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Movements, Immobilization, and Anthropogenic Dietary Histories of Feral Swine in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area

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Movements, Immobilization, and Anthropogenic Dietary Histories of Feral Swine in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area

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ABSTRACT

Great Smoky Mountains National Park (GRSM) and Big South Fork National River and Recreation Area (BISO) need efficient feral swine (*Sus scrofa*) management programs. From April 2015 through September 2018, we trapped, anesthetized and fitted 48 individual feral swine (GRSM, n = 38; BISO, n = 10) with Global Positioning System (GPS) collars. I estimated movements, habitat use, and distribution of feral swine based on >200,000 GPS locations. I used those data to develop a Mahalanobis distance model to predict relative probability of use based on 7 landscape variables. I also evaluated stable isotopes in tooth enamel for estimating the proportion of feral swine in GRSM that consumed anthropogenic diets (e.g., corn) as neonates as a tool to assess the impact of human-mediated augmentations from outside park boundaries. Finally, I evaluated a three-drug combination of butorphanol, azaperone, and medetomidine (BAM^{TM}; Wildlife Pharmaceuticals, Fort Collins, CO, USA) for immobilizing trapped adult feral swine. Male home range sizes in GRSM and BISO were more than twice those of females. Feral swine in GRSM showed a preference for low to mid-elevations with sunny (generally southerly) aspects in the vicinity of water. At BISO, feral swine displayed a strong preference for water at lower elevations but in more shaded aspects. Stable isotope analysis revealed that early diets of domesticated swine had distinctly different carbon ratios from feral swine in GRSM but no feral swine demonstrated a neonate diet of corn. I found BAM^{TM} to be satisfactory for use in collaring and sampling adult feral swine in the field, but I suggest a 50% increase in the initial dose (to 0.9 mg/kg butorphanol, 0.3 mg/kg azaperone, 0.3 mg/kg medetomidine) from what is typically recommended for domestic swine.

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1. INTRODUCTION

Feral swine (*Sus scrofa*) are native to Eurasia and northern Africa and were originally introduced to southern North America as early as the 15th century by Spanish explorers (McClure et al. 2015). Feral swine, otherwise known as “feral hogs”, “wild hogs”, “wild pigs”, or “wild boars”, are an exotic and invasive species to the U.S., whose populations cause billions of dollars in damage annually (Pimentel et al. 2005, Pimentel et al., 2007). Feral swine continue to expand their distribution and numbers, being reported in 48 U.S. states (Mayer and Beasley 2017).

The presence of feral swine can be observed through signs such as tracks, trails, rooting, rubs, wallows, and scat (Barrett and Birmingham 1994, Stevens 1996, Taylor 2003, Mapston 2004, Campbell and Long 2009). Feral swine use their snouts and keen olfaction to search for food within the nutrient-rich soil horizon (Conover 2007). Feral swine lack sweat glands and will wallow several times a day during the warmer months to assist in thermoregulation. Wallows (i.e., depressions in mud, often filled with water) are created by the loafing, rolling, and rooting behavior of feral swine (Stevens 1996). Habitual use of wallows by feral swine can contaminate riparian habitats (Stevens 1996). Invasive feral swine negatively affect ecosystem processes and functions by altering nutrient dynamics (Aplet et al. 1991), disturbing plant communities, impacting sensitive habitats (Barrett and Birmingham 1994, Hone 2002, Cushman et al. 2004, Engeman et al. 2004), and acting as a disease reservoir (Wyckoff et al. 2009).

National Park Service units in the Southeast that have populations of invasive feral swine include Great Smoky Mountains National Park (GRSM) in Tennessee and North Carolina and Big South Fork National River and Recreation Area (BISO) in Tennessee and Kentucky. Feral swine were thought to have originated in GRSM from European wild boar brought in 1912 from

Europe to a hunting camp, located near Hooper Bald in North Carolina (Jones 1959; Peine and Farmer 1990), 45 km southwest of GRSM. By 1920, the wild boar had breached the camp enclosures and bred with local, free-ranging livestock pigs. A combination of hybridized domestic pig and Eurasian boar made their way to GRSM during the 1940s and 50s. Hogs at BISO were thought to have come from a nearby hunting lodge where feral swine were released in 1963, prior to the establishment of the park. The BISO feral swine population that now extends into the surrounding regions (Mayer and Brisbin 1991).

In GRSM, Bratton (1974) found that feral swine uprooted, ate, or trampled up to 50 different plant species, including 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*). Loss of flowering plants such as these can cause areas disturbed by feral swine to change in composition, giving way to plants with deep or poisonous roots (Bratton 1974). Other impacts by feral swine in GRSM include depredation of native fauna, competition with native fauna for resources, and introduction of disease (Salinas et al. 2015). Two sensitive animal species in GRSM that are part of the wild feral swine diet include the red-cheeked salamander (*Plethodon jordani*), which is endemic to the Park, and the Jones middle-tooth snail (*Mesodon jonesianus*, Peine and Farmer 1990).

To date, little is known about the BISO wild hog population, but the damage these animals are causing is threatening park resources including delicate wetland areas where several federally listed species are found including, White Fringeless Orchid (*Platanthera integrilabia*), an endangered endemic (Cumberland Sandwort [*Arenaria cumberlandensis*]), and a threatened species (Cumberland rosemary [*Conradina verticillata*], National Park Service [NPS] 2018).

Natural resource staff at BISO have also received reports of feral swine rooting and damaging private lands near park boundaries (J. Fisher, NPS, personal communication).

Feral swine also serve as reservoirs for infectious and parasitic diseases, which can spread to domestic livestock and humans. Such diseases include hog cholera, swine brucellosis (*Brucella abortus*), trichinosis (*Trichinella spiralis*), hoof and mouth disease, African swine fever, giardia (*Giardia lamblia*), and pseudorabies (Peine and Farmer 1990). Although not previously reported in GRSM (Smith 1979, Zygmont et al. 1982, New et al. 1994), pseudorabies was detected in in the Park in 2005 (Cavendish et al. 2008). Pseudorabies is particularly dangerous because it infects multiple non-swine species and all scavenging mammals that feed on infected carcasses can become infected, resulting in almost 100% mortality. Feral swine are the only known natural reservoirs for the virus (Pedersen et al. 2013). Since 2005, the seroprevalence of pseudorabies in GRSM has ranged from one individual to 22% of feral swine removed by wildlife staff in 2017. Pseudorabies at GRSM is generally increasing in prevalence and distribution. The presence of pseudorabies has not yet been detected at BISO.

Wildlife officials at GRSM and BISO wish to eradicate feral swine populations. In GRSM, the NPS has had a feral swine control program in place since 1959. During that time, >13,000 feral swine have been shot or trapped and killed in GRSM (W. Stiver, NPS, personal communication). Wildlife technicians from 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. However, limited empirical data on the population has made it difficult for managers to determine the effectiveness of these efforts (Salinas et al. 2015). BISO does not presently have a formal feral swine management program, although some limited trapping by NPS officials has occurred. Unlike GRSM, however, the public may legally harvest feral swine at BISO, with no bag limit, from September 22 through February 28. Unfortunately, public hunting pressure within BISO may result in displacement, with groups of feral swine (i.e., sounders) spreading to areas within and outside BISO where they have not previously occurred (J. Fisher, NPS, personal communication).

Recently, GRSM partnered with the National Institute for Mathematical and Biological Synthesis (NIMBios) at The University of Tennessee to form a Feral Swine/Pseudorabies Working Group in GRSM (http://www.nimbios.org/workinggroups/WG_PRV.html). This working group includes 22 individuals from 13 institutional affiliations. The working group is using GRSM feral swine control and disease monitoring data to develop models that will evaluate control efforts and predict consequences for the spread of pseudorabies; this model could ultimately be used to predict the movement and control of emerging foreign animal diseases. It is not known if pseudorabies is spreading across the landscape due to the natural movements of feral swine or through additional illegal releases of feral swine into new areas.

However, model development has been impeded by the lack of biological information related to the movement patterns of feral swine in GRSM and information related to the illegal releases of feral swine near the Park boundary. Studies of seasonal movement and home range size of feral swine in the southern Appalachians has been limited to a study of 14 radio-collared individuals in GRSM conducted in the late 1970s (Singer et al., 1981). Very High Frequency (VHF) radio collars were used in that study, which typically have low positional accuracy (Recio et al. 2011), low numbers of location fixes, and location timing concentrated around daylight hours. Moreover, the vegetation of GRSM has changed since that early work (e.g., hemlock loss [*Tsuga canadensis*] due to hemlock wooly adelgid [*Adelges tsugae*]). In contrast, modern Global Positioning Systems (GPS) tracking allows the collection of animal positions at higher rates and shorter intervals, in remote and poorly accessible areas, during all time and weather conditions, and avoids modified animal behavior due to the proximity of the researcher (Recio et al. 2011).

Illegal releases of feral swine can also hamper control efforts. Credible reports have been received at GRSM that individuals may be illegally stocking feral swine near park boundaries. These reports have been supported by the continued presence of feral swine that appear semi-domesticated and harbor physical characteristics that historically were not found in GRSM (e.g., brindled coloration, short snouts, and curly tails). During the 1990s, 18 pigs were reported wandering along Highway 129 near the western boundary of GRSM (W. Stiver, NPS, personal communication). These conspicuous feral swine displayed similar behavior to domestic swine (e.g., lack of fear of humans) and their physical appearance (e.g., brindled in color and curly tails) also indicated evidence of domestication. Another report indicated that a rented box truck from Florida was returned in Robbinsville, NC (southwestern GRSM) containing swine urine and feces (W. Stiver, NPS, personal communication). Additionally, an individual removed from the western portion of the Park was found to be genetically distinct from other feral swine in GRSM (McCann et al. 2009), providing additional circumstantial evidence of illegal stocking. If human-facilitated augmentation of feral swine is occurring, it could compromise costly and long-term control efforts by officials at GRSM and contribute to the spread of disease. NPS needs information on the level of augmentation that may be taking place.

Stable isotope analysis of feral swine tooth enamel may be useful for determining whether feral swine have been recently released by the public. Stable isotopes (e.g., carbon-12, carbon-13, oxygen-16, and oxygen-18) are isotopes that do not undergo decay. When an animal eats and drinks, the elemental composition of the consumed resource is incorporated into developing tissues (Seger et al. 2013). There are two major photosynthetic pathways used by vegetation that result in distinctly different isotopic ratios of carbon. Most vegetation utilizes a C3 photosynthetic pathway, while some grasses, including corn, utilize a C4 pathway. C4 grasses (e.g., corn) have a distinct carbon signature compared with forbs and feral swine with higher $^{13}C/^{12}C$ ratios suggest the consumption of corn-based products. Corn has become a fundamental basis for human-produced foods and the carbon isotopic composition of feral swine tooth enamel could be used to evaluate its diet early in its lifetime to distinguish human-fed swine from naturally foraging feral swine. In addition, the oxygen isotopic ($^{16}O/^{18}O$) composition of an animal primarily reflects the isotopic composition of the water it has consumed and can yield characteristics about the water sources. Enrichment of $^{16}O/^{18}O$ isotopic ratios generally decreases with latitude but the ratio of rainfall/evaporation or "surface water turnover" can also affect $^{16}O/^{18}O$ isotopic ratios (Inácio and Chalk 2017). Calculating $^{13}C/^{12}C$ and $^{16}O/^{18}O$ isotopic ratios in tooth enamel may enable us to distinguish the type of food and water consumed (i.e., corn vs natural food and livestock water sources vs natural water), and perhaps, in what location.

Finally, methods for immobilizing free-ranging feral swine have previously not been well established. NPS and others working on feral swine need better information on the physiologic and clinical responses of free-ranging feral swine to chemical immobilization. A potentially useful drug mixture to sedate and immobilize feral swine is a combination of butorphanol, azaperone, and medetomidine (BAM^{TM}; Wildlife Pharmaceuticals, Fort Collins, CO, USA). BAM^{TM} is commonly used to immobilize white-tailed deer (*Odocoileus virginianus*) and larger ungulates (Wolfe et al. 2014) but has not been used to anesthetize feral swine. An advantage of BAM^{TM} is that medetomidine is reversible using atipamezole and butorphanol can be reversed using naltrexone. With little clinical data on the use of BAM^{TM} in feral swine, there is a need to investigate the usefulness and appropriate dosages.

The purpose of this project is to collect feral swine movement, habitat, and distribution data to aid GRSM in the advancement of a more efficient and effective feral swine control program. This project will also enable BISO to establish a productive feral swine control program and make informed management decisions in the future. My objectives were to:

1. Capture feral swine to determine movements, habitat use, and distribution based on GPS radio-location data. My goal was to use those data to develop a habitat model to predict relative probability of use based on vegetation, geophysical, and anthropogenic variables, which could be used for targeting control efforts.
2. Evaluate stable isotopes for estimating the proportion of feral swine in GRSM that consumed natural food and water compared with anthropogenic diets as a means for assessing the impact of human-mediated augmentations from outside park boundaries.
3. Evaluate the use of BAM^{TM} for immobilizing free-ranging feral swine.

2. STUDY AREA

GRSM was the most visited national park in the U.S., having >11 million visitors per year. GRSM encompassed nearly 2,114 km^2 and is located along the border between eastern Tennessee and western North Carolina. About 80% of the park was composed of deciduous forest, and major forest types included cove-hardwood, spruce-fir, northern hardwood, hemlock, and pine (*Pinus* spp.)-oak (*Quercus* spp.) forests. GRSM supported 65 mammal, 200 bird, >80 reptile and amphibian species, and >1,600 flowering and 4,000 non-flowering plant species. Elevation in GRSM ranges from 266 to 2,025 m. Average annual rainfall in the highest elevations was about 216 cm (NPS 2015).

BISO was established in 1974 and received about 600,000 visitors annually. BISO was comprised of about 505 km^2 of rugged forested gorge and adjacent forested plateau with an elevation range of 720 to 1,750 m. BISO was located in north-central Tennessee and southeastern Kentucky in the Cumberland Plateau physiographic region. The upland vegetation zone was characterized by gradual rolling slopes and well-drained sandy soils. The distance between GRSM and BISO was about 145 km (Figure 1).

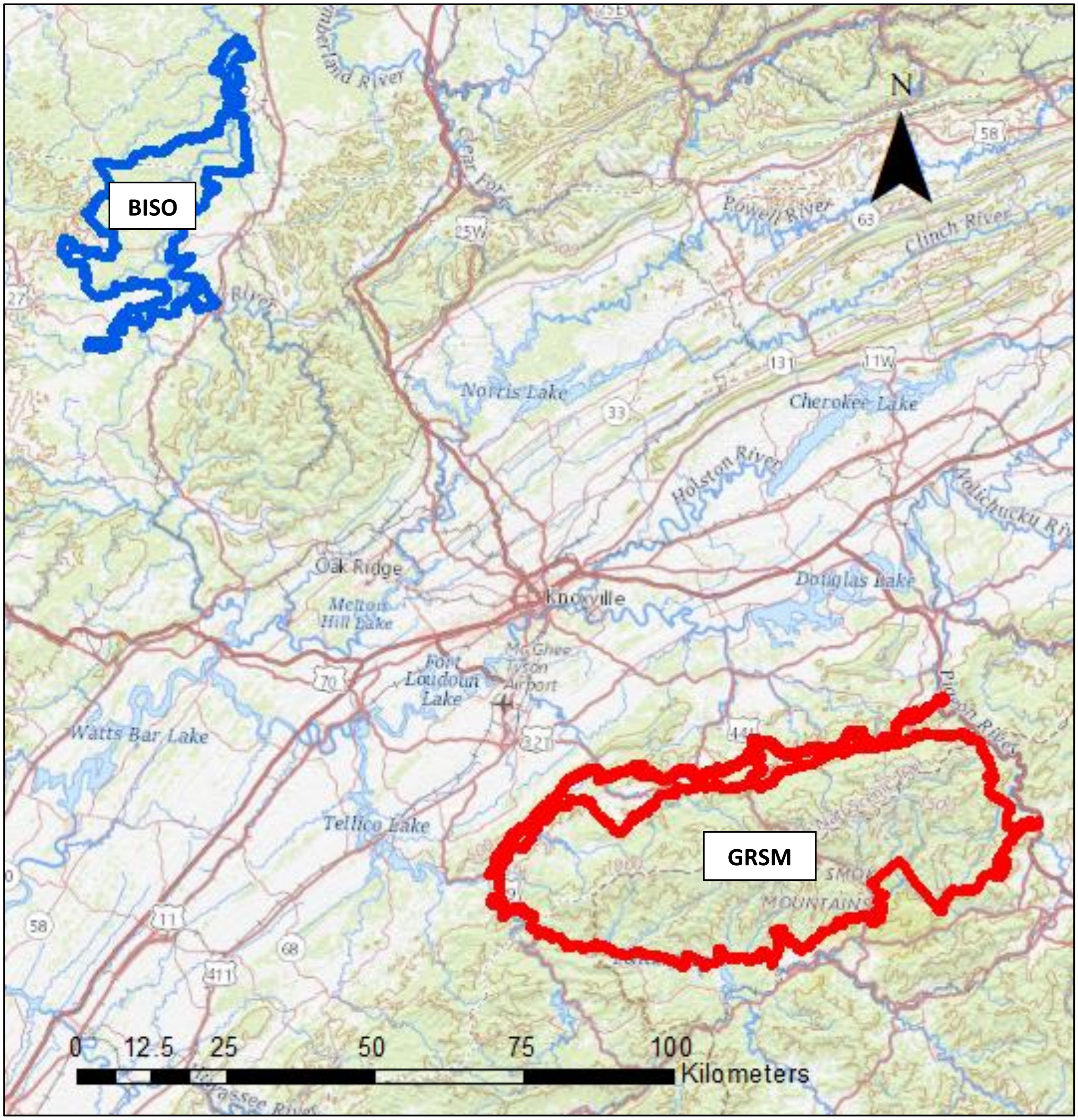


Figure 1. Map of Big South Fork National River and Recreation Area and Great Smoky Mountains National Park.

3. MATERIALS AND METHODS

CAPTURE AND HANDLING

Field crews began trapping feral swine for radio collaring in fall 2015 and continued through summer 2017. We used cage traps and drop nets in GRSM whereas cage traps and corral enclosures were used in BISO. All traps were baited using a mixture of dried, shelled corn and mineral salt. We placed traps near field signs of feral swine; trapping was mostly conducted during winter (November–March). Traps were checked daily, usually in the morning. My goal was to radio collar a relatively even sex ratio of adult feral swine. I avoided collaring younger feral swine because of anticipated weight gain, which could have made collars too restrictive.

To immobilize sample swine, we used the recommended BAM^{TM} dosage by the manufacturer for domestic swine (1 ml BAM^{TM} per 45 kg or 0.6 mg/kg butorphanol, 0.2 mg/kg azaperone, 0.2 mg/kg medetomidine; Wildlife Pharmaceuticals Inc. 2018). Two of the feral swine at GRSM were immobilized using Telazol due to lack of available BAM^{TM} kits in the field. All animal work-up procedures were approved by the University of Tennessee Institutional Animal Care and Use Committee (Protocol # 2461-0516).

We visually estimated body masses while feral swine were in traps based on body condition to calculate the drug dose needed. We delivered the anesthesia via intramuscular injection into the hip or shoulder of each subject. The drug delivery methods used were pole syringe (Cap-Chur, Powder Springs, Georgia, USA), dart projector (Dan-Inject, Dan-Inject North America, Fort Collins, Colorado, USA with darts from Pneu-dart, Williamsport, Pennsylvania, USA), or hand injection with syringe and needle.

Once anesthetized, feral swine were fitted with foot hobbles. We applied sterile artificial tear lubricating ointment (Rugby Artificial Tears, Rugby Laboratories, Inc., Livonia, MI) to feral swine eyes to prevent desiccation and blindfolds were fit over the head and snout for stress reduction. We collected ≥ 2 ml of blood, plucked guard hair samples from the ridge of the back, sampled skin tissue via ear puncture, and pulled a single I3 (incisor) or P1 (premolar) using a tooth extractor tool. We placed an aluminum identification marker in one ear of the hog and a "Do Not Eat Before" tag was placed in the other. The "Do Not Eat Before" tag was a warning to the public that potential residual chemicals may be present in the animal, and not to consume feral swine meat within 45 days of immobilization. The tag indicated the date when the hog would be safe to consume.

We placed an identification tattoo on the inside hind leg of each sampled feral swine that corresponded to the ear tag number, and subcutaneously injected a Passive Integrated Transponder (PIT) into the back between shoulder blades to ensure identification if all other visible markers were lost. We estimated feral swine ages, to the nearest month, based on tooth wear (Kozlo and Nikitenko 1967). We recorded total body length, head length and width, hoof length and width, height at shoulder, torso girth, and neck circumference for each captured feral swine. Feral swine were fit with a GPS/VHF collar (Vectronic Aerospace GmbH, GPS Iridium, Berlin, Germany) programmed to communicate positional data via GPS satellite and/or VHF beacon. Captured feral swine were weighed on site using a field scale. The BAM^{TM} anesthetic was reversed using atipamezole (25 mg/ml or 1 mg/kg) and naltrexone (50 mg/ml or 25 mg/animal) via intramuscular injection based on the recommended dosage for domestic pigs (Wildlife Pharmaceuticals Inc. 2018).

The collar manufacturer provided software that allowed me to change the location collection schedule, check battery capacity, observe clarity/quality of uploads, and view real-time locations through Google Earth (https://earth.google.com). I programmed the collars to record a single point location every hour and upload those data via satellite every 4 hours. Collars were intended to remain on sampled feral swine for up to 1 year. I programmed collars that were stationary for >8 hours to send a VHF mortality signal, and the collar automatically notified me via text and email of its disposition. All collars collected store-on-board data, which made it necessary to locate and kill the collared feral swine for recovery. The collars retrieved from the field were recovered following dropped collar notifications, mortality events, or hunter kills. The data were then downloaded directly from the GPS housing on the collar at the GRSM data management office.

MOVEMENTS, ACTIVITY, AND RESOURCE SELECTION

After recovering the collars, downloading and saving the store-on-board data, I screened the data to eliminate invalid or inaccurate GPS locations and those outside the study period. The data for each individual hog was subset based on deployment dates (i.e., when collars were affixed to sample feral swine) and retrieval dates (i.e., when collars were recovered from the field). All locations outside of those dates were omitted. I minimized GPS location error by screening data for positional dilution of precision (PDOP) values and fix type (2D or 3D; Lewis et al. 2007). I calculated retention values for the data using 4 screening methods: 1) removing 2D locations with a PDOP >5, 2) removing all 2D locations, 3) removing 2D locations with a PDOP >5 and removing 3D locations with a PDOP >10, and 4) removing all 2D locations and removing 3D locations with a PDOP >7. I used ArcMap 10.3 (https://desktop.arcgis.com/en/arcmap/) to plot the location data and extract environmental covariates. Each GPS location was visually screened so that all outlying points such as location uploads from vehicles pre- and post-deployment, and excess mortality locations were eliminated (Leonard 2017).

The GPS data were subset in R based on sex for both Parks. Data from GRSM were then subset into 3 seasons: summer, 1 April–14 August; fall, 15 August–31 October; and winter, 1 November–31 March. The seasonal subsets for GRSM were based on timeframes in which NPS staff prioritize their management efforts. The summer season represents the time period in which black bear (*Ursus americanus*) activity is prevalent and NPS wildlife staff is focused primarily on bear management. The fall season is indicative of an abundance of mast and feral swine activity is focused on foraging in preparation for the coldest months of the year. The winter season is the timeframe when feral swine move to lower elevations in search of food while black bears are in torpor. Data from BISO were subset into 2 seasons: fall-winter, 22 September–28 February; and spring-summer, 1 March–21 September. Again, the seasonal subsets for BISO were based management programs. The fall-winter season represented the period in which public hunting of feral swine was permitted. The spring-summer season took place when there was no public hunting and BISO wildlife staff bait and trap feral swine in the park. Both the GRSM and BISO seasonal subsets were further subset based on time of day (day, night, and crepuscular). I only included data from feral swine that wore a collar for a minimum of 30 days within a season for home range estimation and analyses.

Home range is defined by Burt (1943) as the area traversed by an individual in its normal activities of food gathering, mating, and caring for young. I calculated hog home ranges using the “adehabitatHR” package (Calenge 2006) in R (R Core Team 2018) and utilized code by Leonard (2017). I applied the Kernel Density Estimate (KDE) method with a Gaussian Kernel to compute home ranges. The KDE is a point-based approach that uses individual occurrences (GPS points) as the input and creates an output polygon. The shape and the size of the kernel function (bandwidth) influences the result (Steiniger and Hunter 2013). I used the h_{ref} method for bandwidth estimation, which is an automated reference or default approach. The adehabitatHR package applies a contouring algorithm that calculates a contour line enclosing a desired proportion of the density of all cells (Steiniger and Hunter 2013). I applied a 95% contour to all individuals for all 3 seasons in GRSM, and the fall-winter and spring-summer seasons in BISO. This contour represents a 95% probability of encountering the animal within the output polygon (Steiniger and Hunter 2013). I regressed home range size with number of locations collected in GRSM and BISO to evaluate adequacy of the sample sizes for the $\mathrm{KDE}_{\mathrm{href}}$. My test hypothesis was that the number of locations would not be related to home range size.

To estimate activity, I measured travel rates; the straight-line distance and rate between successive locations in meters per hour. I subset and calculated travel rates based on sex, season, and time of day using the “Amt” package (Signer et al. 2018) in R for both GRSM and BISO datasets. Feral swine travel rates that were measured shared a median sampling rate of 1 GPS location per hour. My assumption was that greater hourly travel rates were associated with greater activity of GPS collared feral swine.

Another movement-related statistic that serves as a trajectory and space-use summary is known as path sinuosity. The sinuosity of a path is determined both by the distribution of changes in direction and by the travel rate (Bovet and Benhamou 1988). Animal sinuosity is the tortuosity of a random search path, ranging between straight-line movement (0) and Brownian motion (1, Benhamou, 2004). Using the “Amt” package in R, I calculated sinuosity based on sex, season and time of day for both Parks to estimate activity suggestive of searching, rooting, or rearing behavior. I tested the calculated home range, travel rate, and sinuosity data for normality of distribution for both Parks using the Shapiro-Wilk test in R. Due to the small sample sizes of the home range and movement data, I used the Mann-Whitney-Wilcoxon Test and the Kruskal-Wallis Test in R to make comparisons based on sex, season and time of day.

I used ArcMap to develop landscape attribute maps for the habitat model. Because some of the hog locations were outside the boundary of both parks, I used the GIS analysis tool to construct a buffer around park boundaries (2.5 km in GRSM, 5 km in BISO) to ensure inclusion of all locations. I downloaded a regional digital elevation model (DEM, NPS 2018) for both parks from the NPS ArcGIS database. Using Spatial Statistics tools in ArcMap, I calculated slope (percent rise) to capture the steepness of the terrain. I utilized the Spatial Analyst tool to determine the area of solar radiation (watt hours/m^2) which represents the amount of exposure to sunlight and heat the terrain receives. I downloaded water polyline layers (NPS 2018) and created a 5-m buffer around the GRSM water polylines (2.5 m in BISO). I then converted the buffered water layers into 10- x 10-m raster layers using the Conversion tool in ArcMap. Using the Reclass operation in ArcMap, I reclassified the water raster into a binary classification (where water was present = 1, where water was not present = 0). I calculated a ridge raster with the regional digital elevation model (DEM) and water raster using the Spatial Analyst tools along with the Hydrology toolset in ArcMap. I converted the ridge polygon into a 10- x 10-m raster and reclassified it to a binary classification (whereby 1 = ridge is present and 0 = ridge not present). Both the water and ridge variables are key to feral swine ecology. Feral swine depend on water sources for hydration and wallowing. Ridges are often used by feral swine for travel and day bedding. I acquired regional land cover data from the USGS Land Cover Data Portal derived from the Appalachian region USGS National Gap Analysis Project (GAP; https://gapanalysis.usgs.gov/gaplandcover/data/download/) and converted the 30- x 30-m cell size to 10- x 10-m.

Feral swine home ranges and behavior are affected by food availability (Howe and Bratton 1976). When mast (e.g., acorns) is abundant, it constitutes up to 84% by volume of the diet of feral swine in the Great Smoky Mountains (Singer et al. 1981). Therefore, I created an oak map layer by reclassifying the Central and Southern Appalachian Oak Forest and Central and Southern Appalachian Oak Forest-Xeric cover types as oak in GRSM (1) and classified Allegheny-Cumberland Dry Oak Forest and Woodland-Hardwood and Southern Interior Low Plateau Dry-Mesic Oak Forest as oak in BISO (1); all other cover types were reclassified as other (0, Tables 2 and 3). During a poor mast year, Singer et al. (1981) and Howe and Bratton (1976) found that feral swine in the Smokies made greater use of stands of yellow poplar (*Liriodendron tulipifera*) and yellow-poplar/Carolina silverbell (*Halesia carolina*) forest. Therefore, I created a second vegetation layer reclassifying all cove forest types (i.e., Southern and Central Appalachian Cove Forest in GRSM and South Central Interior Mesophytic Forest in BISO) as either cove (1) or other (0, Tables 1 and 2).

Table 1. Classification of categories for U. S. Geological Survey Gap landcover in Great Smoky Mountains National Park. The categories were reclassified in ArcMap to represent oak (numeric class 84 and 85) and cove (numeric class 127) forests.

Numeric Classification	Ecosystem/Land Use
34	Deciduous Plantations
38	Evergreen Plantation or Managed Pine
60	Allegheny-Cumberland Dry Oak Forest and Woodland-Hardwood
61	Allegheny-Cumberland Dry Oak Forest and Woodland Pine Modifier
62	Central and Southern Appalachian Montane Oak Forest
63	Central and Southern Appalachian Montane Northern Hardwood Forest
84	Central and Southern Appalachian Oak Forest
85	Central and Southern Appalachian Oak Forest-Xeric
87	Southern Ridge and Valley Dry Calcareous Forest
91	Ruderal Forest
92	Southern Piedmont Dry Oak-(Pine) Forest-Loblolly Pine Modifier
95	Appalachian Hemlock-Hardwood Forest
96	Central and Southern Appalachian Spruce-Fir Forest
110	Southern Appalachian Low Mountain Pine Forest
112	Southern Piedmont Dry Oak-(Pine) Forest-Hardwood Modifier
113	Southern Piedmont Dry Oak-(Pine) Forest-Mixed Modifier

Table 1. Continued

Numeric Classification	Ecosystem/Land Use
126	South-Central Interior Mesophytic Forest
135	Southern Appalachian Montane Pine Forest and Woodland
202	South-Central Interior Large Floodplain-Forest Modifier
203	South-Central Interior Small Stream and Riparian
342	Southern Appalachian Grass and Shrub Bald
343	Southern Appalachian Grass and Shrub Bald-Herbaceous Modifier
344	Southern Appalachian Grass and Shrub Bald-Shrub Modifier
400	Southern and Central Appalachian Bog and Fen
511	South-Central Interior Large Floodplain-Herbaceous Modifier
522	Southern Appalachian Montane Cliff
527	Southern Appalachian Rocky Summit
553	Undifferentiated Barren Land
556	Cultivated Cropland
557	Pasture-Hay
558	Introduced Upland Vegetation-Annual Grassland
563	Introduced Upland Vegetation-Trees
567	Harvested Forest-Grass/Forb Regeneration
568	Harvested Forest-Shrub Regeneration
574	Disturbed/Successional-Grass/Forb Regeneration

Table 1. Continued

Numeric Classification	Ecosystem/Land Use
575	Disturbed/Successional-Shrub Regeneration
579	Open Water
581	Developed, Open Space
582	Developed, Low Intensity
583	Developed, Medium Intensity
584	Developed, High Intensity

Table 2. Classification of categories for U. S. Geological Survey Gap landcover in Big South Fork National River and Recreation Area. The categories were reclassified in ArcMap to represent oak (numeric class 60 and 86) and cove (numeric class 127) forests.

Numeric Classification	Ecosystem/Land Use
38	Evergreen Plantation or Managed Pine
60	Allegheny-Cumberland Dry Oak Forest and Woodland-Hardwood
86	Southern Interior Low Plateau Dry-Mesic Oak Forest
87	Southern Ridge and Valley Dry Calcareous Forest
88	Southern Ridge and Valley Dry Calcareous Forest-Pine Modifier
95	Appalachian Hemlock-Hardwood Forest
110	Southern Appalachian Low Mountain Pine Forest
126	South-Central Interior Mesophytic Forest
127	Southern and Central Appalachian Cove Forest
135	Southern Appalachian Montane Pine Forest and Woodland
202	South-Central Interior Large Floodplain-Forest Modifier
203	South-Central Interior Small Stream and Riparian
523	Southern Interior Acid Cliff
552	Unconsolidated Shore
553	Undifferentiated Barren Land
556	Cultivated Cropland
557	Pasture-Hay

Table 2. Continued

Numeric Classification	Ecosystem/Land Use
568	Harvested Forest-Shrub Regeneration
567	Harvested Forest - Grass/Forb Regeneration
579	Open Water
580	Quarries, Mines, Gravel Pits and Oil Wells
581	Developed, Open Space
582	Developed, Low Intensity
583	Developed, Medium Intensity
584	Developed, High Intensity

I calculated location distances from features and land cover values for each GPS point for all feral swine. I created Euclidean distance buffers around the water and ridge rasters for both Parks using the Spatial Analyst tool. For GRSM, I set the maximum distance to 10,000 m and the output cell size to 100 m. For BISO, the maximum distance was set to 2,000 m with an output cell size of 100 m. Using the Extract Multi-values to Points function in the Spatial Analyst toolset, I calculated values for elevation, slope, and solar radiation for each GPS location in GRSM and BISO. After calculating all GPS point covariates in Arc Map, I exported the data into R and ran a collinearity test to confirm the absence of any correlation between variables ($R < 0.05$).

To estimate percent oak, percent cove, percent water, percent ridge, mean elevation, mean slope, and mean solar radiation within home ranges, I first needed to define a radius for a circular moving window for the Focal Statistics tool in ArcMap. As the circular moving window moves across the Park raster in ArcMap, it calculates the proportion of each landcover variable. Winter female feral swine home ranges in GRSM were the smallest during NPS hog control season; therefore, I used that group to begin the calculations for the radius of the moving window. I utilized fall-winter season feral swine home ranges for the window radius in BISO due to its significantly smaller size compared with all other seasonal subsets (see RESULTS). I subset winter female home ranges in GRSM and fall-winter female home ranges in BISO into weeks (e.g., wk1, wk2, wk3…). For each weekly subset, I calculated KDE_{href} home ranges at a 75% contour density, creating multiple weekly home range polygons for each female that fit the criteria for winter season in GRSM and fall-winter in BISO. All weekly home range polygons were plotted in ArcMap. I calculated the centroid of each weekly home range polygon using the Data Management Feature tool. I measured and averaged the week-by-week distance between each centroid using the ArcGIS Analysis tool. These distances represented the mean week-to-week distances traveled from the weekly home range centroids. The mean centroid distances were used as the radii for the moving windows. Finally, I used the Focal Statistics tool in ArcMap to calculate the average proportion of landcover variables (e.g., percent oak, cove, water) for the entirety of both Parks.

To model resource selection, I used the Mahalanobis (D^2) distance metric (Clark et al. 1993). The D^2 statistic is a presence-only measure of habitat suitability that does not require random samples or identification of a study area extent. Moreover, correlation among variables can occur and the model performs well compared with other presence-only estimators (Farber and Kadmon 2002). The D^2 metric is the squared "distance" from an "ideal" defined by the mean and covariance matrix of the training data set and the covariates at a given set of coordinates. It is a measure of dissimilarity and represents the standard squared distance between a set of sample variates and an ideal habitat (Clark et al. 1993). The habitat model is based on the D^2 distance statistic,

$$D^2 = (\underline{x} - \underline{\hat{u}})' \, \Sigma^{-1} \, (\underline{x} - \underline{\hat{u}}),$$

whereby $\underline{x}$ is a vector of habitat variables associated with each cell; $\underline{\hat{u}}$ is a mean vector of habitat variables estimated from the set of GPS locations; and Σ^{-1} is the inverse of the estimated covariance matrix, also from the GPS locations (Clark 1993, Rao 1952, Morrison 1976). Most feral swine hunting activity takes place in winter in GRSM and BISO, and the smaller winter home ranges of females suggests greater habitat specificity, and presumably, greater success in predicting resource use. Therefore, I restricted my analysis to female feral swine during winter (1 November to 31 March) in GRSM and fall-winter (22 September–28 February) in BISO. To avoid any undue influence of any individual feral swine on the model, I subsampled the radiolocations using the feral swine with the fewest number of fixes as the maximum. Feral swine with greater numbers of locations were randomly thinned so that the number of fixes were consistent across all feral swine.

I used the R package “adehabitatHS” (Calenge 2006) to estimate the D^2 for both Parks based on the following variables: distance to water, distance to ridges, percent cove forest, percent oak forest, slope, solar radiation, and elevation. The estimates were used to produce a map in ArcGIS with D^2 values within each cell of a 10- x 10-m grid. To produce these maps, I exported the covariate raster layers as .tif files into R and plotted the maps for visual inspection. In total, 7 layers for GRSM and BISO were stacked and converted into a “spatial pixels data frame”. The sub-sampled hog data were bound in R to create a data frame of eastings and northings (UTMs) and then converted to a spatial points data frame. Using the previously stacked spatial pixels data frame in combination with the spatial points data frame, D^2 was calculated and saved as a .tif file in ArcGIS. I reclassified the symbology of the D^2 output values into 10 quantiles to make the map more intuitive. Resource selection was evaluated by creating frequency histograms of used versus available resources for each of the map layers.

GRSM STABLE ISOTOPE ANALYSIS

We collected I3 (incisors) or P1 (premolars) teeth from feral swine trapped in GRSM. As a baseline, I collected premolars from domestic hogs at a local livestock slaughterhouse (H&R Custom Slaughtering, Crossville, Tennessee, USA). Dental enamel provides the opportunity to obtain information about the composition of neonate diets ($^{13}C/^{12}C$) and the water source that was used ($^{18}O/^{16}O$, Wright 1998). This was done to evaluate the feasibility of using early dietary histories to identify feral swine that were not born in GRSM, which could be indicative of an

Table 3. Data screening options for positional dilution of precision (PODP) and fix types used to eliminate poor GPS location data, April 2015 through September 2018 in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area. Option 3 was chosen prior to analyses to prevent bias in home range characteristics and maximize data retention.

	Total Data Retention (%)	
Data Screening Options	GRSM	BISO
1 (Remove 2D PDOP >5)	99.9	99.9
2 (Remove all 2-D)	99.8	99.9
3 (Remove 2D PDOP >5 & 3D PDOP >10)	98.4	98.5
4 (Remove all 2D & 3D PDOP >7)	92.9	94.6

illegally released animal. I was primarily interested in diets of feral swine early in their lifetimes to differentiate between individuals born in GRSM with those born elsewhere that were either fed corn-based diets or foraged naturally on corn agriculture. I also wanted to compare oxygen isotope ratios ingested early in life by feral and domestic swine which can indicate differences in composition and location of water sources (Ignácio and Chalk 2017). According to Tonge and McCance (1973), normal pig I3 and P1 development is complete at 8–16 months of age. Thus, isotopic ratios in feral swine tooth enamel should be reflective of diets up to 16 months of age.

I prepared tooth samples for analysis following protocols described by Bocherens et al. (1994), Koch et al. (1997), and Pellegrini and Snoeck (2016). Pretreatment of enamel was used to remove organic tissue and exogenous carbonate material from the tooth. I began the cleaning process by soaking all collected teeth in a sonicator with 15mL of 2% sodium hypochlorite (NaOCl) for 30 min then rinsed them 3 times in deionized water (DI), sonicating 5 min for each rinse. This initial cleaning removed debris and organic tissue from the extracted teeth and made handling of the teeth easier. After air-drying overnight, I cut the cleaned teeth into 2 pieces using a Dremel tool (Dremel, Racine, Wisconsin, USA) to separate tip and base. The pieces were then crushed into powder using an agate mortar and pestle. Each crushed tooth segment (tip and base) yielded about 20 mg of powder. The powder was soaked in 2% NaOCl overnight, rinsed 3 times with DI, then soaked in 1M buffered acetic acid (pH = 4) overnight. The buffered samples were again rinsed in DI 3 times and dried overnight. I weighed approximately 2 mg of each segment powder into separate vials and reacted the samples with 200µL of phosphoric acid at 72°C for $\geq$1.5 hours. The resulting CO_2 gas was analyzed at the University of Tennessee Stable Isotope Laboratory by a Thermo-Finnigan Gas Bench II and Delta+XL mass spectrometer. Isotopic ratios of carbon and oxygen are reported relative to an isotopic standard material (Pee Dee Belemnite) using the delta notation where,

$$\delta^{13}C = [(^{13}C/^{12}C_{\text{sample}}) / (^{13}C/^{12}C_{\text{PDB}}) - 1] \times 1000 \text{ and}$$

$$\delta^{18}O = [(^{18}O/^{16}O_{\text{sample}}) / (^{18}O/^{16}O_{\text{PDB}}) - 1] \times 1000.$$

I used analysis of variance (ANOVA) to compare carbon and oxygen isotope values among wild and domestic hog teeth.

EVALUATION OF BAM^{TM} AS AN ANESTHETIC FOR FERAL SWINE

We recorded 3 phases of the immobilization process to the nearest minute; phase 1, from initial injection to the first sign of wobbling or incoordination; phase 2, from first sign to sternal position (i.e., recumbent); and phase 3, time sternal to time fully anesthetized (i.e., no reaction to stimuli such as physical manipulation of body position and tactile stimulation). I calculated total induction time by summing the 3 timed phases, and total work-up time (i.e., from initial injection to time of capture site exit). We took rectal temperatures (°C; Vet-Temp DT-10, Advanced Monitoring Corp., San Diego, California, USA), along with respirations per minute (based on thoracic movements) and heart beats per minute (via stethoscope at 10-minute intervals). Reversal times were measured from time of reversal injection until the subjects vacated the capture site. Total work-up time was the duration from initial BAM^{TM} injection to capture site departure. I used an ANOVA to compare male and female induction times, and a Tukeys ANOVA test to compare induction times based on capture method.

4. RESULTS

MOVEMENTS, ACTIVITY, AND RESOURCE SELECTION

Forty-eight individual feral swine were captured and collared, 38 in GRSM (19 males, 19 females) and 10 in BISO (5 males, 5 females). Mean age of collared feral swine in GRSM was 34 months (SD = 13.4, range = 6–72 months) and mean mass was 74.5 kg (SD = 18.3, range = 27.2–107.0 kg). Feral swine at BISO had a mean age of 31 months (SD = 15.3, range = 20–72 months) and 67.2 kg in mass (SD = 27.5, range = 45.4–129.7 kg).

Location data from 7 feral swine from GRSM and 1 feral swine from BISO were excluded due to inaccurate and potentially biased locations caused by collar malfunction or habituation to bait. Therefore, 31 individuals in GRSM (18 males, 14 females) and 9 individuals in BISO (5 males, 4 females) were retained for home range analysis. I chose method 3 for screening the location data which removed all 2D fixes with a PDOP >5 and removed all 3D fixes with a PDOP >10; this resulted in 98.4% and 98.5% data retention at GRSM and BISO, respectively (Table 3).

Feral swine in GRSM were radio collared for 9,080 radio-days, with individual feral swine being collared for a mean of 259 days (SD = 147, range = 18–613 days). Feral swine in BISO were radio collared for 2,219 radio-days, with individual feral swine being collared for a mean of 222 days (SD = 124, range = 9–367 days). Regression analyses for GRSM (R^2 = 0.047, P = 0.243) and BISO (R^2 = 0.011, P = 0.785) feral swine indicated that there was no relationship between home range size and the number of radiolocations; thus, sample sizes were adequate and did not bias home range size.

At GRSM, feral swine travel rates did not differ by sex (W = 30.5, P = 0.401) or by season ($\bar{x}$ = 4.355, df = 2, P = 0.113). Seasonal travel rates of feral swine in GRSM were greatest during fall ($\bar{x}$ = 145.3 m/hr, SD = 212.3) followed by winter (118.8 m/hr, SD = 214.4) and summer ($\bar{x}$ = 110.0 m/hr, SD = 178.3; Table 4). Feral swine travel rates at GRSM differed by time of day ($\bar{x}$ = 8.442, df = 2, $P < 0.05$). Feral swine travel rates at GRSM were highest at night ($\bar{x}$ = 151.2 m/hr, SD = 220.8), followed by day (118.0 m/hr, SD = 200.3), and crepuscular hours ($\bar{x}$ = 99.8 m/hr, SD = 180.9). Feral swine travel rates at BISO did not differ by sex (W = 6, P = 0.0649), season (W = 20, P = 0.818), or time of day ($\bar{x}$ = 3.577, df = 2, P = 0.167).

Feral swine path sinuosity at GRSM differed by sex (W = 7323.5, $P < 0.001$), season ($\bar{x}$ = 16.544, df = 2, $P < 0.001$), and time of day ($\bar{x}$ = 6.717, df = 2, $P < 0.05$). Female feral swine mean sinuosity at GRSM was higher ($\bar{x}$ = 0.093, SD = 0.012) than that of males ($\bar{x}$ = 0.083, SD = 0.014). Summer mean sinuosity for male feral swine at GRSM was highest ($\bar{x}$ = 0.065, SD = 0.009; Table 5) while fall and winter means were equal for males at GRSM ($\bar{x}$ = 0.057, SD = 0.011). For female feral swine at GRSM, both summer and winter sinuosity were highest ($\bar{x}$ = 0.070, SD = 0.011) while sinuosity was lowest during fall ($\bar{x}$ = 0.066, SD = 0.010). Male feral swine sinuosity based on time of day at GRSM was highest at night ($\bar{x}$ = 0.058, SD = 0.016), followed by daytime ($\bar{x}$ = 0.057, SD = 0.016), and crepuscular hours ($\bar{x}$ = 0.054, SD = 0.014). Female feral swine sinuosity based on time of day at GRSM was highest at night ($\bar{x}$ = 0.066, SD = 0.019), followed by daytime ($\bar{x}$ = 0.064, SD = 0.020), and crepuscular hours ($\bar{x}$ = 0.061, SD = 0.018).

Feral swine sinuosity also differed between sexes at BISO (W = 518.5, $P < 0.001$). Male feral swine were less sinuous ($\bar{x}$ = 0.073, SD = 0.008) than females ($\bar{x}$ = 0.095, SD = 0.014) at BISO. Female feral swine sinuosity at BISO differed by season with fall-winter having the highest sinuosity ($\bar{x}$ = 0.109, SD = 0.014), followed by spring-summer ($\bar{x}$ = 0.089, SD = 0.013). Male feral swine sinuosity at BISO also differed by season with spring-summer having the

Table 4. Travel rates in meters per hour for male and female feral swine at Great Smoky Mountains National Park during summer (1 April–14 August), fall (15 August–31 October), and winter (1 November–31 March) and at Big South Fork National River and Recreation Area during spring-summer (1 March–21 September) and fall-winter (22 September–28 February) seasons, 2015–2018.

	Male (n=18)		Female (n=14)		Overall (n= 31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
GRSM						
Day	131.0	212.2	89.3	167.6	118.0	200.3
Night	156.6	228.6	138.9	201.5	151.2	220.8
Crepuscular	100.6	187.4	98.0	165.5	99.8	180.9
Summer	112.9	183.9	101.0	158.4	109.1	176.1
Day	120.9	194.8	96.9	167.8	113.1	186.7
Night	143.9	198.3	127.6	173.4	138.6	190.8
Crepuscular	86.4	157.3	85.7	137.7	86.2	151.1
Fall	146.4	215.4	141.6	202.1	145.3	212.3

Table 4. Continued

	Male (n=18)		Female (n=14)		Overall (n= 31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Day	173.0	229.1	137.0	208.2	164.2	224.6
Night	169.1	236.9	170.6	200.8	169.4	228.9
Crepuscular	107.4	187.7	123.2	224.7	111.3	197.5
Winter	126.5	227.4	103.0	184.2	118.8	214.4
Day	117.6	214.2	67.3	147.1	100.9	196.0
Night	159.5	244.2	137.3	218.8	152.2	236.4
Crepuscular	108.5	207.5	99.5	161.7	105.6	194.0

BISO

	Male (n=18)		Female (n=14)		Overall (n= 31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Day	175.1	281.6	114.8	199.1	143.8	244.1
Night	202.8	307.6	130.7	209.7	164.1	262.0
Crepuscular	118.2	229.6	105.6	195.8	111.5	212.3
Spring-summer	145.4	265.2	133.7	230.9	139.6	248.8
Day	173.0	274.0	150.8	239.1	162.3	258.0
Night	166.5	268.5	141.2	235.1	154.0	252.7
Crepuscular	114.9	218.2	117.8	234.3	116.3	226.4
Fall-winter	173.5	295.0	100.0	159.8	131.5	230.6
Day	178.5	293.7	74.0	128.7	118.9	221.8

Table 4. Continued

	Male (n=18)		Female (n=14)		Overall (n= 31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Night	248.5	340.9	120.7	182.0	174.4	268.3
Crepuscular	122.9	244.6	92.7	143.6	105.7	194.2

Table 5. Sinuosity values (0 = straight line, 1 = Brownian movement) for male and female feral swine at Great Smoky Mountains National Park during summer (1 April–14 August), fall (15 August–31 October), and winter (1 November–31 March) and at Big South Fork National River and Recreation Area during spring-summer (1 March–21 September) and fall-winter (22 September–28 February) seasons, 2015–2018.

	Male (n=18)		Female (n=14)		Overall (n=31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
GRSM						
Day	0.060	0.012	0.068	0.015	0.063	0.013
Night	0.061	0.011	0.071	0.009	0.065	0.011
Crepuscular	0.057	0.009	0.065	0.009	0.060	0.010
Summer	0.088	0.013	0.098	0.016	0.091	0.014
Day	0.067	0.010	0.070	0.009	0.068	0.010
Night	0.067	0.010	0.073	0.012	0.069	0.011
Crepuscular	0.063	0.008	0.067	0.009	0064	0.008
Fall	0.078	0.019	0.087	0.014	0.081	0.018

Table 5. Continued

	Male (n=18)		Female (n=14)		Overall (n=31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Day	0.057	0.011	0.067	0.010	0.060	0.011
Night	0.060	0.011	0.068	0.011	0.062	0.011
Crepuscular	0.053	0.009	0.063	0.010	0.056	0.010
Winter	0.079	0.015	0.095	0.011	0.085	0.015
Day	0.056	0.013	0.068	0.016	0.061	0.015
Night	0.054	0.014	0.075	0.009	0.065	0.015
Crepuscular	0.055	0.012	0.067	0.010	0.060	0.013

BISO

	Male (n=18)		Female (n=14)		Overall (n=31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Day	0.060	0.012	0.072	0.009	0.065	0.012
Night	0.053	0.009	0.071	0.008	0.061	0.012
Crepuscular	0.049	0.006	0.066	0.008	0.056	0.011
Spring-summer	0.075	0.009	0.089	0.013	0.083	0.016
Day	0.061	0.012	0.067	0.007	0.064	0.010
Night	0.056	0.009	0.065	0.006	0.060	0.009
Crepuscular	0.051	0.006	0.061	0.006	0.055	0.008
Fall-winter	0.072	0.007	0.109	0.017	0.083	0.016
Day	0.054	0.009	0.083	0.014	0.070	0.019

Table 5. continued

	Male (n=18)		Female (n=14)		Overall (n=31)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Night	0.048	0.001	0.085	0.012	0.069	0.022
Crepuscular	0.047	0.005	0.076	0.011	0.064	0.017

highest sinuosity ($\bar{x}$ = 0.075, SD = 0.009), followed by fall-winter ($\bar{x}$ = 0.072, SD = 0.007). Male feral swine sinuosity based on time of day at BISO was highest at night ($\bar{x}$ = 0.061, SD = 0.011), followed by daytime ($\bar{x}$ = 0.060, SD = 0.012), and crepuscular hours ($\bar{x}$ = 0.057, SD = 0.009). Female feral swine sinuosity based on time of day at BISO was also highest at night ($\bar{x}$ = 0.071, SD = 0.009), followed by daytime ($\bar{x}$ = 0.068, SD = 0.015), and crepuscular hours ($\bar{x}$ = 0.065, SD = 0.009).

Feral swine home ranges in GRSM (95% KDE_{href}) differed based on sex ($W = 47$, $P <$ 0.01), with a male mean home range of 28.2 km^2 (SD = 19.8, range = 3.5–77.8 km^2) and female mean home range of 11.6 km^2 (SD = 9.7, range = 2.9–38.7 km^2; Table 6). At GRSM, winter male mean home range was largest ($\bar{x}$ = 29.9 km^2, SD = 26.6, range = 4.4–103.5 km^2), followed by fall ($\bar{x}$ = 23.5 km^2, SD = 15, range = 6.0–60.4 km^2), and summer ($\bar{x}$ = 14.8 km^2, SD = 10.1, range = 1.4–32.2 km^2). Fall female mean home range was largest ($\bar{x}$ = 10.2 km^2, SD = 6.0, range = 2.4–19.7 km^2) followed by winter ($\bar{x}$ = 9.8 km^2, SD = 5.5, range = 2.9–17.6 km^2) and summer ($\bar{x}$ = 8.9 km^2, SD = 6.0, range = 2.9–20.3 km^2).

Using the Mann-Whitney-Wilcoxon Test, home ranges in BISO did not differ based on sex. Male feral swine mean home range in BISO was 22.0 km^2 (SD = 7.0, range = 6.1–43.3 km^2). Female feral swine mean home range in BISO was 11.8 km^2 (SD = 1.8, range = 7.1–15.4 km^2; Table 6). Fall-winter home range mean for BISO feral swine was 15.1 km^2 (SD = 6.4, range = 3.8 – 49.0 km^2). Spring-summer mean home range in BISO was 16.3 km^2 (SD = 2.8, range = 6.1 – 32.8 km^2). Home range sizes did not differ between BISO and GRSM when data were pooled ($F = 0.325$, $P = 0.572$) or by sex ($F = 0.275$, $P = 0.603$).

The mean centroid distances used as the radii for the moving windows were 612.6 m in GRSM. Frequency histograms describing used versus available land cover layers revealed that

Table 6. Home range sizes (95% Kernel Density Estimates) for male and female feral swine at Great Smoky Mountains National Park during summer (1 April–14 August), fall (15 August–31 October), and winter (1 November–31 March) and at Big South Fork National River and Recreation Area during spring-summer (1 March–21 September) and fall-winter (22 September–28 February) seasons, 2015–2017.

	Male (n=18)		Female (n= 14)		Overall (n=31)	
	$\bar{x}$ (km^2)	SD	$\bar{x}$ (km^2)	SD	$\bar{x}$ (km^2)	SD
GRSM						
All Seasons	28.2	19.8	11.6	9.7	21.2	18.3
Summer	14.8	10.1	8.9	6.0	12.5	9.2
Fall	23.5	15.0	10.2	6.0	20.2	14.5
Winter	29.9	26.6	9.8	5.5	22.9	23.3
BISO						
All Seasons	22.0	7.0	11.8	1.8	17.5	4.2
Fall-winter	28.8	11.2	4.9	0.5	15.1	6.4
Spring-summer	17.3	5.1	15.1	2.1	16.3	2.8

winter females at GRSM showed a slight preference for ridges and water, and for oak and cove species (Figures 2 and 3). These GRSM feral swine tended to prefer somewhat low slopes but there was a relatively strong preference for lower elevations (~500–875 m, Figure 4). Areas with higher solar radiation were selected slightly more than what was available (Figure 5). These characteristics are reflected in the D^2 model for GRSM (Figure 6), with elevation appearing predominant.

The mean centroid distances used as the radii for the moving windows were 476.8 m in BISO. At BISO, fall-winter females showed a tendency to stay close to water (Figure 7). Ridges, oak species, and cove species were selected in proportion to their availability as were ridges (Figures 7 and 8). High slopes and low elevations were selected for as were areas with lower exposure to solar radiation (Figures 9 and 10). The D^2 model for BISO seems to indicate the female feral swine habitat suitability during the fall-winter is mostly determined by distance to water (Figure 11).

GRSM STABLE ISOTOPE ANALYSIS

We collected I3 (incisors) or P1 (premolars) from 30 of the feral swine trapped in GRSM and 13 premolars from domestic feral swine. The δ13C isotope values were significantly lower in feral swine teeth (-17.3 pdb, SD = 1.2, 95% CI = -17.6 – -16.9; $F = 801.4$, $P < 0.001$) than in domestic hog teeth (-5.9 pdb, SD = 1.1, 95% CI = -6.5 – -5.4). Oxygen isotope mean value was -5.0 pdb (SD = 0.2, 95% CI = -5.13 – -4.89) for domestic feral swine and -7.1 pdb (SD = 1.1, 95% CI = -7.4 – -6.8) for feral swine. Oxygen values also differed between wild and domestic hog teeth ($F = 47.8$, $P < 0.001$). The carbon and oxygen isotope values were clearly capable of differentiating between the wild and domestic hog tooth samples (Figure 12). I did not detect

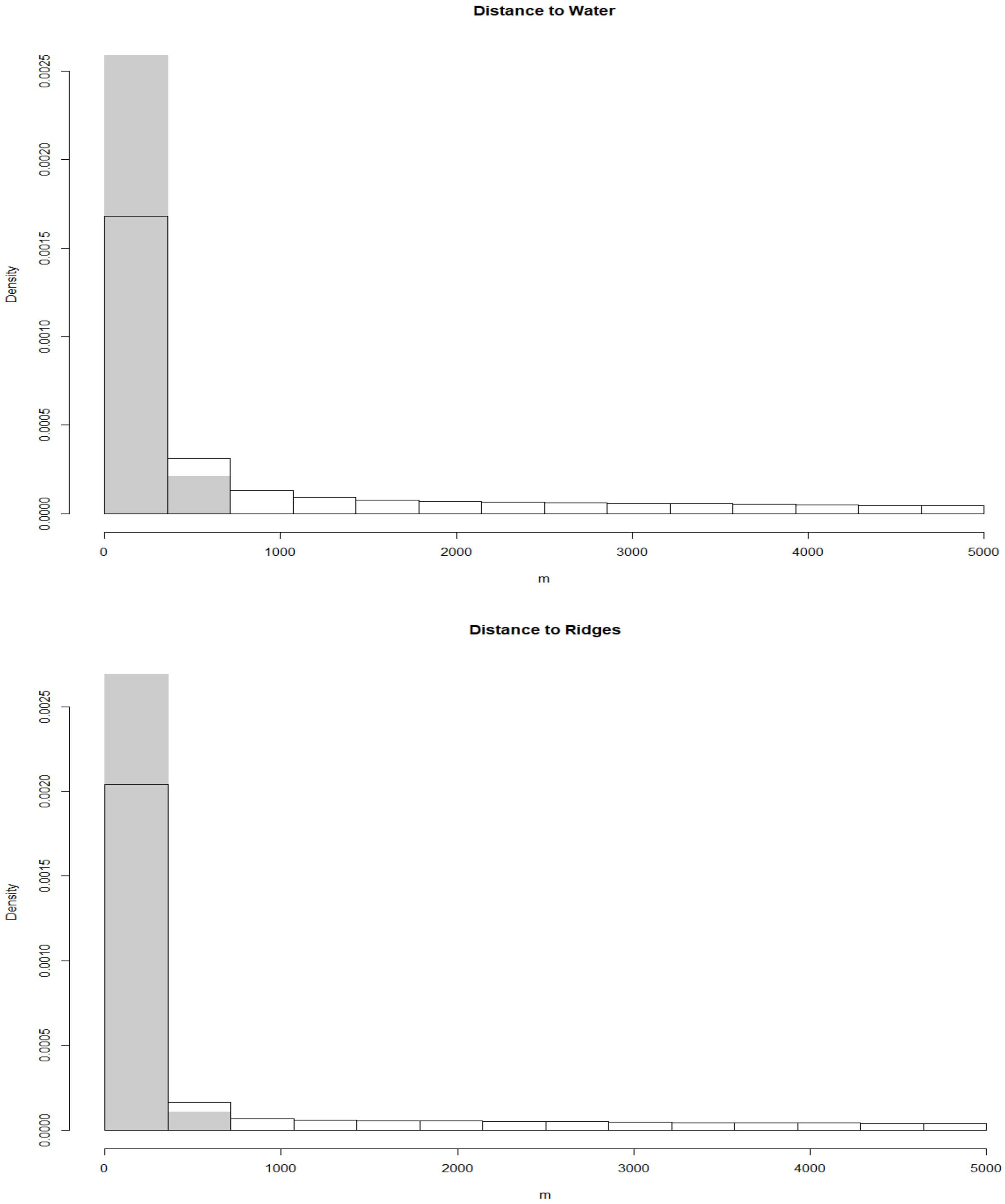


Figure 2. Used (gray) versus available (white) Distance to Water and Distance to Ridges land cover for Great Smoky Mountains National Park by female feral swine based on global positioning system (GPS) radio collar data collected during winter 2015–2017.

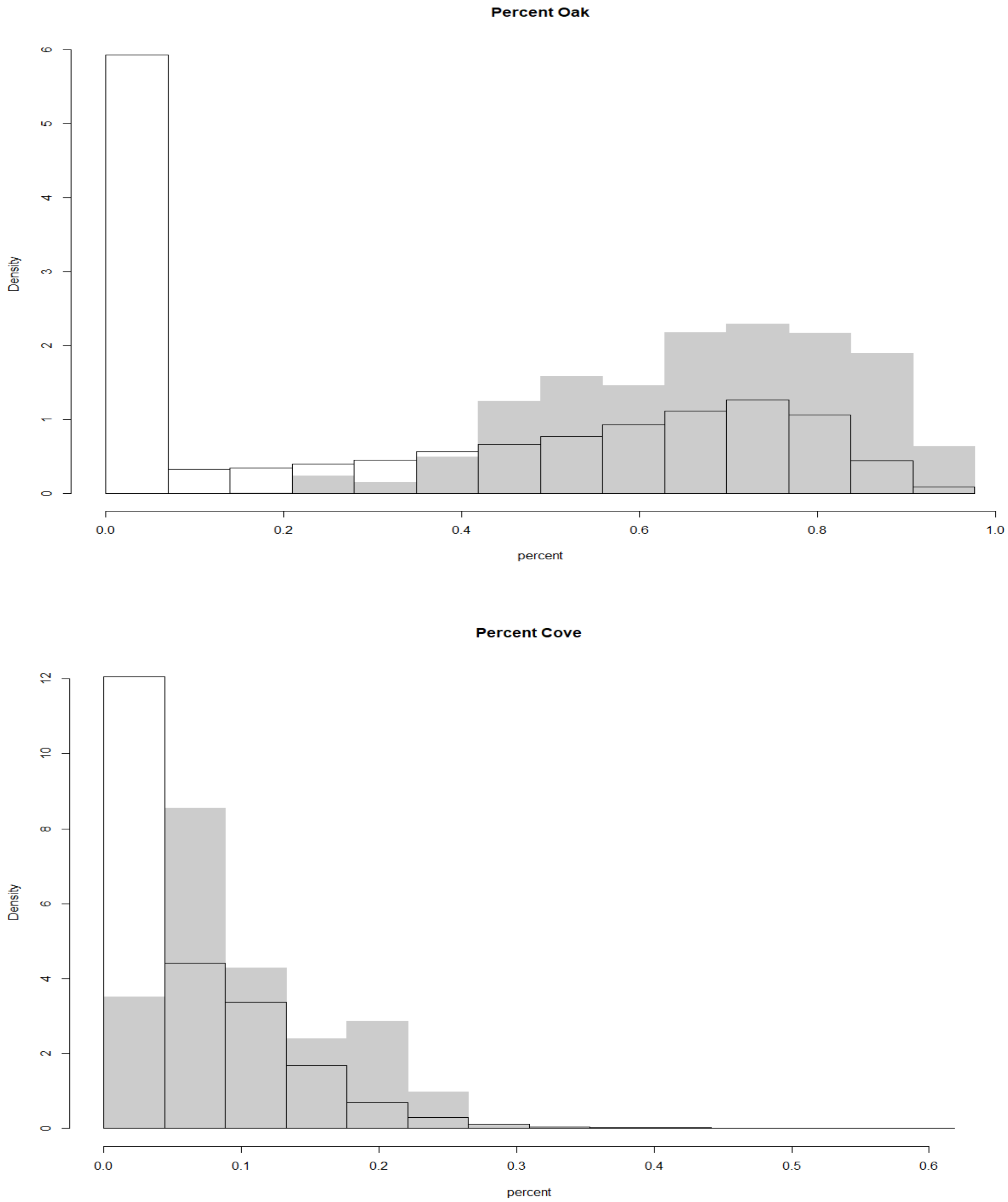


Figure 3. Used (gray) versus available (white) Percent Oak and Percent Cove land cover for Great Smoky Mountains National Park females based on global positioning system (GPS) radio collar data collected during winter 2015–2017.

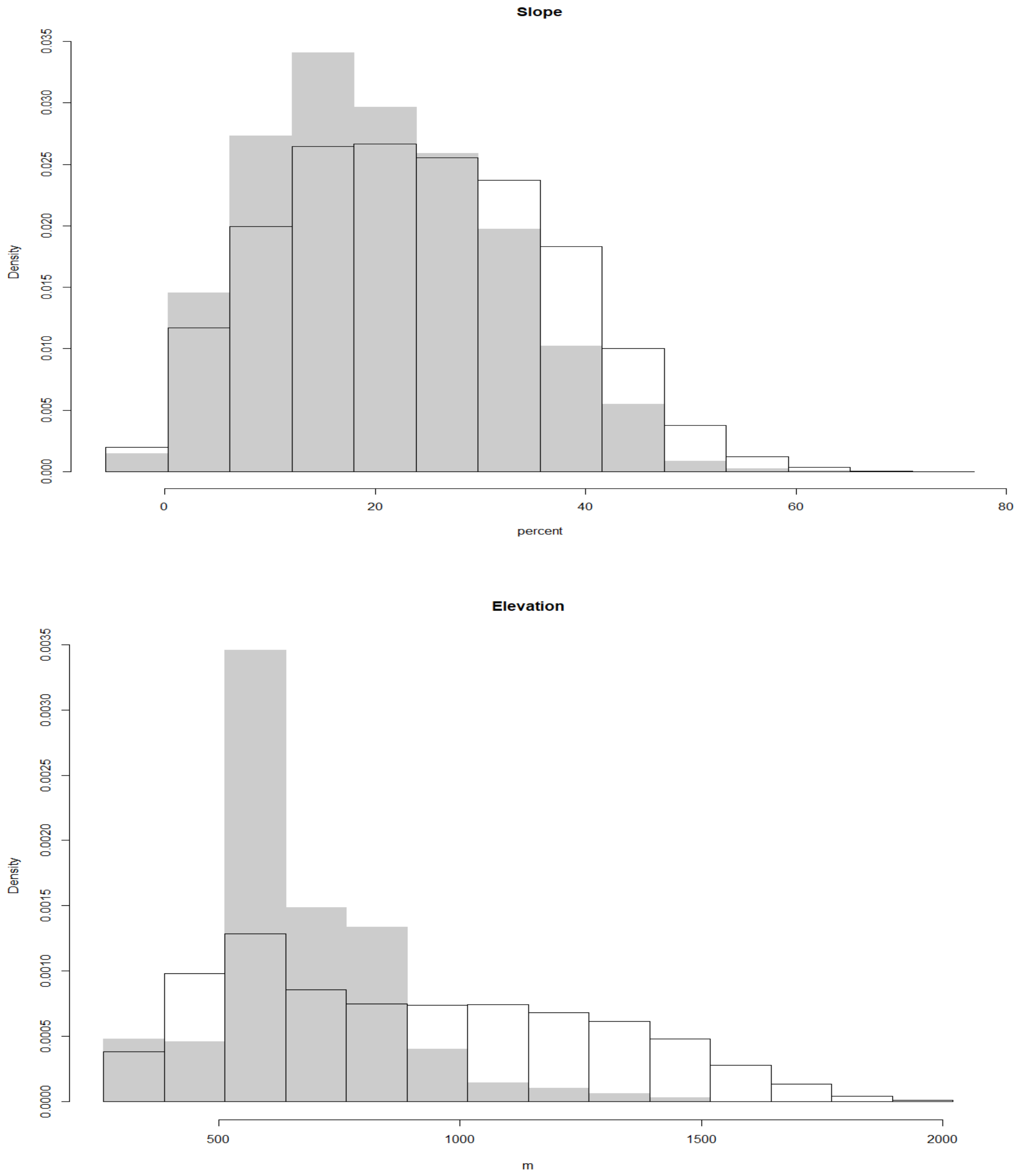


Figure 4. Used (gray) versus available (white) Slope and Elevation land cover for Great Smoky Mountains National Park females based on global positioning system (GPS) radio collar data collected during winter 2015–2017.

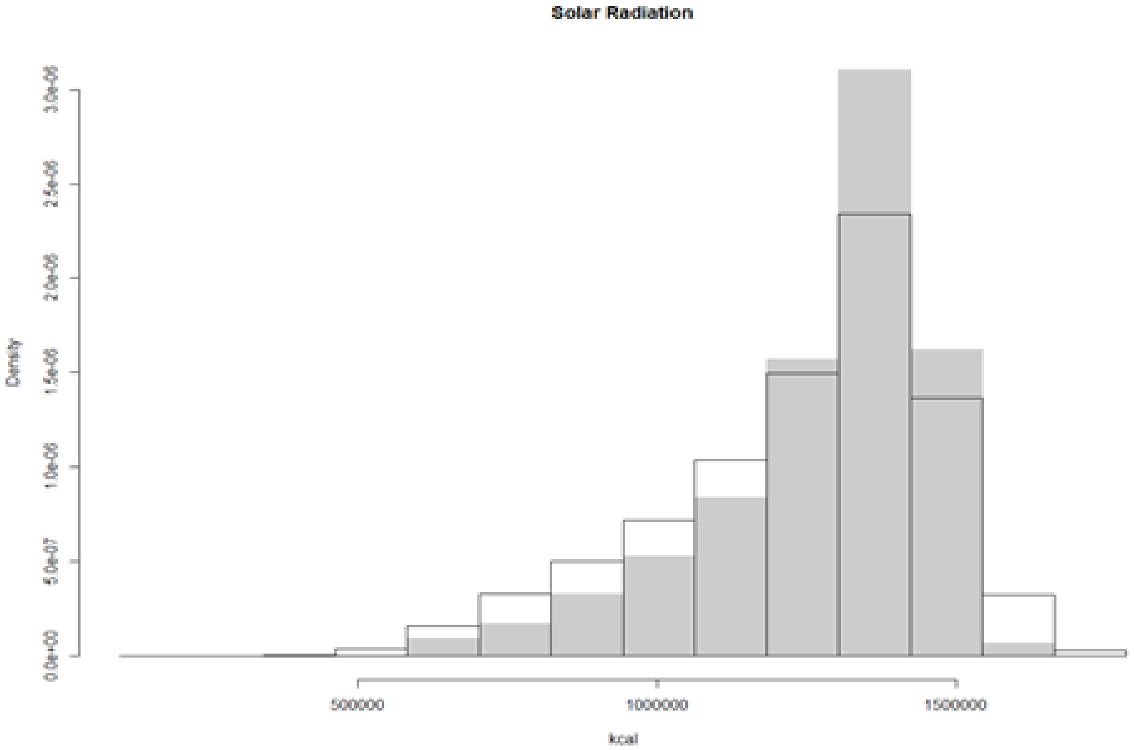


Figure 5. Used (gray) versus available (white) Solar Radiation land cover for Great Smoky Mountains National Park females based on global positioning system (GPS) radio collar data collected during winter 2015–2017.

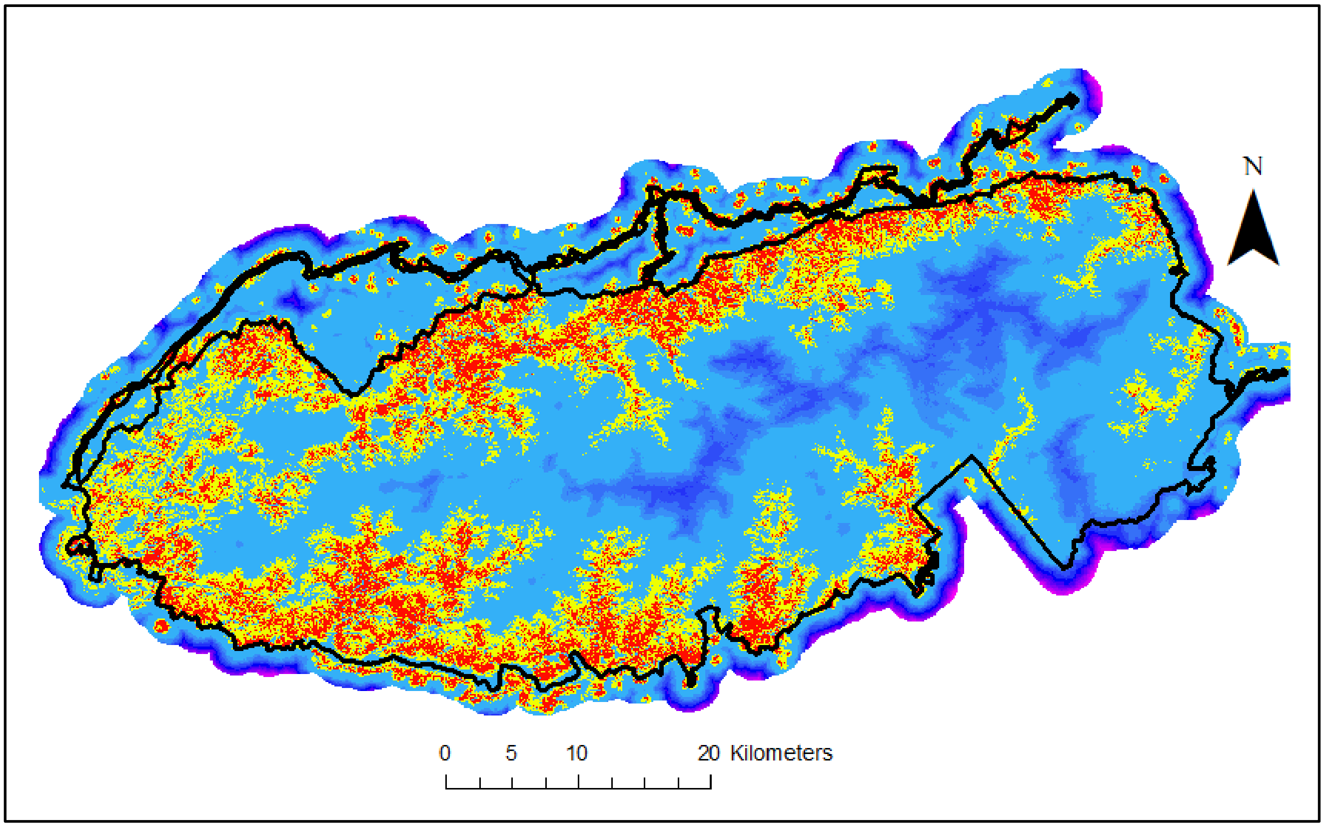


Figure 6. Map showing ArcMap output of Mahalanobis distance in Great Smoky Mountains National Park representing the “ideal” habitat (red and yellow) based on female GPS locations during winters 2015–2018.

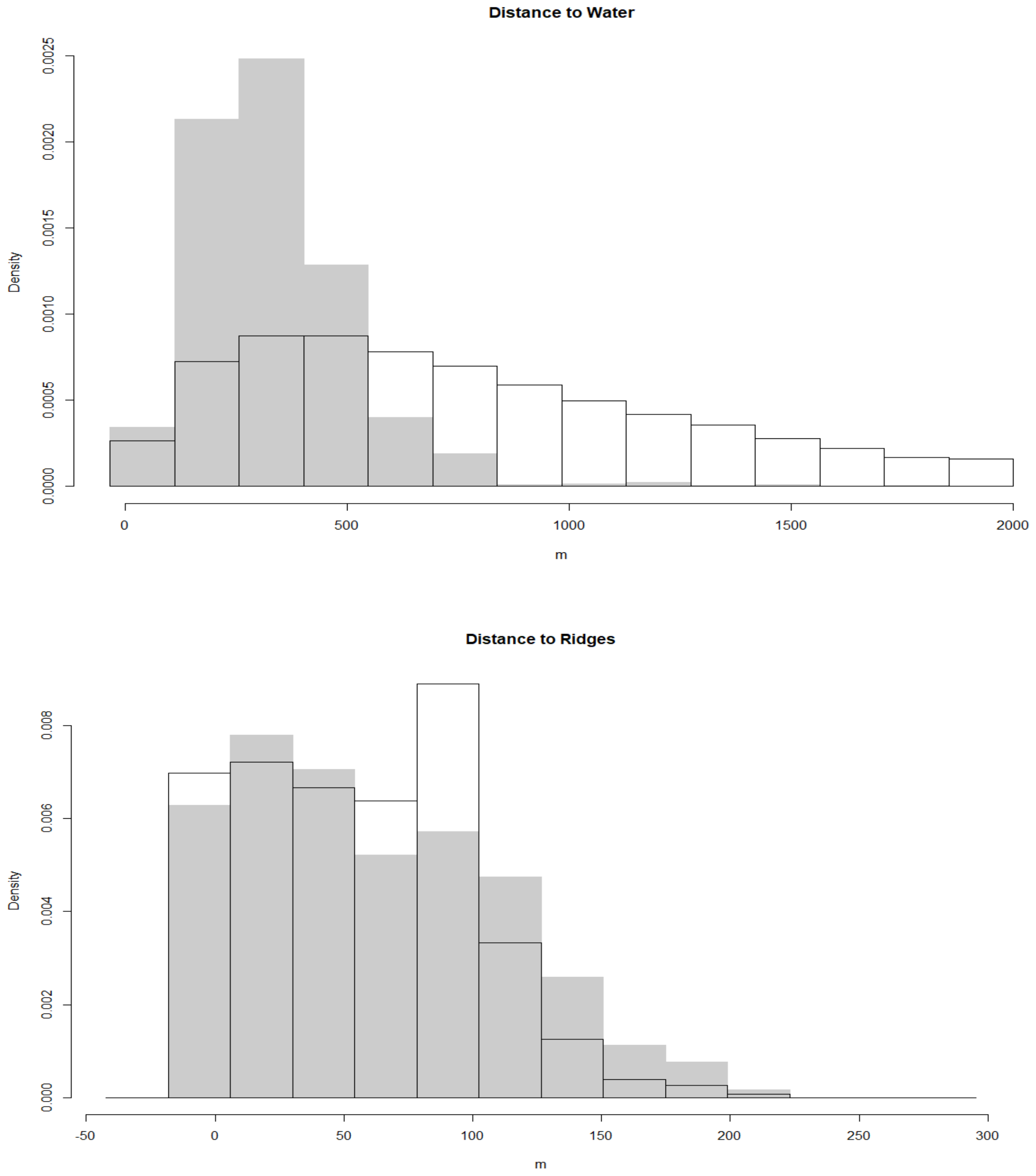
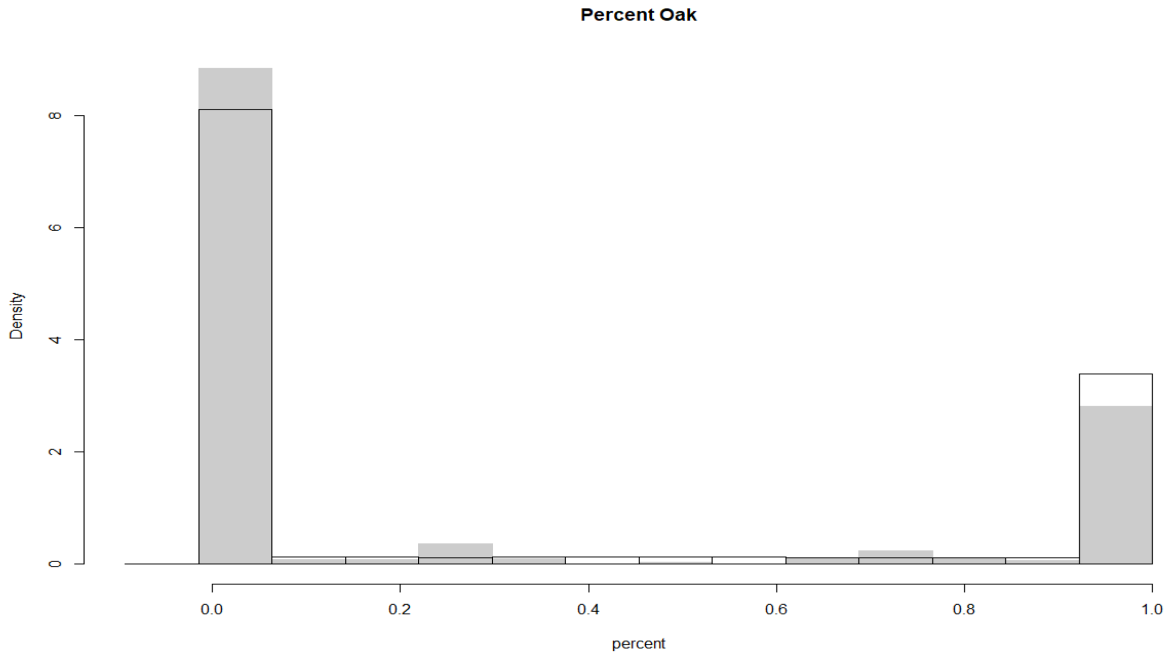


Figure 7. Used (gray) versus available (white) Distance to Water and Distance to Ridges land cover for Big South Fork National River and Recreation Area females based on global positioning system (GPS) radio collar data collected during fall-winter 2015–2017.



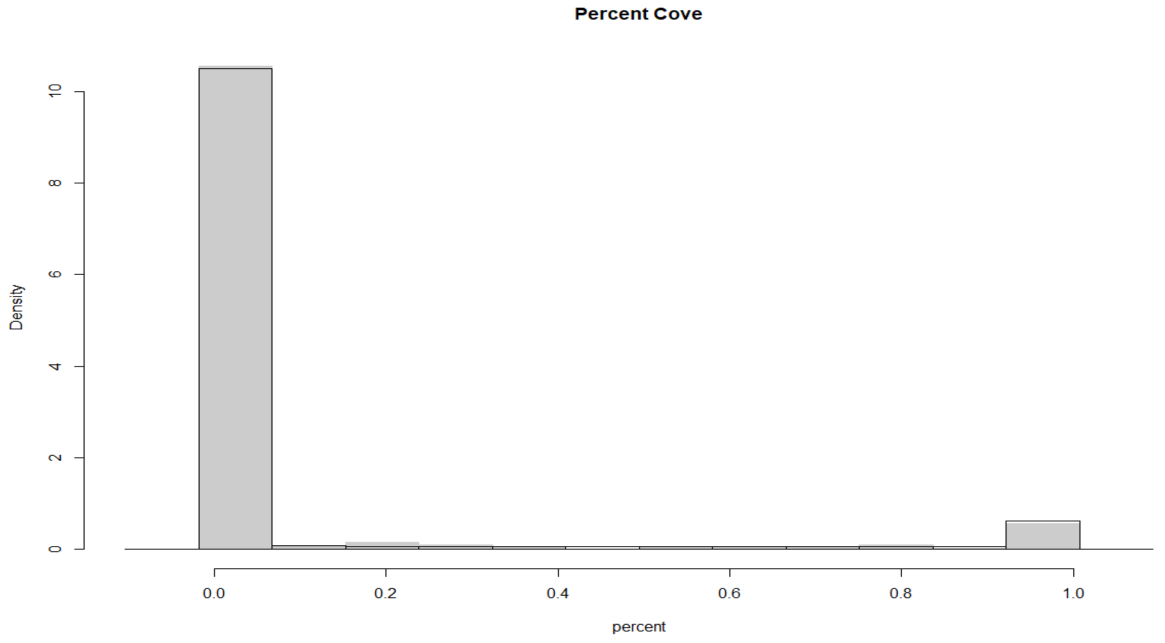


Figure 8. Used (gray) versus available (white) Percent Oak and Percent Cove land cover for Big South Fork National River and Recreation Area females based on global positioning system (GPS) radio collar data collected during fall-winter 2015–2017.

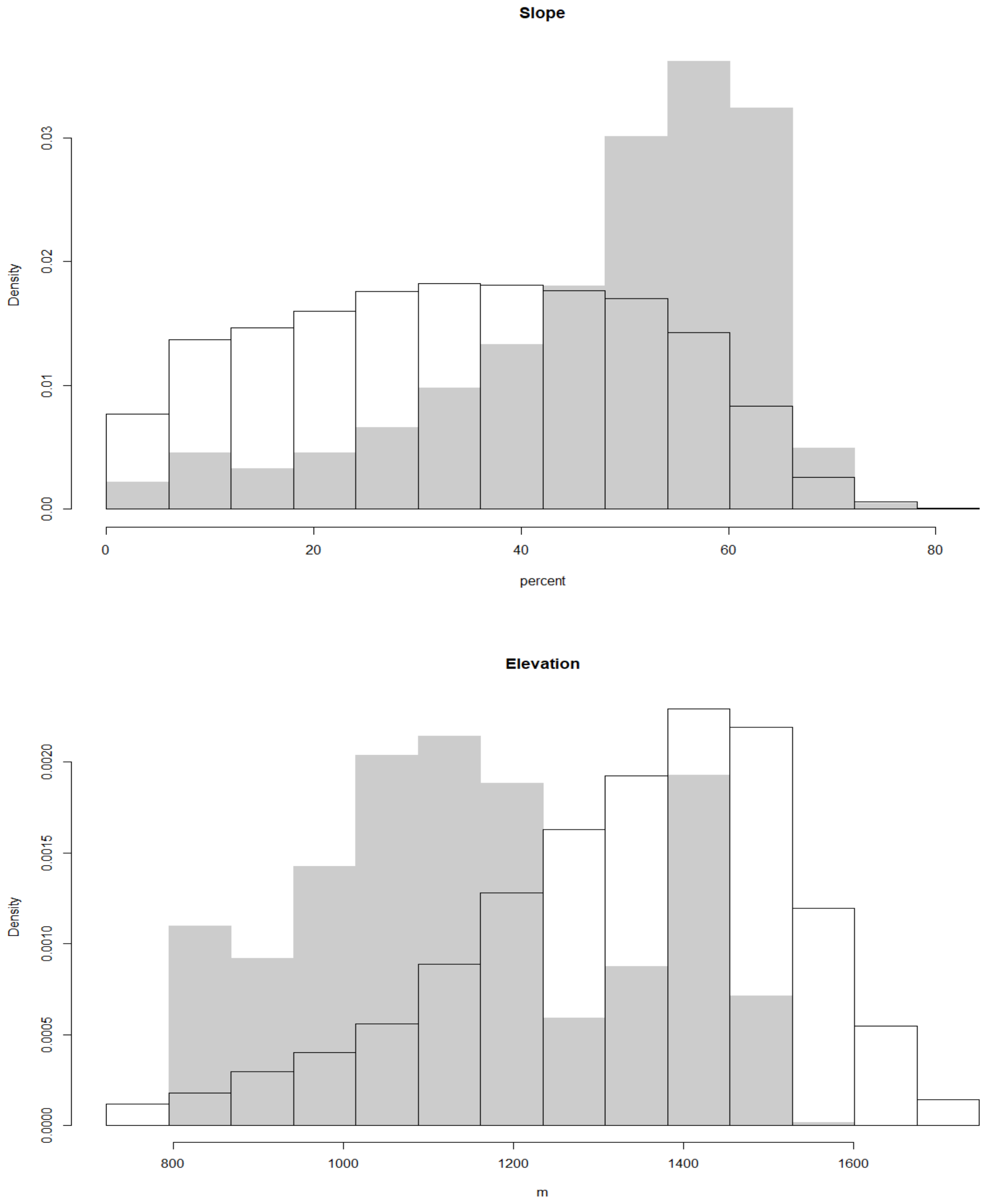


Figure 9. Used (gray) versus available (white) Slope and Elevation land cover for Big South Fork National River and Recreation Area females based on global positioning system (GPS) radio collar data collected during fall-winter 2015–2017.

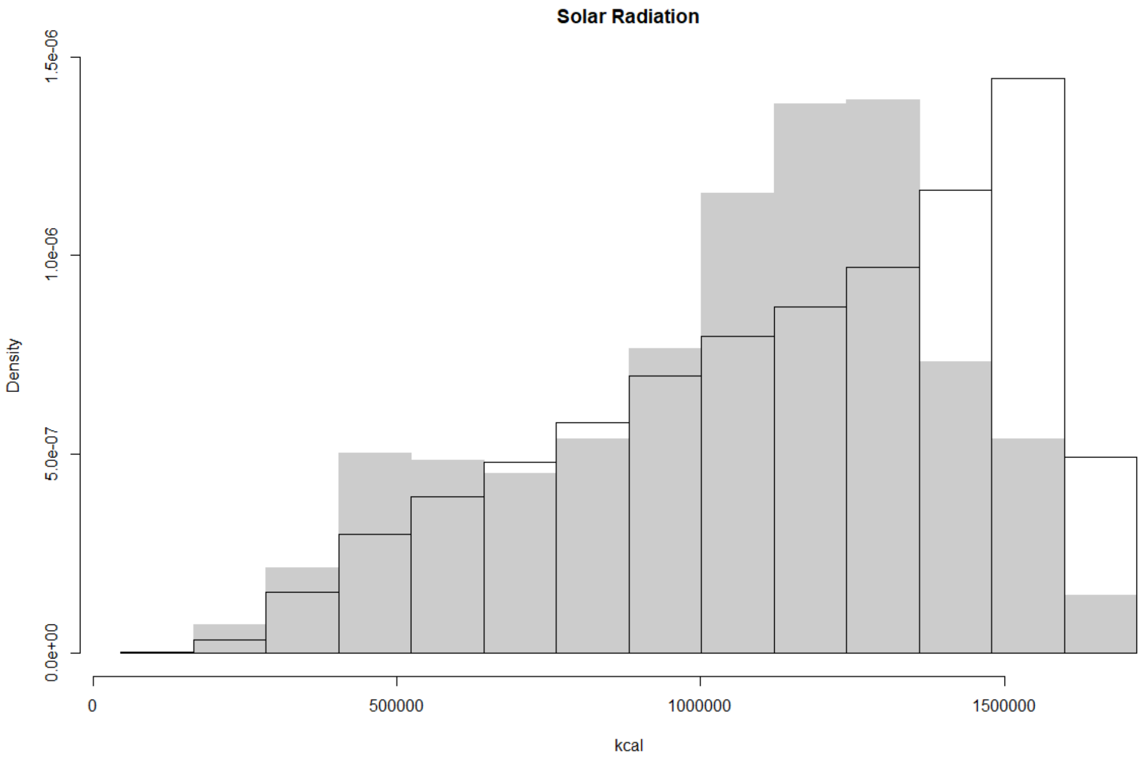


Figure 10. Used (gray) versus available (white) Solar Radiation land cover for Big South Fork National River and Recreation Area females based on global positioning system (GPS) radio collar data collected during fall-winter 2015–2017.

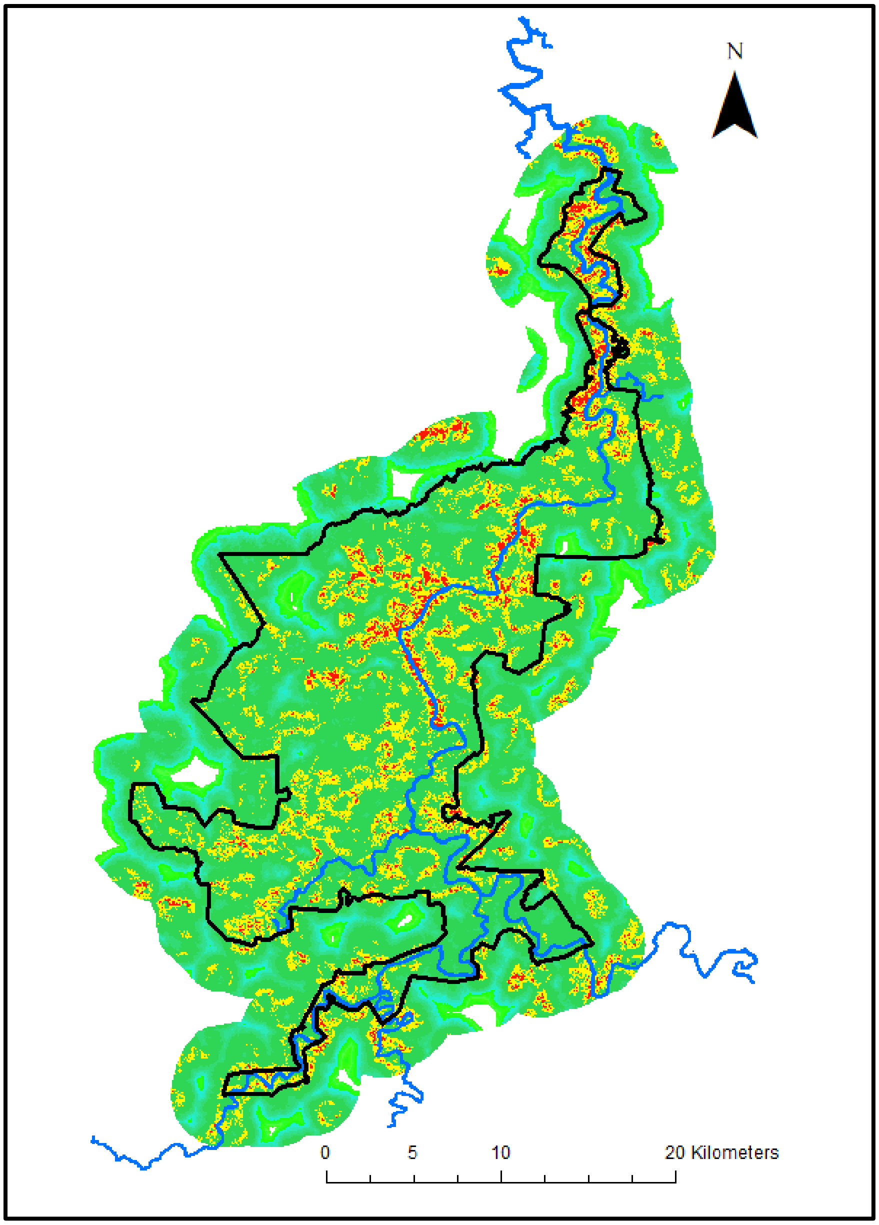


Figure 11. Map showing ArcMap output of Mahalanobis distance in Big South Fork National River and Recreation Area representing the "ideal" habitat (red and yellow) based on female GPS locations during fall-winter, 2016 and 2017.

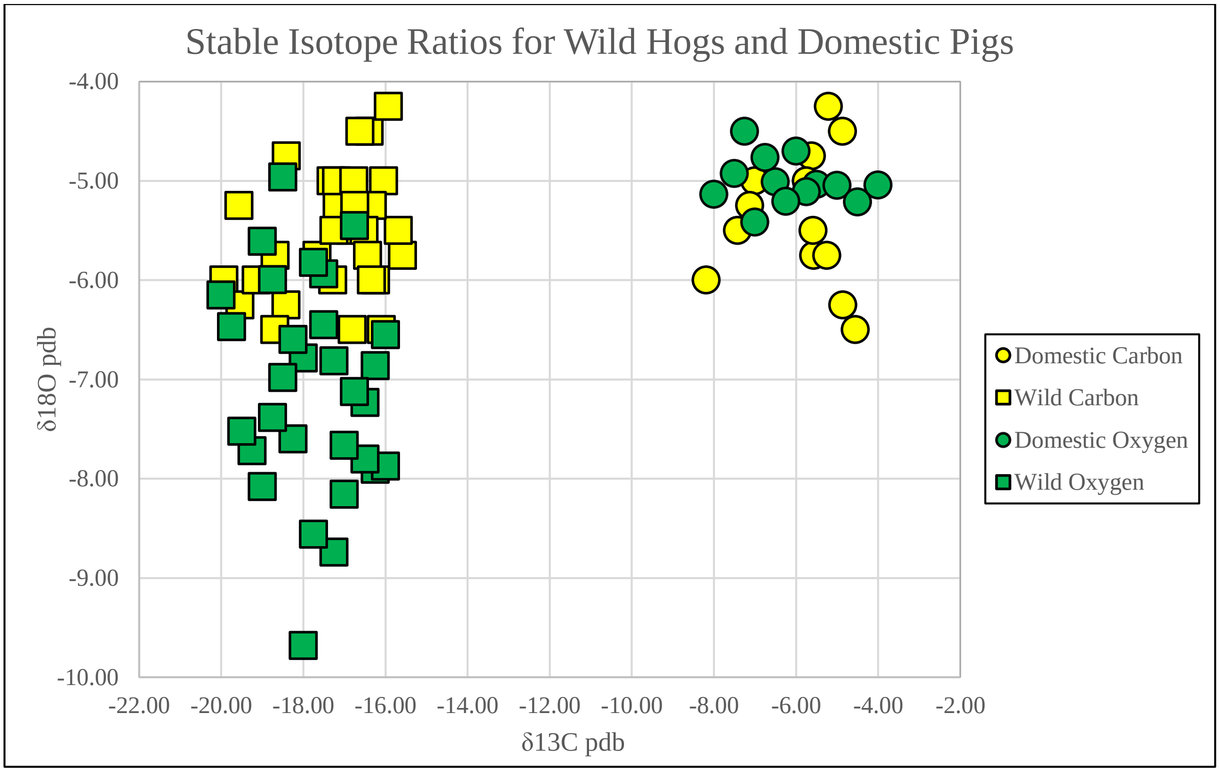


Figure 12. Carbon (δ13C) and oxygen (δ12O) stable isotope ratios from tooth enamel of Great Smoky Mountains National Park wild and local domestic swine

any overlap in carbon isotope ratios for the 2 groups but oxygen isotope ratios for 2 feral hogs overlapped the domestic swine sampled.

EVALUATION OF BAM^{TM} AS AN ANESTHETIC FOR FERAL SWINE

Of the 48 feral swine captured, 41 (20 males, 21 females) were monitored to characterize the physiologic and clinical responses of immobilization with BAM^{TM}. Mean masses of the 41 male and female feral swine were 74.7 kg and 71.6 kg, respectively and mean ages were 36 months and 31 months, respectively. Mean body temperature, heart rate, and respiration rate for males was 38.4°C, 54 bpm, and 15 breaths/min and for females was 38.3°C, 58 bpm, and 15 breaths/m, respectively. Mean work-up time was 60 min (SD = 24.0 min, range = 21–120). Mean induction time (initial injection to anesthesia, Table 7) was 16 min (SD = 15, range = 4.0–42.0) and did not differ by sex ($F = 0.104$, $P = 0.749$). Likewise, mean reversal times did not differ by sex ($F = 0.291$, $P = 0.594$) and averaged 4 min (SD = 4, range = 0.8–23.0 min). Induction time differed by capture method ($F = 10.960$, $P < 0.001$) with induction times being greater for drop nets ($\bar{x}$ = 35.0 min, SD = 8) than single traps ($\bar{x}$ = 16.0 min, SD = 9) and corral traps ($\bar{x}$ = 7.0 min, SD = 3). I observed no mortalities from the drug and induction and recovery was adequate.

Table 7. Time, in observational stages combined for total work-up of male (n = 20) and female swine (n = 21) trapped and collared in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area. The breakdown of time stages served in assessment of potential use of butorphanol, azaperone and medetomidine (BAM^{TM}) drug combination.

	Duration (minutes)			
Stage	Males (n = 20)	SD	Females (n = 21)	SD
1. Injection to 1st Sign	4	0.002	3	0.001
2 Injection to Sternal Position	7	0.003	6	0.002
3 Reversal to Departure	5	0.002	5	0.004
4 Total Induction	15	0.007	6	0.007
5 Total Work-up	61	0.017	59	0.018

5. DISCUSSION

MOVEMENTS, ACTIVITY, AND RESOURCE SELECTION

Female feral swine often exhibit an anestrous period in summer and autumn (Mauget 1981). The social unit peak in January-February reported by Graves et al. (1975) represents females with recently weaned piglets that remain in their sibling groups. Additionally, males pursue females weaning piglets throughout the winter with the goal of reproduction. Graves et al. (1975) observed that the nuclear social unit in swine is based around 1 to several females and their offspring and adult males associate with the female(s) whenever the female(s) exhibits sexual receptivity. Their study stated that solitary individuals were commonly sighted on Ossabaw Island, Georgia, USA during the summer months, but almost never during January-February. Conley et al. (1972), working on feral swine in Tellico Wildlife Management Area in Monroe County, Tennessee, USA, also recorded comparable groups of wild boar. Considering these circumstances, GRSM and BISO feral swine may be in largest assembly during winter seasons as females wean offspring and become receptive to reproduction, likely attracting a following of multiple males.

Feral swine in GRSM traveled faster and used travel routes that were more direct in fall (15 August–31 October). The faster, direct travel in fall are likely associated with feral swine searching for acorns. Conley et al. (1972) reported that feral swine in Tennessee traveled from shaded day beds to wallows and back to shaded cover. Movements from cover to feeding areas in fall could account for the greater rates of travel and lower sinuosity that I found. Graves et al. (1975) concluded in his study on Ossabaw Island that the mast crop has a great impact on the distribution of the animals. Singer et al. (1981) reported that the stomach contents of GRSM feral swine in late fall was made up of 84% hard mast. Singer et al. (1981), Baber and Coblentz, (1986), Saunders and Kay (1991), Hayes et al. (2009), and Franckowiak and Poché (2018) found changes in seasonal home ranges comparable to what I found at GRSM.

Male hog home ranges at GRSM were >2.5 times larger than females, which is consistent with other research on feral swine (Baber and Coblentz 1986, Saunders and Kay 1991, Caley 1997, and Adkins and Harveson 2007). The smallest home ranges and lowest travel rates in GRSM were for females during the day in winter (1 November–31 March) and one of the largest for males were during winter at night. Although feral swine can breed year-round, Taylor et al. (1998) reported that pigs were more likely to conceive litters from September through December, which included my winter period. Females may reduce their home range and become solitary when they are ready to give birth (Kurz and Marchinton 1972) and female movements may be restricted soon after parturition when piglets are too small to travel great distances. Most feral swine births take place in late winter or early spring (Sweeny et al. (1979, Taylor et al. 1998), which would coincide roughly with my winter season. Singer et al. (1981) suggested that greater movements by males in GRSM was due to breeding activity and Barrett (1971) also believed that the large home ranges of males resulted from intensified searches for breeding opportunities. These observations are consistent with my findings. Daily movements in GRSM were smallest during crepuscular hours, and Singer et al. (1981) made similar observations. Whether this is natural behavior or an adaptation by feral swine to competition with black bears (*Ursus americanus*), disturbance by NPS hunters, or other factors is not known.

Home ranges of BISO males were twice those of BISO females. At BISO, male movement rates at night during the fall-winter (22 September–28 February) were more than double the rate of female night movements of the same season. These higher travel rates, coupled with low sinuosity values, suggest directed movements similar to what I observed in

GRSM. As at GRSM, these male movement patterns were likely influenced by hard mast availability and attempts to locate estrous females. Also similar to GRSM, lowest travel rates and highest sinuosity in BISO were by females in the daytime during fall-winter, possibly a result of reproductive behavior and/or farrowing. Interestingly, public hunting pressure at BISO did not seem to increase movement or activity of females.

During the spring-summer (1 March–21 September) at BISO, NPS staff can legally utilize bait and trapping for hog removal and public hunting pressure is low. I found no differences between male and female home ranges at that time. Females from both parks had similar annual home ranges (11.8 km^2 at BISO, 11.6 km^2 at GRSM). Feral swine of both sexes can become habituated to an area that is regularly baited with corn and anecdotal data using field cameras at corral trap sites confirmed that sounders visited multiple sites on the same night on multiple occasions.

Resource selection analyses demonstrated similar relationships among some landscape covariates between BISO and GRSM but differed on others. Feral swine in GRSM selected low to mid-elevations with sunny (generally southerly) aspects and associated with water. These are areas where oaks were predominant but also escape cover in the form of Rhododendron (*Rhododendron maxima*), similar to what Conley et al. (1972) described in other parts of Tennessee. Feral swine at GRSM tended to select aspects with higher solar radiation, which were generally south facing. At BISO, patterns were similar, with feral swine preferring to be near water at lower elevations and in more shaded aspects. Pine and Gerdes (1973) noted that surface water and areas that remain moist throughout the year are essential to good wild hog habitat. The apparent contradiction that GRSM feral swine selected gentle slopes but BISO feral swine selected steeper slopes is probably because streams at BISO are more closely associated with ravines, due to the contrasting geologic histories of the two areas. The same relationship probably accounts for the contradiction in solar radiation as well. Areas near streams and rivers generally receive less sun than areas on top of the plateau. GRSM is in the Blue Ridge physiographic province and, as such, most rock formations are granitic. At BISO, most geologic formations are sedimentary, being in the Appalachian Plateau physiographic province. There is a greater tendency for streams and rivers at BISO to cut through these sedimentary sandstones and thus be associated with steeper slopes (NPS 2019). The selection by BISO feral swine for steep slopes is probably a reflection of the terrain and feral swine preference for habitats near water, as the case in GRSM.

STABLE ISOTOPE ANALYSIS

The lighter δ13C ratios for domestic feral swine compared with wild feral swine supported my hypothesis that domestic swine would have carbon signatures that reflected corn diets early in life. However, I did not sample any feral swine with signatures indicative of an early corn diet prior to enamel formation at GRSM. These results can be interpreted in at least 3 ways. Firstly, feral swine that were translocated to GRSM may have been moved prior to enamel formation (8–16 months of age). That rationale is possible, but probably not likely. In addition, feral swine this young would likely not have high survival rates compared to feral swine released as adults. Secondly, feral swine that were translocated may have had similar diets to GRSM feral swine. This finding is possible if translocated feral swine were from wild stock that had been born outside GRSM without access to corn agriculture. Lastly, the incidence of recently translocated feral swine in GRSM may be low. It is not possible to differentiate between the last two possibilities though it is noteworthy that I found no evidence that domesticated or feral swine from agricultural areas had been released into the GRSM population.

There was a significant amount of variation in δ18O signatures in feral versus domestic swine. The oxygen isotopic ratios in animal tissue depend on a variety of factors. Isotopic fractionation in O_2 takes place as water evaporates or condenses and this leads to changes in the isotopic ratio of water vapor. Consequently, isotopic ratios of O_2 will differ for animals that consumed water from lakes vs streams. This can also result in more negative $^{16}O/^{18}O$ values in precipitation from colder climates and higher elevations. The isotopic variation of waters in GRSM is undoubtedly greater than for domestically raised swine, and the $^{16}O/^{18}O$ ratios of 2 GRSM hogs overlapped those of the domestic swine. Whether this is an indication that these 2 pigs were from domestic stock is not known. However, it has been shown that C3 and C4 plants exhibit different δ18O signatures, which could have confounded my analysis (Kohn 1996). Clearly, more work needs to be done to evaluate O_2 isotopes as an evaluation tool.

EVALUATION OF BAM^{TM} AS AN ANESTHETIC FOR FERAL SWINE

Using BAM^{TM} allowed for safe and effective handling of feral swine during work-ups for both sampled swine and technicians. No work-ups required emergency reversals nor was there evidence of unusual responses while sampled feral swine were sedated; only 1 of the 40 feral swine was responsive to tooth removal. The average duration of anesthesia (60 min) was adequate for collection of all necessary samples. No mortalities or significant injuries were associated with anesthesia.

Dosages recommended by ZooPharm were often inadequate to immobilize the feral swine in my study. Thirteen of 41 (32%) of the feral swine captured for this project required a second injection of BAM^{TM} and 3 required a third injection. For the purpose of GPS collaring and sampling adult feral swine in the field, I suggest a 50% increase in the initial dose, recommended by Zoopharm for domestic swine, to 0.75 ml BAM^{TM} for a 50 lb. (22.7 kg) feral swine (i.e., from 0.6 mg/kg butorphanol, 0.2 mg/kg azaperone, 0.2 mg/kg medetomidine to 0.9 mg/kg butorphanol, 0.3 mg/kg azaperone, 0.3 mg/kg medetomidine).

The duration of recovery was short (14.0 min, max = 23.0 min) which allowed us to process several feral swine in a day. The quality of recovery was also adequate; feral swine did not struggle to stand, walk or vacate trapping sites after the work-ups were complete. After increasing BAM^{TM} doses for adult feral swine in the field, adequate anesthesia was achieved with little to no indication of stress or discomfort. Therefore, I recommend its use for similar studies seeking to fit feral swine with GPS collars and collecting biological samples.

6. MANAGEMENT IMPLICATIONS

Recommendations for BISO:

- Consider closing the public hunting season indefinitely or create alternatives such as informing hunters of the locations of recent feral swine activities. The participation of local hunters can increase feral swine kills and their cooperation with NPS staff can strengthen the relationship between the public and park. It may also be beneficial to allow hunters to bait specifically for feral swine during the hunting season.
- The addition of more wildlife staff is necessary to cover multiple large areas increasing feral swine kills.
- Increase night hunting while feral swine are most active. The use of night vision and thermal scopes allow for more efficient hunting and maximum feral swine removal.
- Begin feral swine control focus based on D^2 map. Confirm the presence of feral swine using bait sites and camera traps. Traps should be placed in areas of highest feral swine activities such as areas close to water at the bottom of steep slopes.
- Increase free range hunting pressure using rifles starting from higher elevations in an effort to strategically pressure feral swine to lower elevations and within proximity of bait and trap sites.
- Continue construction and addition of corral traps in areas depicted by D^2 output map. Trap type and size should depend on amount of feral swine activity confirmed by camera traps.

Recommendations for GRSM:

- Begin management focus on D^2 map results. Trapping and hunting efforts should be focused on locations with the highest likelihood of the presence of feral swine.
- The addition of more corral traps is necessary throughout the lower elevations where the D^2 map depicts as areas of high probability of the presence of feral swine and areas that feral swine traditionally occupy.
- Continue winter hunting and trapping with the addition of traps large enough to capture entire sounders while feral swine numbers are at their seasonal peak.
- Begin baiting heavily and camera monitoring as fall concludes and black bears begin winter torpor. During the winter, competition with bears for food decreases, as well as the availability of hard mast. Therefore, feral swine can become habituated to bait sites and trap locations that are easy to locate, increasing success of capture.
- Hunters, on foot, should also begin aggressive hunting pressure from higher elevations in fall with the goal of pushing feral swine to lower and more accessible bait and trap locations. NPS wildlife staff can gage the success of their efforts based on the number of feral swine captured on camera near bait sites and traps.
- The use of box traps is still beneficial for the removal of feral swine. Continue to place these single traps in locations where solitary feral swine are present.
- In remote areas that are difficult to construct corral traps or place box traps, continue to utilize drop nets for the capture of sounders and/or individuals. These traps can be best used for short-term baiting and trapping at higher elevations with difficult terrain.

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VITA

Patrick Helm was born in Louisville, Kentucky. He is the second oldest of four boys. After 4th grade his family moved to Asheville, NC where he grew up and acquired his passion for the outdoors. He attended Glen Arden Elementary, Valley Springs Middle School and graduated high school from Christ School in Arden, NC. Patrick attended his freshman year in college at Wofford in Spartanburg, SC, where he met his future wife Beth. Feeling a bit unsettled, Patrick relocated to Charleston, SC and attended school at the College of Charleston in pursuit of a studio art degree. While a student in Charleston, Patrick's soon-to-be wife, Beth, was hired as a pharmacist in Juneau, AK. In Juneau, Patrick contemplated his future while working for a local float plane outfit during the summers and as a certified ski technician during the winters. Patrick and Beth had a son, Jimmy, and decided to move back east to be closer to family. Patrick and family relocated to Georgetown, SC where he earned an associate degree in wildlife management at Horry-Georgetown Technical College. While in Georgetown, Patrick began his wildlife career as an intern for the SC Department of Natural Resources at Yawkey Wildlife Refuge, where he trapped his first wild hog. Soon after, he was hired as a wildlife technician at Mount Pleasant Plantation. While working at the plantation, Patrick was also seasonally hired by SCDNR. After graduating, Patrick and his wife had a baby girl, Amelia, and soon relocated to Sylva, NC. Patrick then attended Western Carolina University and received a bachelor's in natural resource conservation and management. After graduating, Patrick was hired by The Nature Conservancy to help eradicate invasive bog species. The following season, Patrick was hired by Great Smoky Mountains National Park as a wildlife intern, where he spent the next eight seasons. Patrick then enrolled at the University of Tennessee Graduate program to research wild hog ecology in Great Smoky Mountains National Park and Big South Fork National River and Recreation Area. After graduating and receiving his master's, Patrick intends to work as a wildlife ecologist in the state of Arizona.