniques, and management. Savannah River National Laboratory, Aiken, South Carolina, USA.

Mayer, J. J., T. J. Smyser, A. J. Piaggio, and S. M. Zervanos. 2020. Wild pig taxonomy, morphology, genetics, and physiology. Pages 7–31 *in* K. C. VerCauteren, J. C. Beasley, S. S. Ditchkoff, J. J. Mayer, G. J. Roloff, and B. K. Strickland, editors. Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, Florida, USA.

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

McNeil, B. J., J. A. Hanley, H. H. Funkenstein, and J. Wallman. 1983. Paired receiver operating characteristic curves and the effect of history on radiographic interpretation. CT of the head as a case study. Radiology 149:75–77.

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

Mersinger, R. C., and N. J. Silvy. 2007. Range size, habitat use, and dial activity of feral hogs on reclaimed surface-mined lands in east Texas. Human-Wildlife Conflicts 1:161–167.

Michigan State Climatologist's Office. 2019. Gladwin (3170). Michigan State University, East Lansing, Michigan, USA. <https://climate.geo.msu.edu/climate_mi/stations/3170/>. Accessed 5 June 2019.

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio-tracking and animal populations: past trends and future needs. Pages 383–393 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Mitchell J., and R. Mayer. 1997. Diggings by feral pigs within the Wet Tropics World Heritage Area of north Queensland. Wildlife Research 24:591–601.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530–539.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445.

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

Morelle, K., and P. Lejeune. 2015. Seasonal variations of wild boar *Sus scrofa* distribution in agricultural landscapes: a species distribution modelling approach. European Journal of Wildlife Research 61:45–56.

Moriarty, K. M., C. W. Epps, and W. J. Zielinski. 2016. Forest thinning changes movement patterns and habitat use by Pacific marten. Journal of Wildlife Management 80:621–633.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105: 19052–19059.

Ohashi, H., M. Saito, R. Horie, H. Tsunoda, H. Noba, H. Ishii, T. Kuwabara, Y. Hiroshige, S. Koike, Y. Hoshino, H. Toda, and K. Kaji. 2013. Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. European Journal of Wildlife Research 59:167–177.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State–space models of individual animal movement. Trends in Ecology and Evolution 23:87–94.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Podgórski, T., M. Apollonio, and O. Keuling. 2018. Contact rates in wild boar populations: implications for disease transmission. Journal of Wildlife Management 82:1210–1218.

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

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior by prairie grouse: implications for development of wind energy. Conservation Biology 23:1253–1259.

R Core Team. 2018. R version 3.5.0. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revilla, E., and T. Wiegand. 2008. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proceedings of the National Academy of Sciences USA 105:19120–19125.

Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 71: 319–392.

Ruiz-Fons, F., J. Segalés, and C. Gortázar. 2008. A review of viral diseases of the European wild boar: effects of population dynamics and reservoir role. Veterinary Journal 176:158–169.

Schley, L., and T. J. Roper. 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. Mammal Review 33:43–56.

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

Schlichting, P. E., C. L. Richardson, B. Chandler, P. S. Gipson, J. J. Mayer, and C. B. Dabbert. 2015. Wild pig (*Sus scrofa*) reproduction and diet in the Rolling Plains of Texas. Southwestern Naturalist 60:321–326.

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

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

Silveira de Oliveira, Ê., M. Ludwig da Fontoura Rodrigues, M. Machado Severo, T. Gomes dos Santos, and C. B. Kasper. 2020. Who's afraid of the big bad boar? assessing the effect of wild boar presence on the occurrence and activity patterns of other mammals. PLoS One 15:e0235312.

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

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

Sjarmidi, A., G. Valet, and F. Spitz. 1996. Autumn frugivory in wild boar (*Sus scrofa*). Pages 213–224 *in* M. L. Mathias, M. Santos-Reis, G. Amori, R. Libois, A. Mitchell-Jones, and M. C. Saint Girons, editors. European mammals. Proceedings of the I European Congress of Mammalogy, Lisboa, Portugal.

Smyser, T. J., M. A. Tabak, C. Slootmaker, M. S. Robeson, R. S. Miller, M. Bosse, H.-J. Megens, M. A. M. Groenen, S. R. Paiva, D. A. de Faria, H. D. Blackburn, B. S. Schmit, and A. J. Piaggio. 2020. Mixed ancestry from wild and domestic lineages contributes to the rapid expansion of invasive feral swine. Molecular Ecology 29:1103–1119.

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

Sparklin, B. D., M. S. Mitchell, L. B. Hanson, D. B. Jolley, and S. S. Ditchkoff. 2009. Territoriality of feral pigs in a highly persecuted population on Fort Benning, Georgia. Journal of Wildlife Management 73:497–502.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: black bears alter movement behaviour in response to hunting pressure. Behavioural Processes 120:30–39.

Swingland, I. R., and P. J. Greenwood. 1983. The ecology of animal movement. Clarendon Press, Oxford, United Kingdom.

Thiebault, A., and Y. Tremblay. 2013. Splitting animal trajectories into fine-scale behaviorally consistent movement units: breaking points relate to external stimuli in a foraging seabird. Behavioral Ecology and Sociobiology 67:1013–1026.

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

Thurfjell, H., G. Spong, and G. Ericsson. 2014. Effects of weather, season, and daylight on female wild boar movement. Acta Theriologica 59:467–472.

Tibshirani, R., G. Walther, and T. Hastie. 2001. Estimating the number of clusters in a data set via the gap statistic. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 63:411–423.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2163–2176.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.

U.S. Geological Survey. 2019. 3D Elevation Program. https://www.usgs.gov/news/usgs-3dep-lidar-point-cloud-now-available-amazon-public-dataset. Accessed 26 May 2021.

Van Moorter, B., D. R. Visscher, C. L. Jerde, J. L. Frair, and E. H. Merrill. 2010. Identifying movement states from location data using cluster analysis. Journal of Wildlife Management 74:588–594.

Welander, J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. Journal of Zoology 252:263–271.

Weterings, M. J. A., M. Zaccaroni, N. van der Koore, L. M. Zijlstra, H. J. Kuipers, F. van Langevelde, and S. E. van Wieren. 2016. Strong reactive movement response of the medium-sized European hare to elevated predation risk in short vegetation. Animal Behaviour 115:107–114.

Wittemyer, G., L. M. Keating, F. Vollrath, and I. Douglas-Hamilton. 2017. Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. Ecography 40:598–605.

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

Wood, G. W., and D. N. Roark. 1980. Food habits of feral hogs in coastal South Carolina. Journal of Wildlife Management 44:506–511.

Wyckoff, A. C., S. E. Henke, T. Campbell, and K. C. VerCauteren. 2006. Is trapping success of feral hogs dependent upon weather conditions? Proceedings of the Vertebrate Pest Conference 22:370–372.

Zhivotovsky, L. A., A. Bergman, and M. W. Feldman. 1996. A model of individual adaptive behavior in a fluctuating environment. Pages 131–154 *in* R. K. Belew and M. Mitchell, editors. Adaptive individuals in evolving populations. Addison-Wesley, Reading, Massachusetts, USA.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Associate Editor: Andrea Litt.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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