




A multi-level modeling approach to guide management of female feral hogs in Great Smoky Mountains National Park

Frances E. Buderman · Patrick J. Helm ·
Joseph D. Clark · Ryan H. Williamson ·
Joseph Yarkovich · Jennifer M. Mullinax 

Received: 1 September 2022 / Accepted: 8 May 2023 / Published online: 16 May 2023
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Abstract We trapped, anesthetized, and fit 16 female feral swine (*Sus scrofa*) with Global Positioning System (GPS) collars in Great Smoky Mountains National Park (GRSM) to develop predictive summer and winter models for more effective population control efforts. Given the highly diverse habitat and topography in GRSM and the spatial extent of our dataset, we employed Step Selection Function

(SSF) to evaluate resource selection at the 3rd-order level and Resource Selection Function (RSF) models at the 2nd-order level for both summer and winter seasons. The summer SSF and RSF models suggested relatively similar levels of selection, whereas the winter models differed by method. We created a straightforward consensus model to better visualize the agreement and constraints of each set of models. In summer, feral swine used lower slopes regardless of elevation, especially those closer to human-dominated spaces such as along paved and gravel roadways. In winter, feral swine maintained preference for lower slopes but preferred oak-dominated forest areas and selection for human development was less than in summer. Wildlife managers can use these models to better focus feral swine surveillance and management in GRSM. Managers can identify areas of high use by season and plan control activities that are both accessible and highly efficient. The combination and consensus framework presented here can be applied to other systems where species' habitat selection may result in incongruous results across different levels of selection or seasons of interest.

F. E. Buderman
Department of Ecosystem Science and Management,
Pennsylvania State University, 401 Forest Resources Bldg,
University Park, PA 16801, USA

P. J. Helm
Department of Forestry, Wildlife and Fisheries, University
of Tennessee, 427 Plant Biotechnology Building, 2505 E.
J. Chapman Drive, Knoxville, TN 37996, USA

J. D. Clark
U.S. Geological Survey, Northern Rocky Mountain
Science Center, Southern Appalachian Research Branch,
University of Tennessee, 427 Plant Biotechnology
Building, 2505 E. J. Chapman Drive, Knoxville,
TN 37996, USA

R. H. Williamson · J. Yarkovich
National Park Service, Great Smoky Mountains National
Park, 107 Park Headquarters Road, Gatlinburg, TN 37738,
USA

J. M. Mullinax (✉)
Department of Environmental Science and Technology,
University of Maryland, 1433 Animals Sciences Bldg,
College Park, MD 20742, USA
e-mail: wildlife@umd.edu

Keywords Feral swine · Great Smoky Mountains National Park · Habitat use · Hogs · Invasive · Resource selection · Step selection · *Sus scrofa*

Wild boar (*Sus scrofa*) are native to Eurasia and northern Africa and were originally introduced to

southern North America as early as the sixteenth century by Spanish explorers (McClure et al. 2015). These animals are a nonindigenous, invasive species in the U.S. and are typically referred to as feral swine, feral hogs, or wild hogs. The International Union for Conservation of Nature (IUCN) considers feral swine to be in the top 100 invasive species most damaging to the world's biodiversity (Lowe et al. 2000). Feral swine negatively affect ecosystem processes and functioning by altering nutrient dynamics (Aplet et al. 1991), disturbing plant communities, impacting sensitive habitats (Barrett and Birmingham 1994; Stevens 1996; Hone 2002; Cushman et al. 2004; Engeman et al. 2004; Seward et al. 2004; Siemann et al. 2009; Porter et al. 2014), and acting as a disease reservoir (Wyckoff et al. 2009). Unfortunately, feral swine continue to expand their distribution and numbers in the contiguous United States where they cause billions of dollars in damage annually (Pimentel et al. 2005; Pimentel 2007; Mayer and Beasley 2017).

In 1912, Eurasian boars (*S. scrofa scrofa*) were released into pens on a hunting camp in North Carolina, USA, 45 km southwest of what is now Great Smoky Mountains National Park (hereafter GRSM or Park; Peine and Farmer 1990). Within 10 years, those animals escaped the camp enclosures and began breeding with local, free-ranging livestock pigs (*S. scrofa domestica*), and by the 1940s and 50 s, the feral hogs had colonized the newly designated GRSM (Henry and Conley 1970, 1972; Bratton 1974, 1975; Singer et al. 1981; Peine and Farmer 1990).

Populations of feral hogs pose a significant threat to the > 70 unique plant community associations consisting of > 1,600 flowering plants, over 450 bryophytes, > 60 ferns, and 833 known species of lichens of the GRSM ecosystem (Bates et al. 2018). Bratton (1974) documented feral swine in GRSM uprooting, eating, and trampling 50 plant species. These plants included sensitive species such as Virginia spring beauty (*Claytonia virginica*), Dutchman's breeches (*Dicentra cucullaria*), Turk's-cap lily (*Lilium superbum*), fringed phacelia (*Phacelia fimbriata*), star chickweed (*Stellaria pubera*), and red trillium (*Trillium erectum*). Feral swine have also negatively impacted sensitive fauna of GRSM, including the red-cheeked salamander (*Plethodon jordani*) and the Jones middle-tooth snail (*Mesodon jonesianus*, Peine and Farmer 1990). Rossell (2016) found that rooting by hogs in rich montane seeps in the Park negatively

affected associated plant species richness and salamander density on the soil surface. Feral swine can also serve as a reservoir for several diseases that can spread to domestic livestock and humans, such as swine brucellosis (*Brucella abortus*), trichinosis (*Trichinella spiralis*), hoof and mouth disease, giardia (*Giardia lamblia*), and pseudorabies (Peine and Farmer 1990). Unfortunately, pseudorabies was detected in the Park in 2005, and resident feral swine are the only known natural reservoirs for the virus (Cavendish et al. 2008). In 2017, the seroprevalence of pseudorabies from feral swine culled by Park staff was 22% (W. Stiver, NPS, unpublished data).

Because of the negative impacts of feral hogs, officials at GRSM started a population control program in 1959. Over the decades, officials at GRSM have utilized numerous control techniques such as free-range hunting, trapping (i.e., box traps and corrals), and drop nets to capture and kill feral swine; > 13,000 feral swine have been lethally removed from GRSM. Still, the large size of the Park and large areas of rugged and inaccessible topography make trapping and hunting of feral hogs extremely difficult. Although the control efforts have required extensive working hours and monetary and training resources, hogs continue to occupy and damage the natural resources of the Park. No direct studies on population size or growth have been conducted on feral swine in GRSM, and local studies on movements and home range size of feral swine have been limited to a study of 14 radio-collared individuals in GRSM in the late 1970s (Singer et al. 1981). In that study, feral swine were located using Very High Frequency (VHF) radio collars, which had low positional accuracy (Recio et al. 2011), and data were collected manually, which typically results in low numbers of location fixes collected only during daylight hours (Singer et al. 1981). The advent of Global Positioning System (GPS) collars has enabled researchers to collect animal position data at higher frequencies (i.e., shorter time intervals between locations), with greater spatial accuracy, in remote areas, and during all weather conditions and time of day (Recio et al. 2011).

To assist resource managers in understanding where feral swine are more likely to be vulnerable to trapping and hunting control efforts, our objective was to develop models of relative probability of use for feral swine in the Park based on remotely sensed landscape data and GPS telemetry data. Johnson

(1980) described a hierarchical framework for studying habitat selection at four levels of resource selection. First order is selection of the physical or geographical range of a species; 2nd order is selection of a home range of an individual or social group; 3rd order is selection of various habitat patches within the home range; and 4th order is selection of specific resources within a habitat patch. We considered the 2nd and 3rd orders of selection to be most relevant to management of feral hogs in our study. Previous work on feral hog habitat selection has focused on assessing only one order of selection (e.g., Thurfjell et al. 2009, Oliveira-Santos et al. 2016, Kramer et al. 2022) or has not accounted for the temporally varying landscape that is available for selection during within-home-range movements (e.g., Clontz et al. 2021). We hypothesized that the relative probability of use by feral hogs would be influenced by the order of selection (2nd vs 3rd orders), in addition to vegetation type, elevation, and general landform. By comparing models across the 2nd and 3rd order of habitat selection (Johnson 1980), we assessed the potentially hierarchical nature of feral swine habitat selection (i.e., multi-level; McGarigal et al. 2016) within the unique and highly variable habitats of GRSM. Opposing effects of habitat variables across the two orders of selection or across seasons could produce sub-optimal management actions if only one level of selection or one season were used for inference. Our goal was to help managers plan and focus feral hog control resources in areas with higher likelihoods of success.

Study area

Great Smoky Mountains National Park was chartered by the U.S. Congress in 1934. GRSM lies in the southern Appalachian highlands, which are in the Blue Ridge, Ridge and Valley, and Piedmont physiographic regions. The Park is 2114 km² in size and is located along the border of eastern Tennessee and western North Carolina. Elevation in GRSM ranges from 266 to 2025 m. Dominant forest types included montane alluvial, early successional, cove, hemlock (*Tsuga canadensis*), montane oak-hickory (*Carya* spp., *Quercus* spp.), xeric ridge, and high-elevation hardwoods. Oaks were the predominant tree species with hickory, ash (*Fraxinus* spp.), and yellow poplar

(*Liriodendron tulipifera*) being other common species. Frasier fir (*Abies fraseri*) and red spruce (*Picea rubens*) occurred at the highest elevations where rainfall averaged 215 cm/year (Bates et al. 2018). The floral and faunal assemblages of the Park are highly diverse owing to highly variable microclimates associated with high spatial heterogeneity from widely varying elevations, slopes, and aspects. The high ecological diversity of the area led to GRSM being designated as an International Biosphere Reserve in 1988.

Materials and methods

Capture and handling

We began trapping feral swine for radio collaring in fall 2015 and continued through summer 2017. We placed cage traps and drop nets baited with a mixture of dried, shelled corn and mineral salt (Helm 2019) near signs of feral swine activity. We checked traps daily during morning hours from November to March. To immobilize swine, we used 1 ml BAMTM per 45 kg estimated body mass (i.e., 0.6 mg/kg butorphanol, 0.2 mg/kg azaperone, 0.2 mg/kg medetomidine; Wildlife Pharmaceuticals/ZooPharm, Fort Collins, Colorado, USA). We used pole syringes (Cap-Chur, Powder Springs, Georgia, USA), dart projectors (Dan-Inject North America, Fort Collins, Colorado, USA, with darts from Pneu-dart, Williamsport, Pennsylvania, USA), or a hand injection with syringe and needle to deliver the anesthetic intramuscularly into the hip or shoulder of each animal.

Anesthetized feral swine were fitted with foot hobbles. We applied sterile artificial tear lubricating ointment (Rugby Artificial Tears, Rugby Laboratories, Inc., Livonia, Michigan, USA) to prevent desiccation of the eyes and placed blindfolds over the head and snout for stress reduction. We equipped adult feral swine with GPS/VHF collars (Vectronic Aerospace GmbH, GPS Iridium, Berlin, Germany) programmed to communicate positional data via GPS satellite and VHF beacon. We did not collar juvenile feral swine because of anticipated weight gain, which could have made collars too restrictive (Kozlo and Nikitenko 1967). We reversed the effects of the BAMTM anesthetic with atipamezole (25 mg/ml or 1 mg/kg) and

naltrexone (50 mg/ml or 25 mg/animal) via intramuscular injection.

We programmed the collars to record a single point location every hour and to upload those data via satellite every 4 h. Collars that were stationary for > 8 h sent a VHF mortality signal, and the collar would automatically notify us via text message and email. All location data could not be uploaded via satellite, which made it necessary to physically retrieve the collar to access the full dataset. Collars were recovered following dropped collar notifications, (i.e., mortality signal) mortality events, or management kills.

GPS data

After recovering the collars and downloading the full on-board dataset, we minimized GPS location error by excluding locations based on positional dilution of precision (PDOP) values and position fix type (2D or 3D; Lewis et al. 2007). Specifically, we removed 2D locations with a PDOP > 5 and 3D locations with a PDOP > 10. All pre- and post-deployment locations as well as multiple locations at mortality sites were eliminated (Leonard 2017). We classified the locational data by sex and season and we only retained data from feral swine for which we had ≥ 30 days of locations within a season.

Helm (2019) reported that home ranges of male feral hogs in GRSM averaged 28.2 km² (SD=19.8, range=3.5–77.8 km²) and female home ranges averaged 11.6 km² (SD=9.7, range=2.9–38.7 km²). Given the assumed generalist nature of the species, the smaller home ranges of females suggested greater habitat specificity, and presumably, greater success in predicting resource use. Moreover, the nuclear social unit of swine is based around one to several females and their offspring, and adult males associate with the females when they are sexually receptive (Conley et al. 1972; Graves et al. 1975). Lastly, female swine mortalities have a greater impact on population growth than male mortalities in this polygamous species (Bieber and Ruf 2005). Therefore, we restricted our modeling analysis to female feral swine. We focused on summer and winter nocturnal periods when most feral swine trapping and hunting in GRSM has taken place. Specifically, we subset location data to females, from dusk to dawn (using the definition of civil dawn and dusk), during summer (20 June–21 September 2015 to 2017) and winter (15

December–15 April from 2015 to 2017), within the Park boundary (Signer et al. 2019).

Environmental variables

We created 12 predictors of resource use based on landscape characteristics reported in the literature that could be important to feral swine. The predictors quantified landforms, land cover types, and human influences on the landscape. To facilitate comparison of effect sizes, all continuous variables were standardized to have a mean of zero and standard deviation of one.

We created three variables representative of landform characteristics: elevation, slope, and aspect. To reduce skewness in the locational data and facilitate maximum likelihood estimator convergence, we converted the elevation data from a regional digital elevation model (DEM) using a natural log. We used the original DEM to calculate slope and aspect with a Beers transformation within the Park boundary (Beers et al. 1966).

We created six layers to account for land cover-related metrics relevant to feral hogs at fine and coarse scales. When hard mast (e.g., acorns) was abundant, it constituted up to 84% by volume of the documented diet of feral swine in the Great Smoky Mountains (Howe and Bratton 1976; Singer et al. 1981). To account for this major diet component, we used 30-m² regional land cover derived from the 2011 Appalachian region USGS National Gap Analysis Project (<https://gapanalysis.usgs.gov/gaplandcover/data/download/>). From those data, we created a binary oak presence layer by reclassifying the Central and Southern Appalachian Oak Forest and Central and Southern Appalachian Oak Forest-Xeric cover types as “oak”; all other cover types were reclassified as “other.” Similarly, we created a binary cove forest presence variable by reclassifying the Southern and Central Appalachian Cove Forest types into a raster, including “cove” and “other” (Singer et al. 1981; Howe and Bratton 1976). We found no seasonal difference in feral hog average daily movement, so we used a circular moving-window analysis with a radius of 612.6 m, based on average winter weekly shifts of home range centroids of female feral swine home ranges in GRSM, to create coarser estimates of percent oak and percent cove from the fine-scale binary layers (Helm 2019). Next, we created percent

canopy and percent human development layers using the same structured moving window analysis. The percent canopy cover layer was based on the 2016 National Land Cover Dataset Canopy Cover Dataset (NLCD, USDA Forest Service 2019), and the percent development layer was calculated by combining the land cover categories of barren land, developed open space, developed low-intensity, developed medium-intensity, and developed high-intensity (Yang et al. 2018). In GRSM, these categories primarily comprised roadways, parking lots, camping areas, paved trails, and Park buildings and residential areas.

Lastly, we calculated three distance-based variables; all were log transformed to address skewness. We calculated Euclidean distance from the land cover categories designated as development as previously described. Given that feral swine depend on water for hydration and wallowing, we created a 5-m buffer around the GRSM water polylines from the USA Detailed Streams dataset (Esri 2018). We then calculated the Euclidean distance to the buffered water layer. Lastly, we used TIGER/Line® roads data (U.S. Census Bureau 2017) to calculate a Euclidean distance to trails layer.

Habitat selection models

We anticipated that the high spatial heterogeneity of the landscape in GRSM may impact modeling in unique ways. We hypothesized that wild hogs may select different habitat attributes when selecting areas within their home-range (3rd order) when compared to selection of broader home-range placement (2nd order). We used a resource selection function (RSF, Manly et al. 2007) to evaluate habitat selection at the 2nd order level and a step selection function (SSF, Fortin et al. 2005) for 3rd order selection for both the summer and winter seasons. The two techniques differ in how available resources are defined. The SSF defines available resources conditional on the location of an individual at a given point in time and their movement ability given the time between observations; SSFs are typically used when the time between observations is small relative to the size of the home-range and there is serial dependence in the locations (Fieberg et al. 2021). In contrast, the interpretation of the RSF is dependent on the definition of the available points in the used-available study design framework (e.g., we chose available points from within a

study area to describe home-range placement; DeCesare et al. 2012).

Given that we had data on multiple individuals, we fit both types of models using random-effects models as proposed by Muff et al. (2020). The random-effects models allowed us to account for the inter-individual heterogeneity of space use. For the SSFs, only pairs of locations that were collected within 1 h (± 10 min) of each other were used for creating the sequence of used steps. We generated nine random step lengths and turning angles for each observed step by fitting the observed step lengths to a gamma distribution and observed turning angles to a von Mises distribution (Avgar et al. 2016; Signer et al. 2019). We fit the model with a Poisson likelihood with stratum-specific random intercepts and a large, fixed prior variance, which is likelihood-equivalent to the more traditional SSF analysis using a conditional logistic regression but allows for efficient estimation of random effects (Muff et al. 2020). We included individual-specific random slopes for each predictor to account for individual variation in responses to landscape attributes. We used landscape data from the end of each observed and random step thereby relaxing the assumption that movement pathways between consecutive locations consisted of a straight line (Fortin et al. 2005). Lastly, we also used standardized step length as a fixed effect in the model to account for any bias induced by using parametric distributions to sample available step lengths (Forester et al. 2009; Avgar et al. 2016; Fieberg et al. 2018).

For the RSFs, we thinned the used locations to one location per night to minimize the effects of spatial autocorrelation; we only retained individual hogs that had a minimum of 15 nightly locations per season. To approximate the placement of alternative home-ranges available to hogs (2nd-order selection), we calculated the average weekly distance moved using the average daily movement distance (sum of the Euclidean differences between observed locations within 24 h. across the entire set of locations for an individual, minus the day of collaring and the last day of acquired data) multiplied by seven. Then, we used that value to buffer a 95% minimum convex polygon (MCP) of all used locations for each individual. Next, we sampled ten times the number of used locations per individual to create an “available” background random subsample. This available background sample therefore included locations from a significantly

larger area than the 95% MCP, and represented local areas available for alternative home ranges.

To fit the RSF models, we used the logistic regression formulation of the resource selection function without case–control pairing (Johnson et al. 2006; Aarts et al. 2012). We used individual-specific, random intercepts with a large, fixed prior variance to account for the sampling ratio of used versus available points and the unequal distribution of habitat among home ranges (Warton and Shepherd 2010; Muff et al. 2020). We also used individual-specific random slopes for the landscape predictors of interest to account for inherent individual variation in responses. To estimate the coefficients, we used the weighted likelihood approach in which used points received a weight of one and available points received a large weight (1000), ensuring that the statistical connection between the logistic regression formulation and the inhomogeneous Poisson point process held (Fithian and Hastie 2013; Muff et al. 2020; Fieberg et al. 2021).

For both the SSF and the RSF models, we fit a series of models in which each predictor was included as the sole predictor of interest and used a p -value of 0.05 to determine if a predictor should be retained in the full model. No retained predictors were correlated above a threshold of 0.6; therefore, we fit a full model for the SSF and RSF, for both seasons, with all predictors that were significant in the single-predictor models. We used the R (R Core Team 2021) package `amt` (Signer et al. 2019) to process the location data for the SSF and RSF analysis and the `glmmTMB` (Brooks et al. 2017) package to fit the mixed-effects models in R.

Model validation

Given the lack of independent test data and small sample size of feral hogs, we evaluated the general predictability of both our SSF and RSF models via both the Boyce Index (BI) based on a k -fold cross validation process (Boyce et al. 2002). For our k -fold cross-validation, we removed one set of locations for a given hog and the rest of the hogs were considered as the training set to compare with the background points. Then, we calculated the Spearman rank correlation between the realized versus expected proportion of predictions in each class, based on the proportion of the landscape that fell in

each class. Correlation values near zero indicate the model is equivalent to a random model. Positive values closer to 1 indicate the model is reflecting true probability of presence and values closer to -1 indicate the output is representing the areas of absences or pseudo-absences. Because of our relatively small sample sizes and the arbitrary nature of selecting a number of classes or bins for ratio comparisons, we calculated the Boyce ratio for 5 equally distributed bins (quantiles) of the scaled SSF/RSF values from the random background locations. Spearman-rank correlations ($r_s > 0.5$) between bin ranks and area-adjusted frequencies for model sets would indicate a strong relationship and supported the validity of the model. We note that there are concerns that the BI are not generalizable to SSFs due to the stratified nature of the presence-background data, but to our knowledge there is no proposed alternative metric for summarizing the predictive ability of an SSF (Fieberg et al. 2018).

Next, to facilitate a useful interpretation of the magnitude of the selection coefficients, we used an approach that related the strength of selection to change in habitat conditions across space. To do so, we compared two metrics, the relative selection strength (RSS; $\exp(\beta)$) and the log-RSS (β), where β is a regression coefficient or effect size, across the SSF and RSF models. These metrics helped interpret the effect size of the various habitat covariates and identify mismatches between the levels of analyses and relevant ecological processes (Avgar et al. 2017; Fieberg et al. 2021). Because our predictor variables were standardized, the RSS was interpreted as the relative intensity of use of locations that differed by 1 SD unit of the predictor variable and was equivalent to the exponentiation of the predictor coefficient, keeping all other predictors constant. The log-RSS was interpreted such that positive values represented selection for and negative values represented avoidance of larger values of the predictor variable (Avgar et al. 2017; Fieberg et al. 2021). We used the estimated log-RSS values and the values of each set of covariates to calculate the SSF (excluding the effect of step length) and RSF (excluding the intercept term) surfaces of relative selection strength across GRSM; both selection functions were scaled by their maximum value such that the area with the greatest relative selection strength was equal to one.

Combining levels of selection

We considered two methods for combining relative selection probabilities across levels of selection for each season. The first method is multiplicative, where multiple levels of selection can be multiplied together if one assumes they are conditionally independent (Johnson et al. 2004; DeCesare et al. 2012). Given this approach, we multiplied the scaled SSFs by the scaled RSFs to create an integrated visualization of selection across the two levels for each season. For visualization, these values were also scaled such that the greatest relative selection strength was equal to one.

For the other method, we generated a consensus model, which identified areas where the two levels of selection agreed on areas of high relative selection strength. We reclassified the SSF and RSF according to median, with values greater than the median being equal to 1 and values less than the median being equal to 0. Then, we added both models together to create a simple consensus model with resulting values of 0 (neither model selected), 1 (one model selected), or 2 (both models selected; Fielding and Bell 1997; Araújo and New 2007; Zhang et al. 2015; Poor et al. 2020). We used this simple consensus or frequency approach as well as the comparison of the relative probability of selection for both models to understand the limits of each model as well as areas of model agreement.

Results

Sixteen female feral swine were captured and collared from 2015 to 2017. Female feral swine in GRSM were radio collared for an average of 191 days (range=18–380 days). Ten individually collared females were available during summer and twelve individuals during winter from 2015 to 2017. The average number of locations per individual for summer was 602 (range=74–1,019); when thinned to one location per night for the RSF, each individual averaged 70 used locations (range=13–111; Fig. 1). The average number of locations per individual for winter for the SSF was 945 (range=121–1,527); when thinned to one location per night for the RSF, each individual averaged 82 used locations (range=17–128). For buffering of the 95% MCP,

the average weekly distance moved by feral hogs was 2,255 m in winter and 2,073 m in summer.

Summer models

For the summer SSF, we found that slope, aspect, presence of oak, distance to development (log), and distance to water (log) were significant predictors in the model (Table 1). All significant parameters had a negative relationship with feral hog presence except distance to water. The SSF BI average correlation was 0.58 (range=−0.34 to 0.97). The RSF for the summer season identified only slope, percent canopy, and distance to development (log) as significant predictors (Table 1), and the mean BI correlation was 0.58 (range=−0.02 to 1.00). Slope and distance to development were two consistent predictors in both models for summer. Across both scales of summer models, a negative relationship with slope and distance to development resulted in similar individual maps of relative selection strength (Table 1, Fig. 2).

Winter models

For the winter SSF, we found that elevation (log), slope, percent oak, percent development, distance to trail (log), and distance to water (log) were significant predictors in the model (Table 2). The average BI correlation was 0.53 (range=−0.06 to 0.93). The winter RSF identified elevation (log), slope, presence and percentage of oak, percent canopy, and the distance to development (log) as significant predictors (Table 2). The mean of the BI correlation statistic was 0.75 (range=−0.09 to 1.0). As opposed to the summer models, the parameters included in these two models reflected different levels of selection, with only elevation, slope, and percent oak supported in both the RSF and SSF models. Based on the log-RSS values, elevation was positive at the finer SSF level but negative at the RSF level (Table 2); however, both models had a negative mean effect size for slope, as did the summer models (Table 1). Percent oak also had different relationships across the two models, negative at the 3rd level but positive at the 2nd level of selection (Table 2). Because of these opposing relationships, the maps of relative selection strength differed. Specifically, the SSF predicted high relative selection strength in the center of the Park, where elevations were highest and percent oak and canopy cover were

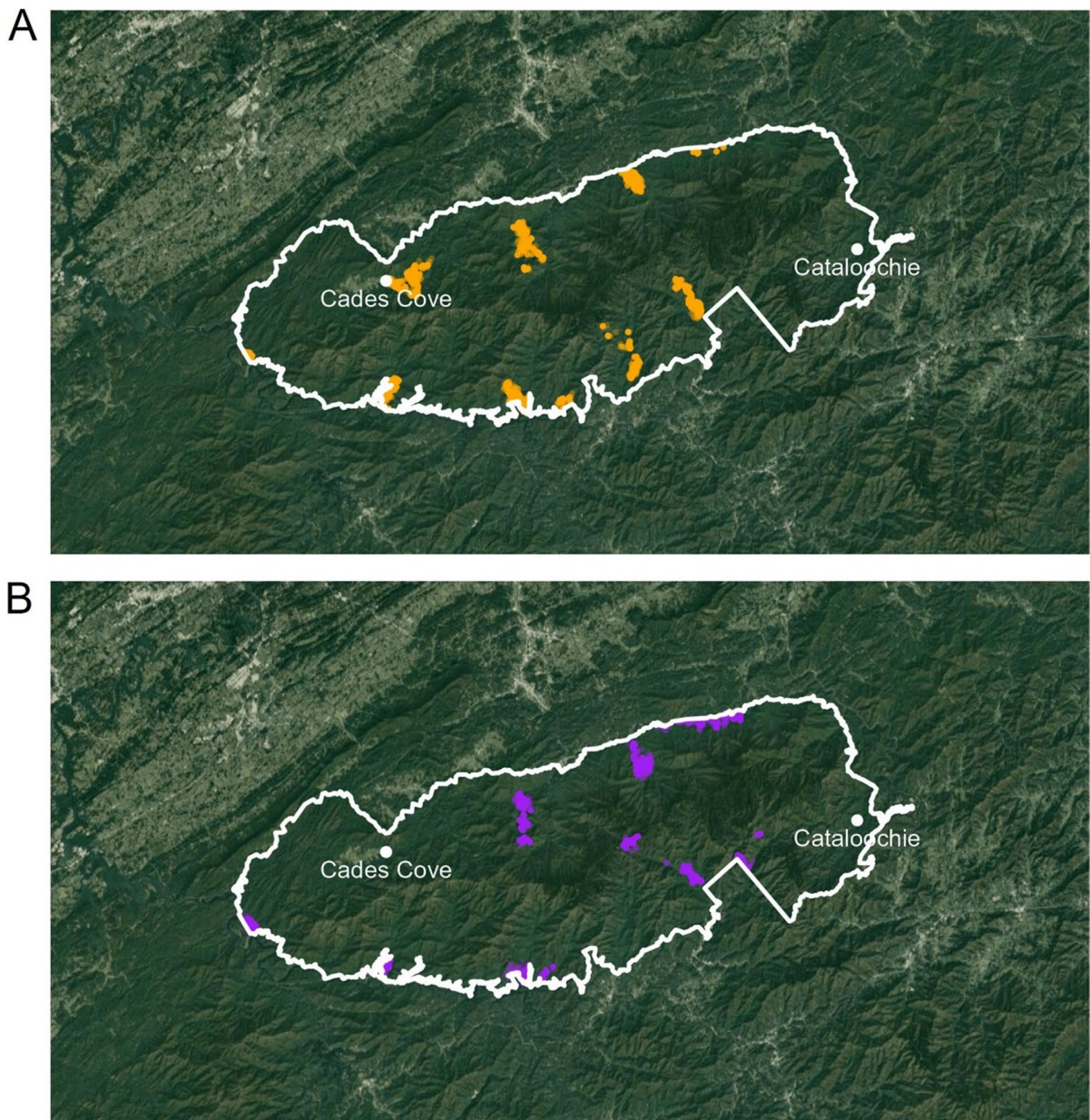


Fig. 1 Female feral swine winter, dusk and night locations (orange; A) and summer, dusk and night (purple; B) within in Great Smoky Mountains National Park, 2015–2017

lower than surrounding areas. In contrast, the RSF indicated low selection in the same area (Fig. 3).

Combined and consensus models

We identified small nuanced changes when the summer RSF and SSF models were combined, whereby

lower slopes and areas along roads were selected, regardless of elevation (Fig. 4). When we combined the obviously divergent winter models, the low RSF values generally negated the fine-scale selection characterized by the SSF, but the SSF added more nuance to the patterns of selection in areas where the RSF indicated high relative selection (Fig. 4).

Table 1 Relative selection strength (i.e., $\exp(B)$), log relative selection strength (i.e., β) and 95% confidence intervals for the summer season SSF and RSF analyses for feral hogs in Great Smoky Mountains National Park, 2015–2017

Predictor	Mean SSF	95% CI	Mean RSF	95% CI
<i>Relative selection strength</i>				
Slope	0.58	0.44:0.76	0.66	0.44:0.99
Aspect	0.96	0.92:0.99		
Oak presence	0.89	0.76:1.04		
Distance to development (log)	0.78	0.60:1.03	0.60	0.40:0.92
Distance to water (log)		1.37	1.11:1.68	
Percent canopy			3.40	1.06:10.85
<i>Log relative selection strength</i>				
Slope	-0.55	-0.83:-0.27	-0.42	-0.82:-0.01
Aspect	-0.05	-0.27:-0.08		
Oak presence	-0.12	-0.27:0.04		
Distance to development (log)	-0.24	-0.52:0.03	-0.50	-0.92:-0.09
Distance to water (log)		0.31	0.11:0.52	
Percent canopy			1.22	0.06:2.38

When identifying consensus across the models, the summer consensus model reflected moderate to moderately high agreement among the two models for what would be considered high-quality hog habitat, based on the median model value as a threshold for “selected” habitat (Summer RSF=1.35; Summer SSF=3.83; Fig. 5). In comparison, the winter consensus model reflected the low agreement between the winter models in terms of what would be considered high-quality hog habitat, based on our median threshold (Winter RSF=0.005, Winter SSF=0.06; Fig. 5).

Discussion

Modeling

Our study was the first in-depth, telemetry-based resource selection study of feral hogs in GRSM. However, this required a multi-level modeling approach given the unique variability, specifically in elevation and slope, of the ecosystem. Interestingly, contradictory results across the two levels of selection have been reported by others (DeCesare et al. 2012; Wilson et al. 2014). Given that landscapes created from stationary SSFs assume that an individual is equally likely to be anywhere within the area being evaluated, even if in reality individuals are non-randomly

distributed, contradictory results are logical (Signer et al. 2017). We anticipated the potential issue of divergent models given (1) we were modeling a species in a relatively small portion of a highly diverse study area and (2) we had a priori knowledge from Park staff that feral swine were not distributed equally across the landscape. Regardless, we found straightforward consistencies from the two scales of summer models and the multiplication of the SSF and RSF created a more nuanced, but logical map of selection. However, when this multiplication was attempted for the winter season, very high levels of selection occurred in highly specific, clustered areas with very low availability across the Park, such as the lowest and flattest areas along the western edge. Those combinations resulted in significant scaling issues in the resulting product, which led us to quantify relative selection using quantiles, as recommended by Morris et al. (2016). The degree of divergence and the relatively few areas of consensus between the two models was surprising given the previously documented generalist nature of feral swine and supported recent findings of some degree of scale-dependence in their decision making with respect to specific landscape attributes (Mahoney et al. 2018; Paolini et al. 2018; Whittington et al. 2022). When we combined the winter models, low RSF values generally negated the fine-scale selection characterized by the SSF. That is, hogs would not select for a home-range in winter in

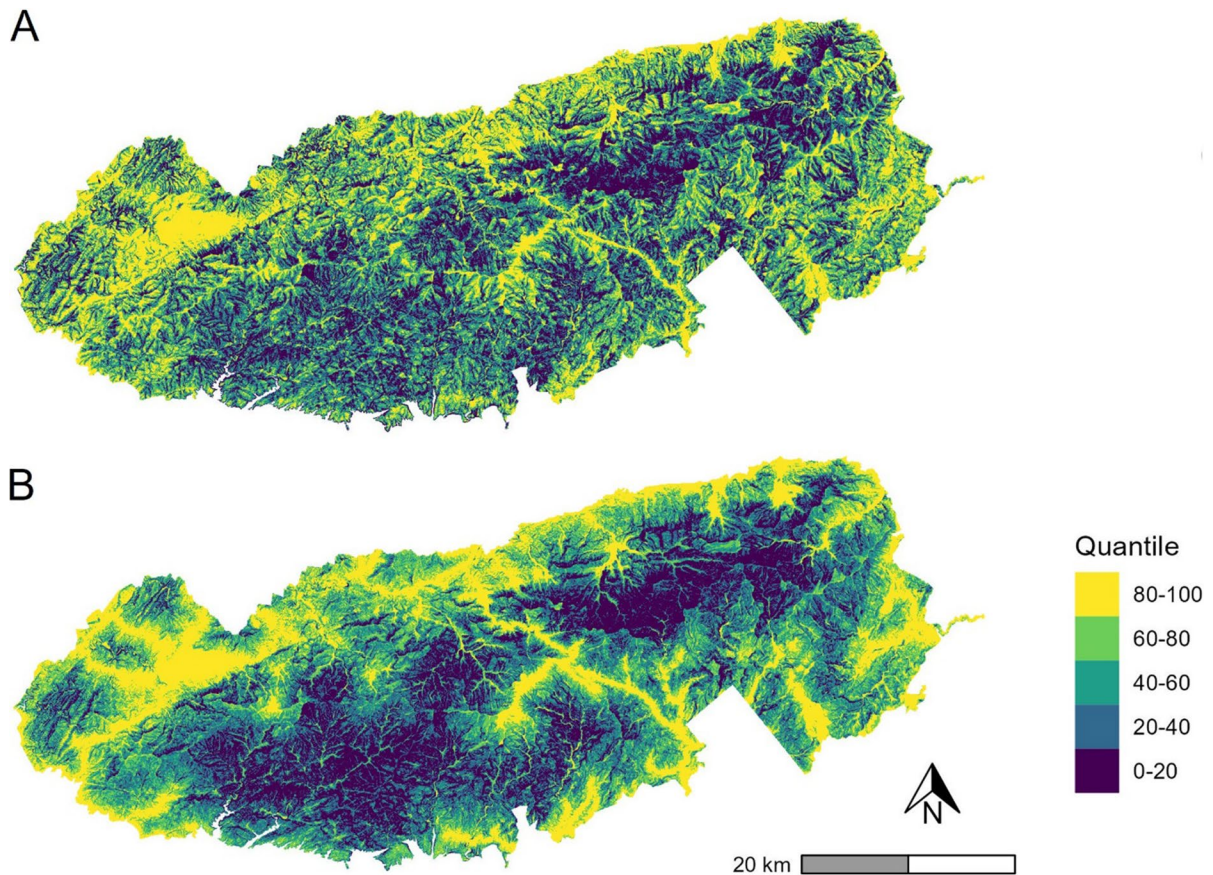


Fig. 2 Relative selection surface generated by the summer season SSF analysis (**A**) based on the predictors of elevation (log), slope, percent canopy, percent development, distance to water (log), and distance to trail (log) and the RSF analysis (**B**) including elevation (log), slope, oak presence, percent

oak, percent canopy, distance to water (log), and distance to trail (log). The model predictions, illustrated in quantiles, were based on the fixed-effect log-relative selection strength values for feral hogs in Great Smoky Mountains National Park, 2015–2017

some areas, so they would not be there to select at the local level. However, we also saw that in areas where the RSF indicated high relative selection strength, the SSF added more nuance to the patterns of selection (i.e., because the RSF indicated that hogs were likely there at the broad scale, these were the local areas that would be selected).

Creating independent SSF and RSF models can be useful because one may be more relevant for management purposes than the other (Froehly et al. 2020). The RSF represents larger-scale selection that may inform initial settlement behavior but not how selection might shift after a feral swine had selected an acceptable area for wintering behavior and energetic requirements. If users need to extrapolate to a larger, diverse area without existing knowledge of species

presence, we suggest the RSF. The SSF represents selection along a path traversed by a feral swine within their home range; however, because there was no adjustment for areas where feral swine were present at the landscape-level, it could provide counterintuitive inference. However, if site-specific management is the primary goal and users have a priori knowledge that the species is in the area, the SSF may provide better insight into specific management options. The 3rd-2nd order comparisons and consensus models created more clarity around constraints of fine-scale habitat selection given the large-scale home range placement within GRSM (DeCesare et al. 2012; Jakes et al. 2020) and allowed us to see where selection behavior was manifesting as divergences and agreements across seasons and ecological levels. This

Table 2 Relative selection strength (i.e., $\exp(B)$), log relative selection strength (i.e., β), and 95% confidence intervals for the final SSF and RSF analysis for feral hogs in the winter seasons Great Smoky Mountains National Park, 2015–2017

Predictor	Mean	95% CI	Mean	95% CI
	SSF		RSF	
<i>Relative selection strength</i>				
Elevation (log)	5.35	2.38:12.03	0.11	0.03:0.39
Slope	0.65	0.55:0.77	0.77	0.609:1.00
Oak presence			1.41	0.77:2.56
Percent oak	0.32	0.15:0.71	3.07	1.06:8.87
Percent canopy			3.97	0.90:17.47
Percent development	1.18	0.95:1.47		
Distance to development (log)			0.74	0.36:1.51
Distance to trail (log)	1.57	1.31:1.89		
Distance to water (log)		1.22	1.06:1.40	
<i>Log relative selection strength</i>				
Elevation (log)	1.68	0.87:2.49	-2.19	-3.42:-0.95
Slope	-0.43	-0.60:-0.26	-0.26	-0.52:0
Oak presence			0.34	-0.26:0.94
Percent oak	-1.13	-0.92:-0.34	1.12	0.06:2.18
Percent canopy			1.38	-0.10:2.86
Percent development	0.16	-0.06:0.38		
Distance to development (log)			-0.30	-1.02:0.41
Distance to trail (log)	0.45	0.27:0.64		
Distance to water (log)	0.19	0.06:0.33		

analysis framework can be applied to other systems to highlight areas in which different levels of habitat selection may result in incongruous results when observing only one level of selection.

If data limit the ability to do intensive modeling that explicitly integrates both levels of selection, we present a simple solution of comparison and consensus. Additionally, as seen here, representing the relative probability surface with quantiles (Morris et al. 2016) may be more appropriate when deciding where to expend limited management resources. We note recent efforts have been made to address the potential disconnect between SSFs and RSFs using complex approaches, such as Markov chain Monte Carlo algorithms to account for the different levels of use (Michelot et al. 2019) or simulation approaches to relate SSF results to utilization distributions (Signer et al. 2017). Unfortunately, creating a useable joint utilization distribution is not yet straightforward, especially when modeling multiple individuals using random-effects models. So, we illustrate one simple, non-integrated, useful method for combining relative probability of use from an SSF and an RSF by

multiplying the two relative probability surfaces together (DeCesare et al. 2012; Jakes et al. 2020).

We recognize that the predictability of these models, especially the SSFs, was limited. That result was not completely surprising given past documented variability in individual habitat usage, especially for female feral hogs (Keuling et al. 2008). We had several individuals that were highly varied in their selection pattern and while we included random effects that allowed individual deviations from any overall tendency, when we predicted to a “random” subset, we predicted using the mean fixed effects across all individuals. Interestingly, the two combined maps were still consistent with past research, past culling locations, and qualitative information received by Park rangers and Park biologists (Levy 2016, Keller et al. 2003, W. Stiver, NPS, personal communication). Additionally, we considered the possibility that trapping efforts were preferentially sampling feral hogs that preferred low elevations, due to ease of access; however, to assess this, we fit the RSF models without elevation and the overall seasonal patterns remained the same.

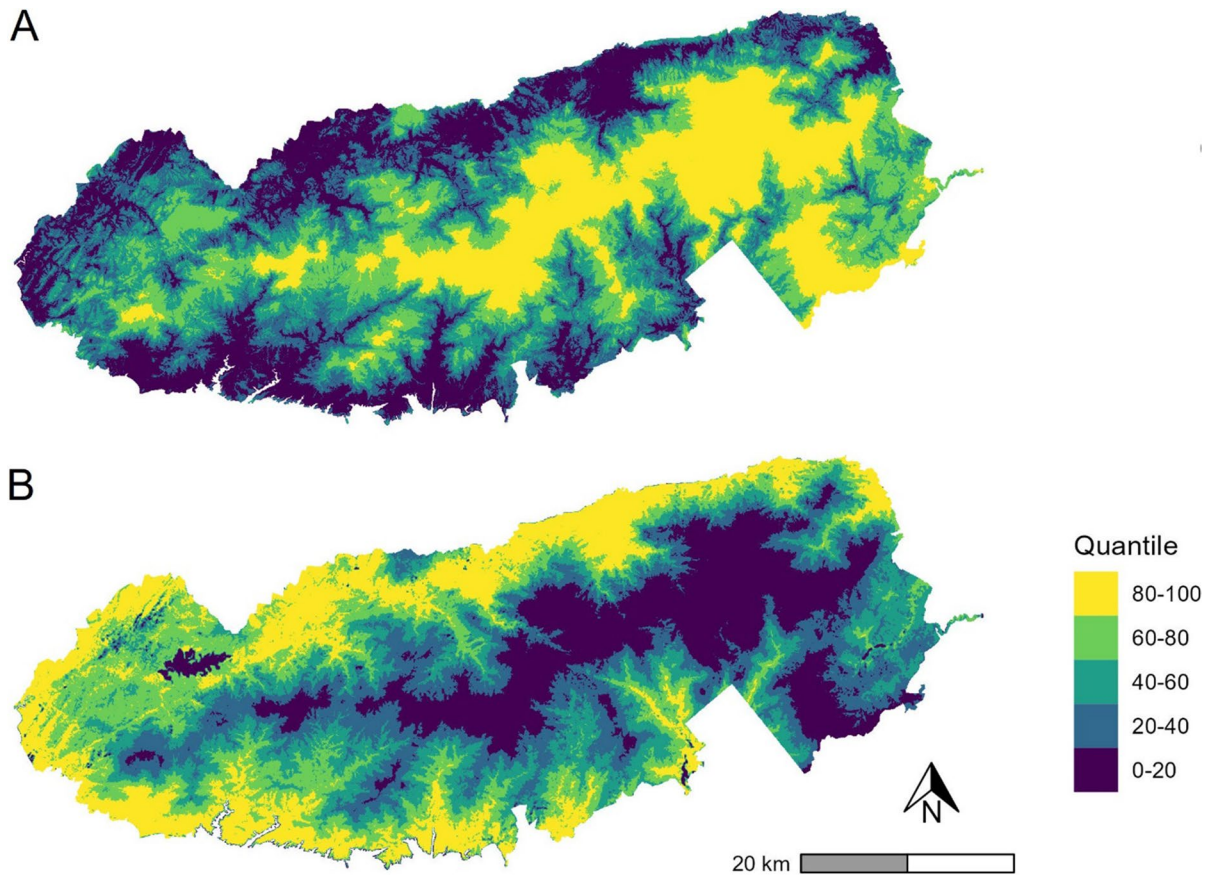


Fig. 3 Relative selection surface generated by the winter season SSF analysis (A) based on the predictors of elevation (log), slope, percent canopy, percent development, distance to water (log), and distance to trail (log) and the RSF analysis (B) including elevation (log), slope, oak presence, percent

oak, percent canopy, distance to water (log), and distance to trail (log). The model predictions, illustrated in quantiles, were based on the fixed-effect log-relative selection strength values for feral hogs in Great Smoky Mountains National Park, 2015–2017

Feral hog habitat selection

As seen in past studies of feral hog habitat use, the relative selection strengths in our models illustrated the influence of the interrelated covariates of elevation, land cover type, and slope on their resource selection (Levy 2016; Raoul et al. 2019; Clontz et al. 2021). Our findings support changes in selection driven by temporally dynamic resources, indicating a likely seasonal habitat functional response. Generally, feral hogs in GRSM used flat areas along trails and roadsides in the summer, while in winter, they shifted to more remote, flatter areas at lower elevations with large amounts of oak, presumably for foraging on acorns. Area of high selection in the two combined models corresponded greatly with areas hogs were

routinely culled over the last few decades (Keller et al. 2003).

The development predictor in the summer model is consistent with Raoul et al. (2019), who concluded that feral swine in pastoral land were frequently found along roadsides, used roadways to traverse other habitats, and even suggested roads could be an efficient means to collect population monitoring data. In terms of water, the topographic nature of GRSM creates areas with higher elevation and often higher slopes that are intrinsically closer to water, and as the land flattens out, water sources spread farther apart. So, hogs being found farther from water could be an artifact of the modeling process that is driven by slope. Conversely, other studies have supported the non-selection of streams during high-forage seasons at

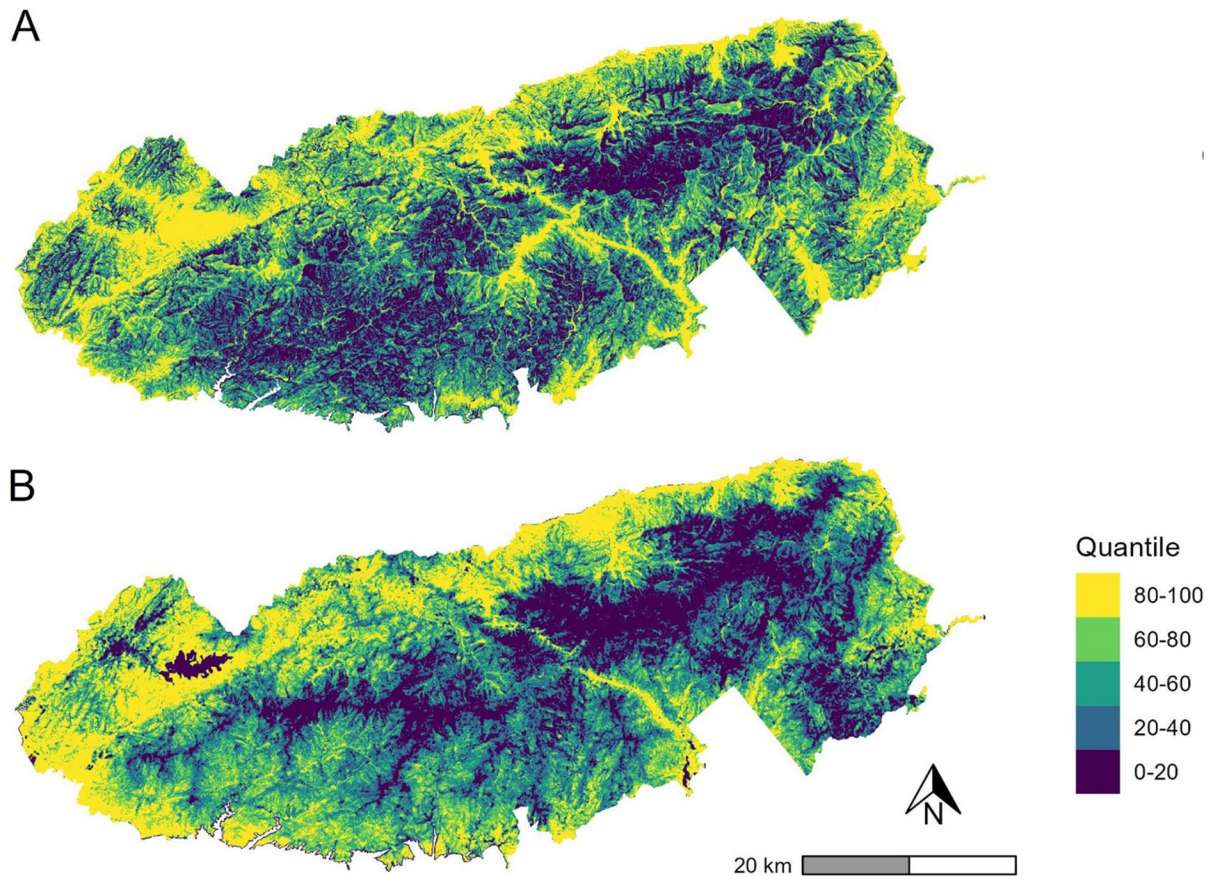


Fig. 4 Relative selection surface for summer (A) and winter (B) generated by multiplying the relative selection surface from the seasonal SSF analysis by that from the corresponding seasonal RSF analysis. The model predictions, illustrated in

quantiles, were based on the fixed-effect log-relative selection strength values from each of the models for feral hogs in Great Smoky Mountains National Park, 2015–2017

the home-range scale, which may be due to the availability of dense cover for thermoregulation (Thurfjell et al. 2009; Clontz et al. 2021).

Feral hogs can establish populations and home ranges in a wide array of landscapes, and our winter models reflected very different levels of selection, with only slope being inversely related with selection on a consistent basis. In winter, elevation was a primary determinant in the feral hog SSF, creating an unexpectedly large area of high relative selection in the center of the Park, even as non-oak forests (e.g., spruce-fir) became more dominant. We suggest that a combination of having high variability in individual hog selection behavior, high levels of selection occurring in unique and clustered areas of the Park, and the conditional availability of resources in the SSF created a lack of

clear modeling at that scale. In contrast, the more predictive winter RSF relative selection strengths were dominated by the covariates representing lower slopes and the closed canopied pine-oak, oak-hickory, and cove hardwood forests in low-mid elevations in GRSM. Selection in the winter RSF rapidly decreased with increasing elevation as the northern hardwood forests became more prevalent, which typically have a much lower percentage of oak species. We expected the SSF and RSF could be impacted by variables associated with hard mast availability (Singer et al. 1981, Baber and Coblenz 1986, Saunders and Kay 1991, Hayes et al. 2009, Franckowiak and Poché 2018, and Helm 2019). Fortunately, the combination of the SSF with the RSF likely dampened any biased results from the SSF, but in the future, including more understory

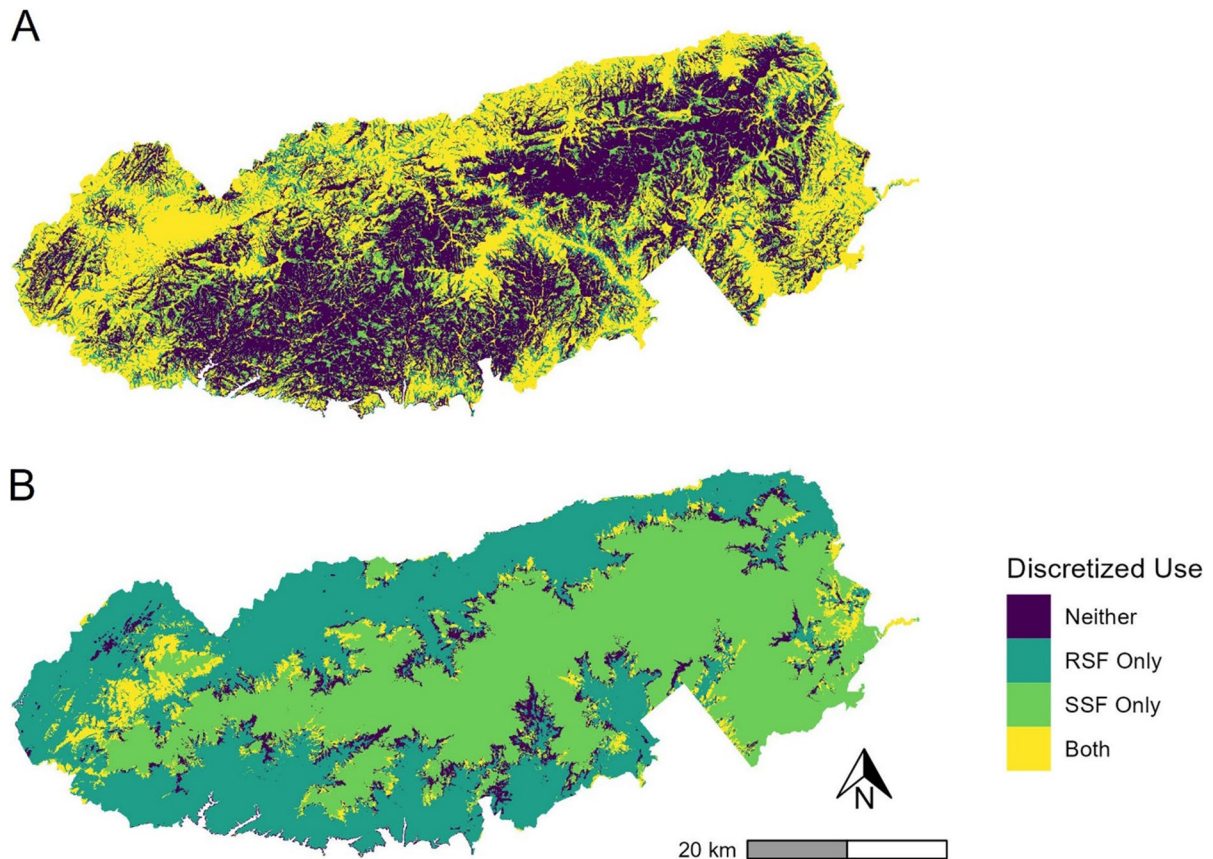


Fig. 5 Consensus model based on reclassified SSF and RSF models for feral hogs in the summer (**A**) and winter (**B**) seasons in Great Smoky Mountains National Park, 2015–2017.

The Discretized Use values indicate areas where neither model indicated selection, either the RSF or SSF model indicated selection, or both models were in agreement

variables, such as *Rhododendron* cover may better enable the 3rd-order selection modeling.

We documented another interesting pattern in the winter RSF model, and in a lesser degree in the SSF, around large open fields in GRSM including Cades Cove and Cataloochee Valley (Figs. 1, 2 and 3). The open fields had very low levels of selection in winter, likely from a complete lack of canopy cover, but the edges of the fields had very high preference. However, the low slope seemed to override any issues associated with an open canopy in the summer models.

Though feral swine are typically considered more of a generalist species throughout their range, our findings and others suggest that, their habitat selection can be constrained by season, topography, and land cover type (Keuling et al. 2008; Gray et al. 2020, Wilbur 2020). Our winter model differences confirmed our suspicions that the two models could

reveal levels of selection, and that the RSF would be more general, and the SSF, while informative within areas with feral swine, identified large areas that likely have very low hog selection. Furthermore, our study supported not only seasonality but also high individual heterogeneity. Though it may seem counter-intuitive, in certain species that do not have a narrow niche, there is more individual freedom of selection, which can create high individual heterogeneity, as we saw in our SSF. Regardless, these findings illustrated an in-season variation in selectivity that could be expected for a generalist as well as likely seasonal differences in selection.

Management implications

The seasonal combinations of the 3rd and 2nd order selection can more clearly guide the management of

this invasive species across the larger study area of GRSM. Managers can use these maps to determine where to focus their efforts given their knowledge about species presence, the timing of implementing control efforts, as well as the amount of effort and resources they have to expend. Our results imply that the most efficient hunting strategies would likely differ by season (Fig. 4). In fall, along with trapping efforts, any backcountry stalking efforts could occur in slightly higher elevations with the goal of pushing feral swine to lower, more preferred, and more accessible bait and trap locations. In winter, focusing on flat areas of deciduous forests and coves and around all field openings would be effective. Based on our study, focusing the highest concentration of hunting on the western and southwestern edges of the Park, as well as the eastern half of the northern border, would more effectively meet management goals. While trapping around fields like Cades Cover and Cataloochee Valley would still be areas of selection in the summer season, shifting hunting and trapping to lower sloped flats and areas around paved or gravel roads and trails, regardless of elevation, would be effective. More specifically, an effective management strategy would include hunting areas along all the major scenic drives in the Park (e.g. U.S. Route 441), areas along the Appalachian Trail, and areas around Balsam Mountain Campground.

The available background habitat in the SSF/RSF did not include any significant areas of the highest elevations in GRSM as available habitat. When feasible, future efforts to document any feral hog signs, along with potentially trapping and collaring/tracking feral hogs in the highest elevations, far off trails and away from roads would be beneficial. That locational information would be useful to understand if and how feral hogs utilize spaces in remote, higher elevations and would help clarify our limited inference regarding feral swine at the higher elevations in GRSM.

Acknowledgements The authors thank Bill Stiver for administrative assistance and the numerous technicians who assisted with data collection. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions RW, JY and JC conceptualized the study. PH, JC, FB, and JM designed the analysis. FB and JC performed the statistical analysis. PH, JC, FB and JM wrote the manuscript. All authors participated in editing of the final

version of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding Funding for this study was provided by the National Park Service, Eastern Band of Cherokee Indians, the Tallassee Fund, and was also supported by USDA National Institute of Food and Agriculture and Hatch Appropriations under Project #PEN04758 and Accession #1024904. This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use.

Declarations

Conflict of interest The authors declare no conflict.

Ethical approval The feral swine trapping protocol was approved by University of Tennessee Institutional Animal Care and Use Committee (Protocol # 2461-0516).

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References

- Aarts G, Fieberg J, Matthiopoulos J (2012) Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods Ecol Evol* 3:177–187
- Aplet GH, Anderson SJ, Stone CP (1991) Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. *Vegetation* 95:55–62
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Avgar T, Lele SR, Keim JL et al (2017) Relative selection strength: quantifying effect size in habitat-and step-selection inference. *Ecol Evol* 7:5322–5330
- Avgar T, Potts JR, Lewis MA et al (2016) Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods Ecol Evol* 7:619–630
- Baber DW, Coblentz BE (1986) Density, home range, habitat use and reproduction in feral hogs on Santa Catalina Island. *J Mammal* 67:512–525

- Barrett RH, Birmingham GH (1994) Wild pigs. In: Hygnstrom SE, Timm RM (eds) Prevention and control of wildlife damage, vol 2. University of Nebraska-Lincoln Press, Lincoln, Nebraska, USA, pp 65–70
- Bates PC, Miller JR, Styers DM et al (2018) Natural resource condition assessment Great Smoky Mountains National Park. Natural Resource Report NPS/GRSM/NRR—2018/1626 <http://npshistory.com/publications/grsm/nrr-2018-1626.pdf>
- Beers TW, Dress PE, Wensel LC (1966) Aspect transformation in site productivity research. *J For* 64(10):691–692
- Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *J Appl Ecol* 42(6):1203–1213
- Boyce MS, Vernier P, Nielsen S et al (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300
- Bratton SP (1974) The effect of the European wild boar (*Sus scrofa*) on the high-elevation vernal flora in Great Smoky Mountains National Park. *Bull Torrey Bot Club* 101:198–206
- Bratton SP (1975) The effect of the European wild boar, *Sus scrofa*, on gray beech forest in the Great Smoky Mountains. *Ecology* 56:1356–1366
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9(2):378–400. <https://doi.org/10.32614/rj-2017-066>
- Cavendish TA, Stiver WH, Delozier EK (2008) Disease surveillance of wild hogs in Great Smoky Mountains National Park- a focus on Pseudorabies. In: Proceedings of the 2008 feral hog conference, St. Louis, Missouri, USA. April 13–15
- Conley RH, Henry VG, Matschke GH (1972) European hog research project W-34. Tennessee Game and Fish Commission. Nashville, Tennessee, USA
- Clontz LM, Pepin KM, VerCauteren KC, Beasley JC (2021) Behavioral state resource selection in invasive wild pigs in the Southeastern United States. *Sci Rep* 11:1–14
- Cushman JH, Tierney TA, Hinds JM (2004) Variable effects of feral pig disturbances on native and exotic plants in a California grassland. *Ecol Appl* 14:1746–1756
- DeCesare NJ, Hebblewhite M, Schmiegelow F et al (2012) Transcending scale dependence in identifying habitat with resource selection functions. *Ecol Appl* 22:1068–1083
- Engeman RM, Smith HT, Severson R et al (2004) Damage reduction estimates and benefit-cost ratios for feral swine control from the last remnant of a basin marsh system in Florida. *Environ Conserv* 31:207–211
- Esri (2018) USA detailed rivers and streams. Layer developed by Esri and U.S. Geological Survey in cooperation with U.S. Environmental Protection Agency <https://www.arcgis.com/home/item.html?id=1e29e33360c8441bbb018663273a046e>
- Fieberg JR, Forester JD, Street GM et al (2018) Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. *Ecography* 41:737–752
- Fieberg J, Signer J, Smith B et al (2021) A ‘How to’ guide for interpreting parameters in habitat-selection analyses. *J Anim Ecol* 90:1027–1043
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49
- Fithian W, Hastie T (2013) Finite-sample equivalence in statistical models for presence-only data. *Ann Appl Stat* 7:1917–1939
- Forester JD, Im HK, Rathouz PJ (2009) Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90:3554–3565
- Fortin D, Beyer HL, Boyce MS et al (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330
- Franckowiak GA, Poché RM (2018) Short-term home range and habitat selection by feral hogs in northern Texas. *Am Midl Nat* 179:28–38
- Froehly J, Beane N, Evans D, Cagle K, Jachowski D (2020) Using multi-scale behavioral investigations to inform wild pig (*Sus scrofa*) population management. *PLoS ONE* 15(2):e0228705
- Graves HB, Wilson M, Elicker J (1975) Behavior of feral swine on Ossabaw Island, Georgia. In: Proceedings of Pennsylvania Livestock Day AS-SW-75-14, pp. 149–150
- Gray SM, Roloff GJ, Montgomery RA et al (2020) Wild Pig Spatial ecology and behavior, invasive wild pigs in North America: ecology, impacts, and management 33–56
- Hayes R, Riffell S, Minnis R et al (2009) Survival and habitat use of feral hogs in Mississippi. *Southeast Nat* 8:411–426
- Helm P (2019) Movements, immobilization, and anthropogenic dietary histories of feral swine in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area. University of Tennessee, Knoxville, TN, USA
- Henry VG, Conley RH (1970) Some parasites of European wild hogs in the southern Appalachians. *J Wildl Manag* 34:913–917
- Henry VG, Conley RH (1972) Fall foods of European wild hogs in the southern Appalachians. *J Wildl Manag* 36:854–860
- Hone J (2002) Feral pigs in Namadgi National Park, Australia: dynamics, impacts and evolution and management. *Biol Cons* 105:231–242
- Howe TD, Bratton SP (1976) Winter rooting activity of the European wild boar in the Great Smoky Mountains National Park. *South Appalach Bot Soc* 41:256–264
- Jakes AF, DeCesare NL, Jones PF et al (2020) Multi-scale habitat assessment of pronghorn migration routes. *PLoS ONE* 15(12):e0241042
- Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *J Appl Ecol* 41:238–251
- Johnson CJ, Nielsen SE, Merrill EH et al (2006) Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *J Wildl Manag* 70:347–357
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71

- Keller RD, Litchford RG, Brinson JC, Carroll AD, Houck JM, Mauney HF, McDonald MT (2003) Hog wild: using GIS to examine 26 years of wild boar control efforts (1976–2001) in the Great Smoky Mountains National Park. *ArcUser* 6:12–13
- Keuling O, Stier N, Roth M (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *Eur J Wildl Res* 54:403–412
- Kramer CJ, Boudreau MR, Miller RS, Powers R, VerCauteren KC, Brook RK (2022) Summer habitat use and movements of invasive wild pigs (*Sus scrofa*) in Canadian agroecosystems. *Can J Zool* 100:494–506
- Kozlo P, Nikitenko MF (1967) Methods for ageing wild boar (in Russian). *Ecology of mammals and birds*. Nauka, Moscow pp. 209–221
- Leonard J (2017) Analyzing wildlife telemetry data in R. <<https://www.ckwri.tamuk.edu/publications/technical-publication/analyzing-wildlife-telemetry-data-r>>. Accessed 6 May 2018
- Levy B (2016) Modeling feral hogs in Great Smoky Mountains National Park. University of Tennessee, Knoxville, TN, USA
- Lewis JS, Rachlow JL, Garton EO et al (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. *J Appl Ecol* 44:663–671
- Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 45:255–268. <https://doi.org/10.2307/2532051>
- Lowe SM, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's worst invasive alien species: a selection from the global invasive species database. Published by the invasive species specialist group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). First published as special lift-out in *Aliens* 12
- Mahoney PJ, Liston GE, LaPoint S, Gurarie E, Mangipane B, Wells AG, Brinkman TJ, Eitel JU, Hebblewhite M, Nolin AW, Boelman N (2018) Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties. *Ecol Appl* 28(7):1715–1729
- Manly BFL, McDonald L, Thomas DL, McDonald TL, Erickson WP (2007) *Resource selection by animals: statistical design and analysis for field studies*, 2nd edn. Kluwer, New York, New York, USA
- Mayer JJ, Beasley JC (2017) Wild pigs. In: Pitt WC, Beasley JC, Witmer GW (eds) *Ecology and management of terrestrial vertebrate invasive species in the United States*. CRC Press, LLC, Taylor and Francis Group, Boca Raton, Florida, USA, pp 219–248
- McClure ML, Burdett CL, Farnsworth ML et al (2015) Modeling and mapping the probability of occurrence of invasive wild pigs across the contiguous United States. *PLoS ONE* 10(8):e0133771
- McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol* 31(6):1161–1175
- Michelot T, Blackwell PG, Matthiopoulos J (2019) Linking resource selection and step selection models for habitat preferences in animals. *Ecology* 100(1):e02452
- Morris LR, Proffitt KM, Blackburn JK (2016) Mapping resource selection functions in wildlife studies: concerns and recommendations. *Appl Geogr* 76:173–183
- Muff S, Signer J, Fieberg J (2020) Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. *J Anim Ecol* 89:80–92
- Oliveira-Santos LGR, Forester JD, Piovezan U, Tomas WM, Fernandez FA (2016) Incorporating animal spatial memory in step selection functions. *J Anim Ecol* 85:516–524
- Paolini KE, Strickland BK, Tegt JL, VerCauteren KC, Street GM (2018) Seasonal variation in preference dictates space use in an invasive generalist. *PLoS ONE* 13(7):1–18
- Peine JD, Farmer JA (1990) Wild hog management program at Great Smoky Mountains National Park. In: *Proceedings of the fourteenth vertebrate pest conference vol 67*, pp. 221–227
- Pimentel D, Ziniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273–288
- Pimentel D (2007) *Environmental and economic costs of vertebrate species invasions into the United States*. University of Nebraska, Lincoln, Nebraska, USA
- Poor EE, Scheick BK, Mullinax JM (2020) Multiscale consensus habitat modeling for landscape level conservation prioritization. *Sci Rep* 10:17783
- Porter KM, DePerno CS, Krings A et al (2014) Vegetative impact of feral horses, feral pigs, and white-tailed deer on the Currituck National Wildlife Refuge, North Carolina. *Castanea* 79:8–17
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/Accessed> 1 January 2021
- Raoul B, Allen B, Tillman E, Wisely S, Engeman R (2019) Road hogs: Implications from GPS collared feral swine in pastureland habitat on the general utility of road-based observation techniques for assessing abundance. *Ecol Ind* 99:171–177
- Recio MR, Mathieu R, Denys P et al (2011) Lightweight GPS-Tags, one giant leap for wildlife tracking? an assessment approach. *PLoS ONE* 6(12):e28225
- Rossell CR (2016) Description of rich montane seeps and effects of wild pigs on the plant and salamander assemblages. *Am Midl Nat* 175:139–154
- Saunders G, Kay B (1991) Movements of feral pigs (*Sus scrofa*) at Sunny Corner, New South Wales. *Wildl Res* 18:49–61
- Seward NW, VerCauteren KC, Witmer GW et al (2004) Feral swine impacts on agriculture and the environment. *Sheep Goat Res J* 19:34–40
- Siemann E, Carrillo JA, Gabler CA et al (2009) Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *For Ecol Manage* 258:546–553
- Signer J, Fieberg J, Avgar T (2019) Animal movement tools (amt): R-Package for managing tracking data and conducting habitat selection analyses. <<https://arxiv.org/pdf/1805.03227.pdf>> Accessed 4 December 2018

- Signer J, Fieberg J, Avgar T (2017) Estimating utilization distributions from fitted step-selection functions. *Ecosphere* 8:e01771
- Singer FJ, Otto DK, Tipton AR et al (1981) Home ranges, movements, and habitat use of European wild boar in Tennessee. *J Wildl Manag* 45:343–353
- Stevens RL (1996) The feral hog in Oklahoma. Samuel Roberts Noble Foundation, Ardmore, Oklahoma, USA
- Thurfjell H, Ball JP, Åhlén PA, Kornacher P, Dettki H, Sjöberg K (2009) Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. *Eur J Wildl Res* 55:517–523
- USDA Forest Service (2019) NLCD 2016 Tree Canopy Cover (CONUS). Salt Lake City, UT
- U.S. Census Bureau (2017) TIGER/Line Shapefiles (machine readable data files)/prepared by the U.S. Census Bureau. <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>
- Warton DI, Shepherd LC (2010) Poisson point process models solve the “pseudo-absence problem” for presence-only data in ecology. *Ann Appl Stat* 4:1383–1402
- Whittington J, Hebblewhite M, Baron RW, Ford AT, Paczkowski J (2022) Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Mov Ecol* 10(1):1–8
- Wilber MQ, Chinn SM, Beasley JC et al (2020) Predicting functional responses in agro-ecosystems from animal movement data to improve management of invasive pests. *Ecol Appl* 30(1):e02015
- Wilson RR, Horne JS, Rode KD, Regehr EV, Durner GM (2014) Identifying polar bear resource selection patterns to inform offshore development in a dynamic and changing Arctic. *Ecosphere* 5:1–24
- Wyckoff AC, Henke SE, Campbell TA et al (2009) Feral swine contact with domestic swine: a serologic survey and assessment of potential for disease transmission. *J Wildl Dis* 45:422–429
- Yang L, Jin S, Danielson P et al (2018) A new generation of the United States National Land Cover Database: requirements, research priorities, design, and implementation strategies. *ISPRS J Photogramm Remote Sens* 146:108–123
- Zeller KA, McGarigal K, Beier P et al (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. *Landscape Ecol* 29:541–557
- Zhang L, Liu S, Sun P et al (2015) Consensus forecasting of species distributions: the effects of niche model performance and niche properties. *PLOS ONE* 10(3):e0120056. <https://doi.org/10.1371/journal.pone.0120056>

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