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Home range and habitat use of feral hogs in Congaree National Park, South Carolina

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Abstract: Feral hogs (Sus scrofa) are a widespread exotic species that currently occur in most states within the United States and are common throughout the southeastern United States. We radio-collared and tracked feral hogs from April 2005 to November 2006 in Congaree National Park (CNP), South Carolina, USA. The CNP is one of the largest and most intact tracts of old-growth, bottomland hardwood forest remaining in the United States. We measured home range size and determined habitat use for male and female hogs. The mean (± SE) home range sizes for male hogs (n = 7) and female hogs (n = 9) were 218 ± 43 ha and 191 ± 31 ha, respectively. These home range estimates are relatively small compared to estimates from other studies of feral hogs. Habitat use models indicated that high use areas for hogs included habitat types best characterized as bottomland hardwoods and that hog locations were distributed in a relatively uniform manner throughout the study area within CNP. The small home ranges and habitat use patterns we observed suggest that habitat quality in CNP is good for feral hogs. Radio-collared hogs also moved readily between park and private lands. Thirteen of 23 collared hogs were found on private lands adjacent to CNP at least once. At least eight of the 23 collared hogs were shot and killed by hunters and one of these was taken on CNP land. If control of hogs in CNP were a goal of resource managers, then it would likely succeed or fail based in large part on the incorporation of adjacent private lands into the program.

Key Words: Congaree National Park, feral hog, habitat use, home range, human–wildlife conflicts, invasive species, national park, Sus scrofa

Range expansion and population increase of feral hogs (Sus scrofa) in the United States has generated much concern among natural resource managers (Chavarria et al. 2007, Engeman et al. 2007). Feral hogs currently occur in 40 of the 50 states, can strongly influence ecosystem processes, and often directly or indirectly affect native flora and fauna, as well as crops and soil (Mayer and Brisbin 1991, Ditchkoff and West 2007, Kaller et al. 2007, Hartin et al. 2007). Due to the strong and often negative effects feral hogs have on natural systems, as well as economically valued commodities, managers are often tasked with developing and implementing control programs for this species (Engeman et al. 2007, Rollings et al. 2007). In general, such programs typically are expensive and time-consuming to develop, logistically difficult to implement, and often meet with limited success (Dziecolowski et al. 1992, Waithman et al. 1999, Hone 2002).

Along with being considered a nuisance species, however, feral hogs also are prized as game, and numerous efforts exist to manage lands and habitat for hog hunts. Potential conflicts may arise when public lands managed for ecosystem protection, such as national parks, border private lands where hogs are abundant and where control measures are not in place or are not being considered. In these situations, hogs may move regularly between hunted private lands and protected public lands, hence, creating challenges for those tasked with managing or controlling their populations. The opportunity for control programs to succeed, however, is enhanced when ample life history and location-specific data can be gathered prior to the design or implementation of control efforts. Data gathering often requires location-specific research that is directed toward understanding habitat use and movement patterns.

We examined the home range patterns and habitat use of feral hogs in Congaree National Park (CNP), South Carolina, USA. Feral hogs are abundant in the state of South Carolina, occurring in 42 of 46 counties, with nearly 27,000 individual hogs harvested in 2006 (South Carolina Department of Natural Resources, unpublished data). Hogs occur throughout most areas of the CNP (Zengel
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2005) and are common on adjacent lands, as well. Our objectives were to (1) measure individual home ranges of radio-collared adult male and female feral hogs trapped within the CNP, (2) determine the extent to which hogs moved between the park and adjacent private lands, and (3) determine habitat use patterns of these same individuals. We also compared these measures to similar data from both the southeastern United States and from outside of the region to lend insight into the quality of feral hog habitat within CNP.

Study site
The CNP encompasses about 9,000 ha, is located 32 km south of Columbia, South Carolina (Figure 1), and supports a high density of feral hogs (Zengel 2005). The CNP is best described as old-growth, bottomland hardwood forest and is one of the largest tracts of its kind remaining in the eastern United States. The area is best characterized as a flood-pulse system that is driven by responses of the Congaree River to seasonal rains. During 2005 and 2006, the mean annual rainfall was about 112 cm. During summer months, the mean maximum and minimum temperatures were about 33° and 20° C, respectively. During winter months, the mean maximum and minimum temperatures were about 19° and 3° C, respectively. Common tree species of CNP include sugarberry (Celtis laevigata), sweetgum (Liquidambar styraciflua), American hornbeam (Carpinus caroliniana), bald cypress (Taxodium distichum), American sycamore (Platanus occidentalis), red maple (Acer rubrum), loblolly pine (Pinus taeda), longleaf pine (Pinus palustris), and various oaks (Quercus spp.). Much of the surrounding land is privately-owned and leased for hunting (including feral hog hunts).

Methods
Trapping and relocations
We conducted field work between April 2005 and November 2006. We captured feral hogs in live traps. Portions of the CNP interior were not trapped because traps were difficult to move (3.5 m, 32 kg) and because vehicle use is prohibited throughout much of the park. Trap sites were located in the southern section of the park along the Congaree River (Figure 2), which provided boat access. The northern sections of the park were accessed from nearby roads outside the park. We spaced traps at least 2.4 km apart, baited them with corn or mash, set them in the evenings, and checked them as early as possible the subsequent morning. Upon capture, each hog was immobilized with an intramuscular injection of telazol (1 ml per 23 kg of body mass) delivered with a jab stick. Hogs with a body mass >45 kg were ear-tagged and fitted with a 420-g radio collar (model M2520B, Advanced Telemetry Systems, Isanti, Minn.). If multiple hogs were simultaneously captured in a trap, no more than two were collared. We allowed approximately 48 hours for hogs to adjust to collaring and handling prior to obtaining the first relocation. We tracked animals until they were observed directly or, if hidden in vegetation, until vocalizations or movements confirmed their presence. Once hogs were located, we recorded the dominant vegetation type in the area to serve as verification for habitat modeling. We also recorded behavior and noted whether signals were stationary or moving. We relocated hogs approximately once per week; we collected all relocations during daylight hours, due to logistical and safety constraints, and we used a
handheld GPS to obtain relocation coordinates. We obtained the majority of relocations either between April 2005 and September 2005 or between January 2006 and June 2006.

**Home range**

We used the animal movement analysis extension in ArcView (Hooge and Eichenlaub 1997) and the National Park Service Alaska Pak extension to calculate 95% fixed kernel (Silverman 1986, Worton 1989) and 100% minimum convex polygon (MCP) home ranges. Core areas were calculated as 50% fixed kernel estimators. For each individual, we estimated a total home range that included all relocations for that individual. We also estimated home range from shorter time intervals where sample sizes allowed (i.e., sufficient relocations within individuals to calculate home ranges and sufficient individuals to conduct a statistical analysis comparing home range size among groups). These shorter time intervals did not necessarily follow strict definitions of seasons due to the need for sufficient sample sizes and due to the skewed trapping success we experienced. Therefore, time periods are defined for each comparison. The minimum number of relocations we used to calculate these partial home ranges was determined by assessing the stability of the size of each 95% kernel home range in relation to the number of relocations. Prior to any analysis, we constructed a cumulative curve of home range size in relation to sample size for each individual and only included individuals where curves were relatively stable (i.e., home range not increasing with increasing sample size) for the time period under consideration. The resulting number of relocations used to calculate kernel home range estimates was similar to values recommended for this technique (Seaman et al. 1999, Adkins and Harveson 2007).

We also calculated individual indices of home range dispersion and shifts in the central tendency of home range locations. To calculate the dispersion index for a home range, we
calculated the mean distance from all relocations to the weighted mean of the center of the home range polygon. Hence, a low dispersion value indicates that the home range was compact.

We assessed home ranges for shifts in location by comparing home range centers between time periods following procedures described by Plowman et al. (2006). We first constructed individual MCPs for 2 time periods of interest (spring 2005 and 2006). We then calculated the weighted mean of points for each home range polygon using the Jenness (2004) extension in ArcView. For each individual, we then calculated the weighted mean of the center of the polygon for time periods 1 and 2 and the dispersion index during time period 1. Next, we compared the distance between the weighted mean center of each home range polygon from each of the 2 time periods of interest with the dispersion index for the first time period of interest. If the distance between weighted means was $>0.5 \times$ dispersion index (hereafter referred to as the threshold value), we considered the shift to be significant (i.e., $>0.5$ of an individual’s home range shifted to a new area; Plowman et al. 2006). We calculated the overlap in home ranges between individuals with temporally sympatric relocation data. For each hog, we calculated an MCP and then determined the proportion of each individual’s home range polygon that was occupied by a second individual; we reported this as percentage of overlap.

Table 1. Total area (ha) in each of the 6 primary vegetation classes in the entire Congaree National Park (CNP), South Carolina, and in the subset of those cells in which radio-collared hogs were relocated (i.e., used cells).

<table>
<thead>
<tr>
<th>Vegetation class*</th>
<th>Area (ha) CNP</th>
<th>Used cells</th>
<th>% total CNP</th>
<th>Used cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugarberry, sweetgum, laurel oak, ironwood</td>
<td>5651.3</td>
<td>1015.5</td>
<td>62.9</td>
<td>69.2</td>
</tr>
<tr>
<td>Bald cypress, water tupelo, Carolina ash, swamp tupelo</td>
<td>1244.0</td>
<td>115.0</td>
<td>13.8</td>
<td>7.8</td>
</tr>
<tr>
<td>Plantation pine (longleaf and loblolly pine)</td>
<td>390.4</td>
<td>80.5</td>
<td>4.3</td>
<td>5.5</td>
</tr>
<tr>
<td>Sweetgum, water oak, laurel oak</td>
<td>296.5</td>
<td>49.1</td>
<td>3.3</td>
<td>3.3</td>
</tr>
<tr>
<td>Bald cypress, green ash, red maple, swamp oak</td>
<td>281.6</td>
<td>39.9</td>
<td>3.1</td>
<td>2.7</td>
</tr>
<tr>
<td>Muscadine grape, peppervine, trumpet creeper</td>
<td>239.1</td>
<td>11.4</td>
<td>2.7</td>
<td>0.1</td>
</tr>
<tr>
<td>All other</td>
<td>881.1</td>
<td>155.6</td>
<td>9.9</td>
<td>11.4</td>
</tr>
</tbody>
</table>

*Scientific names for species not previously mentioned in text: water tupelo (*Nyssa aquatica*), Carolina ash (*Fraxinus caroliniana*), swamp tupelo (*Nyssa biflora*), water oak (*Quercus nigra*), swamp oak (*Quercus bicolor*).
only considers habitat at sites known to be used and that it retains the information in the ordered ranking of the dependent variable (North and Reynolds 1996).

First, we projected all hog relocations onto a vegetation map of the CNP that was comprised of 22 vegetation types (American Geographic Data, Inc. 2001). We determined the total area of each of the original vegetation types and then created a smaller number of classes comprised of similar vegetation (n = 6) to be used in subsequent analyses (Table 1). We then created a 300 × 300 m grid overlay. Center points were delineated for each cell. We chose this grid cell size to be small enough to allow an individual hog to move between cells in 1 day, but large

![Figure 3: Determination of 3 categorical use-intensity levels for analysis of habitat association of (A) male and (B) female feral hogs radio-collared in Congaree National Park, South Carolina, April 2005 to November 2006.](image)
enough so that approximately 50% of cells had >1 relocation (North and Reynolds 1996, Cross and Petersen 2001). We determined the intensity of use for each cell by radio-collared hogs by tallying the number of relocations within each cell. We did this separately for male and female hogs. For each data set, we then created a frequency distribution that included both the number of relocations within a cell as the independent variable and the number of cells containing that number of relocations as the dependent variable. We then determined classification of use-intensity levels as high, medium, or low based on clumping patterns observed from these frequency distributions (Cross and Petersen 2001; Figure 3). These 3 classes of use served as the dependent variables. For each cell, we also determined the proportion of occurrence for each of the 6 vegetation classes and the elevation and the distances from the center of the cell to the nearest trail, road, permanent water source, and park boundary. These were used as independent variables.

We then used a forward selection process with the multinomial logistic regression models to assess the intensity of hog habitat use in relation to the independent variables. Prior to analysis, we examined all pairwise correlations among independent variables. To avoid multicollinearity, pairs of variables with $r > 0.6$ were not entered into a model together. Instead, we made the variable producing the strongest result from a single variable multinomial logistic regression model available for entry into the final model. We set the entrance criteria to 0.10 and the criteria for keeping a variable in the model at 0.05. We report coefficient estimates (±1 SE) and odds ratios (95% CI) for final models. The odds ratios from these models provide the odds of a cell moving up 1 level (i.e., from a low-use cell to a medium-use cell, or from medium-use cell to a high-use cell), with each unit increase in the independent variable. All means are presented ± 1 SE unless stated otherwise. All home range comparisons were conducted using kernel estimators unless stated otherwise.

Results

There were 115 trap nights between April 2005 and April 2006 within CNP. Hogs were captured at 5 of 6 trap locations along the river and at 6 of 9 trap locations in the uplands. Trapping success was 21% (11 of 52 trap-nights) along the river and 19% (12 of 63 trap nights) in the uplands. We radio-collared 11 male and 12 female hogs. There was a temporal difference in trapping success by gender. During the first trapping period (April to September 2005), we captured 8 male and 4 female hogs. Of those,

<table>
<thead>
<tr>
<th>Hog ID</th>
<th>Relocation dates (years)</th>
<th>Number of relocations</th>
<th>% locations on private property</th>
<th>Fate as of Nov 2006</th>
<th>Kernel home range</th>
<th>MCP home range</th>
<th>Core area</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>May 05–Oct 06</td>
<td>53</td>
<td>0</td>
<td>Dropped collar</td>
<td>136.7</td>
<td>140.6</td>
<td>15.7</td>
</tr>
<tr>
<td>M2</td>
<td>May 05–Sept 05</td>
<td>20</td>
<td>0</td>
<td>Unknown</td>
<td>180.2</td>
<td>118.6</td>
<td>40.0</td>
</tr>
<tr>
<td>M3</td>
<td>May 05–Sept 06</td>
<td>49</td>
<td>0</td>
<td>Alive</td>
<td>159.8</td>
<td>116.3</td>
<td>29.0</td>
</tr>
<tr>
<td>M4</td>
<td>May 05–Sept 05</td>
<td>18</td>
<td>6</td>
<td>Shot</td>
<td>145.7</td>
<td>62.8</td>
<td>45.3</td>
</tr>
<tr>
<td>M5</td>
<td>June 05–Feb 06</td>
<td>27</td>
<td>4</td>
<td>Shot</td>
<td>180.1</td>
<td>129.3</td>
<td>45.7</td>
</tr>
<tr>
<td>M6</td>
<td>June 05–June 06</td>
<td>31</td>
<td>23</td>
<td>Shot</td>
<td>269.7</td>
<td>232.5</td>
<td>39.1</td>
</tr>
<tr>
<td>M7</td>
<td>July 05–Aug 05</td>
<td>5</td>
<td>0</td>
<td>Shot</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>M8</td>
<td>Aug 05–Aug 05</td>
<td>0</td>
<td>0</td>
<td>Died</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>M9</td>
<td>Feb 06–Aug 06</td>
<td>22</td>
<td>77</td>
<td>Shot</td>
<td>455.5</td>
<td>225.4</td>
<td>59.9</td>
</tr>
<tr>
<td>M10</td>
<td>Mar 06–May 06</td>
<td>6</td>
<td>50</td>
<td>Dropped collar</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>M11</td>
<td>April 06–June 06</td>
<td>12</td>
<td>25</td>
<td>Shot</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* A dash indicates that too few relocations were collected to estimate home range. Shot = killed. Died = cause of death unknown.
6 male and 2 female hogs were relocated frequently enough to allow estimation of home ranges. In the second period (January to April 2006), we captured 3 male and 8 female hogs. Of those, we relocated 1 male and 7 female hogs frequently enough to allow estimation of home ranges. This difference in trapping success limited the comparisons that we could make in home range sizes within and between season, year, and sex.

**Home range size**

We obtained 512 relocations of radio-collared hogs between April 2005 and November 2006 (Tables 2 and 3). We estimated total home ranges for 7 male and 9 female hogs (Figure 2). Maps of relocations for each individual can be found in Friebel (2007). Total home range estimates were based on relocations obtained over a period of 98 to 516 days. The mean duration between relocations was 5.3 (± 0.4) days for male hogs and 5.6 (± 0.4) days for female hogs.

Estimates of 95% kernel home range size ranged from 66 ha to 456 ha for all individuals, and core areas ranged from 10 ha to 60 ha (Tables 2 and 3). Estimates of MCP home range size ranged from 45 ha to 262 ha (Tables 2 and 3). There was no significant difference ($t_{12} = 0.5, P = 0.7$) in the total home range size (i.e., all relocations included) for male hogs ($218 ± 43$ ha, $n = 7$) compared to female hogs ($191 ± 31.0$ ha, $n = 9$). There also were no significant differences ($t_{14} = 1.1, P = 0.3$) in core areas between male hogs ($39 ± 5$ ha) and female hogs ($31 ± 5$ ha), in distance traveled from trap site to the farthest relocated position ($t_{14} = 0.28, P = 0.4$) between male hogs ($1,661 ± 192$ m) and female hogs ($1,593 ± 155$ m), or in dispersion ($t_{13} = 0.2, P = 0.9$) between male hogs ($508 ± 54$ m) and female hogs ($496 ± 47$ m).

Temporal comparisons of home range size within and between genders were limited to those time periods for which a sufficient sample of individuals and relocations were available. We compared home range size between 5 male and 9 female hogs from January to November 2006. Home range sizes of male hogs ($279 ± 72$ ha) were not significantly different ($t_{14} = 1.1, P = 0.3; \text{resampled } P = 0.12$) from that of female hogs during this same time period ($190 ± 38$ ha).
range in home range sizes was nearly identical for both genders during this time period, as well (male hogs 78 to 456 ha, female hogs 66 to 452 ha). There also was no significant difference ($t = 1.0, P = 0.4$) in home range dispersion of male hogs from January to November 2006 (596 ± 91 m) compared to female hogs during this same time period (493 ± 47 m).

We compared home ranges for female hogs during winter to spring (i.e., January to May) with home range for female hogs during summer to fall (May to November 2006). There was no significant difference ($t = 0.3, P = 0.8$) in the winter to spring home range size for 9 female hogs (164 ± 56 ha) compared to summer to fall home ranges of 6 female hogs (147 ± 27 ha). Mean dispersion for female hogs from January to May 2006 (429 ± 69.5 m) also was not significantly different ($t = 0.1, P = 0.9$) compared to female hogs during May to November 2006 (421 ± 52 m).

We examined temporal shifts in central tendency of home ranges within individuals between time periods. Individuals often shifted home ranges between seasons, although the range in the magnitude of shifts was wide (Table 4). For example, 6 of 7 individuals had shift distances that were 2.5 to 5.5 times as great as threshold values. We also examined the proportion of overlap of home ranges between individuals with sympatric sets of relocations. This analysis was restricted to February to June 2006 when sufficient data were available to compare home range overlaps. Overlap within female or within male hogs captured in different trap locations never exceeded 1%. The home range of male hog number 3 overlapped that of male hog number 6 (captured in the same trap) by 21%, while the home range of male hog number 6 overlapped that of male hog number 3 by 37%. Overlap within female hogs captured in the same trap locations ranged from 25 to 100% ($n = 8$ pairs of overlaps). Three male and 3 female hogs had no overlap with members of the same sex during this time period.

**Habitat use**

Locations (i.e., map cells) used by radio-collared hogs were uniformly positioned throughout the portion of CNP where traps were originally set (Figure 4). All but one of the high and medium-use cells were connected (including diagonally) to low-use cells. All of the isolated cells (i.e., cells not connected to any other cells) were low-use cells. All high-use cells occurred inside home ranges that encompassed ≥34 relocations from either a single hog or a group of hogs.

We examined habitat use for 10 male hogs with a total of 219 relocations across 76 cells. Low-use cells had 1 to 3 relocations per cell ($n = 58$ cells); medium-use cells had 4 to 5 relocations per cell ($n = 9$ cells); and high-use cells had 6 to 15 relocations per cell ($n = 9$ cells; Figure 3a). The final model indicated that hog use in a cell increased in intensity levels as three of the vegetation classes increased within that same cell ($P < 0.02$ for each). These three were: the proportion of the muscadine grape (*Vitis rotundifolia*), pepper vine (*Ampelopsis arborea*), trumpet creeper (*Campsis radicans*) vegetation group (odds ratio 1.12, 95% CI 1.03 to 1.22), the proportion of the sugarberry, sweetgum, laurel oak (*Quercus laurifolia*), ironwood (*Carpinus caroliniana*) vegetation group (odds ratio 1.08, 95% CI 1.01 to 1.15), and the proportion of the sweetgum, water oak, laurel oak vegetation group (odds ratio 1.13, 95% CI 1.02 to 1.26).

We examined habitat use for 10 female hogs with a total of 258 relocations across 99 cells. Low-use cells had 1 to 3 relocations per cell ($n = 77$ cells); medium-use cells had 4 to 6 relocations per cell ($n = 11$ cells); and high-use cells had 6 to 10 relocations per cell ($n = 11$ cells; Figure 3b). The final model indicated that hog use in a cell increased in intensity levels as the proportion of the bald cypress, green ash (*Fraxinus pennsylvanica*), red maple, swamp oak vegetation group increased within a cell ($P = 0.03$, odds ratio $= 1.04$, 95% CI 1.00 to 1.08, 18% discordant).

**Use of private property**

Of the 23 hogs collared, we relocated thirteen on private land adjacent to CNP at least once. For hogs that had ≥1 location on private property there was no significant difference ($t = 0.7, P = 0.5$) in the percentage of relocations on private property for male hogs (30.8 ± 11.3%) compared to female hogs (21.4 ± 5.7%). As of November 2006, when fieldwork ceased, eight of the 23 hogs collared had been shot, 7 collars were found without hogs, 3 hogs died from unknown causes, 1 hog disappeared for
Table 4: Spatial shifts in central tendency for feral hogs in Congaree National Park, South Carolina, April 2005 to November 2006.

<table>
<thead>
<tr>
<th>Hog ID</th>
<th>Time period 1</th>
<th>Time period 2</th>
<th>Threshold value (m)</th>
<th>Shift distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>April 05–Aug 05</td>
<td>Jan 06–Jun 06</td>
<td>147.3</td>
<td>708.5</td>
</tr>
<tr>
<td>M3</td>
<td>May 05–Aug 05</td>
<td>Jan 06–Jun 06</td>
<td>195.7</td>
<td>80.7</td>
</tr>
<tr>
<td>M6</td>
<td>June 05–Aug 05</td>
<td>Feb 06–Jun 06</td>
<td>160.0</td>
<td>713.0</td>
</tr>
<tr>
<td></td>
<td>± SE</td>
<td></td>
<td>167.6 ± 14.5</td>
<td>500.72 ± 210.0</td>
</tr>
<tr>
<td>F5</td>
<td>Jan 06–Mar 06</td>
<td>April 06–Aug 06</td>
<td>140.0</td>
<td>786.8</td>
</tr>
<tr>
<td>F8</td>
<td>Feb 06–May 06</td>
<td>May 06–Nov 06</td>
<td>417.4</td>
<td>1032.5</td>
</tr>
<tr>
<td>F10</td>
<td>Feb 06–May 06</td>
<td>May 06–Oct 06</td>
<td>241.4</td>
<td>581.0</td>
</tr>
<tr>
<td>F11</td>
<td>Mar 06–May 06</td>
<td>June 06–Nov 06</td>
<td>192.3</td>
<td>665.1</td>
</tr>
<tr>
<td></td>
<td>± SE</td>
<td></td>
<td>247.8 ± 60.2</td>
<td>766.4 ± 98.3</td>
</tr>
</tbody>
</table>

* Threshold value = mean dispersion value of all relocations during time period 1 multiplied by 0.5.

b Shift distance is calculated as the distance between the weighted mean of points (i.e., weighted center) of 2 home range polygons for 2 separate time periods using the weighted mean of points extension (ArcView 3.3, Jenness 2004). The significant shift distances appear in boldface.

Figure 4: Use-intensity levels for male and female feral hogs in Congaree National Park, South Carolina, April 2005 to November 2006. Values for intensity of use defined in results (also see Figure 3). Only cells in which hogs were relocated are categorized for levels of use.
unknown reasons, and 4 hogs were still alive and with collars (Tables 2 and 3). Of the 8 hogs that were shot and killed, 75% were males; three of these were shot and killed within 7 weeks of moving to private land, and four were shot and killed 5 to 7 months after moving to private land. One hog appeared to be shot and killed on CNP property within approximately 3 weeks of being collared.

Discussion

Home range

All of the movement data we examined suggest that home ranges of hogs in the CNP were compact. Furthermore, the mean 95% kernel and MCP home range sizes (203 and 143 ha, respectively) in our study appeared to be smaller than most home range estimates previously reported for this species. For example, Adkins and Harveson (2007) found MCP home ranges >30 km² for hogs in a desert environment in Texas; Saunders and Kay (1991) and Caley (1997) reported MCP home range sizes from 490 to 3,500 ha in Australia; and Gabor et al. (1999) reported kernel estimates for female hog home ranges of 590 ha in Texas. Estimates of home range size for feral hogs in other locations within South Carolina appear to be slightly larger than, or in some cases, similar to (but not smaller than) estimates from this study. Kurz and Marchinton (1972) in upstate South Carolina and Wood and Brenneman (1980) in coastal South Carolina found MCP home range sizes for hogs in bottomland hardwood forests and marshes to be between 123 and 799 ha and 181 and 226 ha, respectively.

The degree of overlap and spatial shifts in home range locations also suggest that space use by individual hogs during our study was compact (Lesage et al. 2000). For example, overlap in home ranges for hogs caught at the same traps in CNP ranged from 21 to 100%, and we observed overlap in both males and females. We observed significant spatial shifts in home range locations in only 6 of the 23 individuals we tracked. These shifts occurred from 7 to 14 months post-collaring, and once these individuals shifted their home range locations, their new home ranges also appeared to stabilize. Shifts in home range locations of feral hogs in the southeastern United States have been attributed to changes in food availability (Sweeney 1970, Kurz and Marchinton 1972, Ackerman et al. 1978). The lack of large spatial shifts in our study suggests, therefore, that food resources within home ranges were relatively consistent throughout the annual cycle.

We did not find a difference in home range size between male and female hogs. In contrast, most other studies have found male hogs to have significantly larger home ranges compared to female hogs (Baber and Coblentz 1986, Saunders and Kay 1991, Caley 1997, Adkins and Harveson 2007). Differences in home range size between genders in hogs are often related to population density or young rearing (Saunders and Kay 1991, Caley 1997, Russo et al. 1997, Adkins and Harveson 2007). The lack of difference we observed in home range sizes may be due in part to a relatively high population density in CNP (Zengel 2005), which in turn would reduce the degree of movement and home range size required by male hogs when searching for mates. Results from other studies also showed that female hogs restricted their movements when raising young. All female hogs tracked during our study were observed with young at some point during the study. If females in CNP can successfully raise young while relying upon small home ranges, then it would appear that habitat quality in the park is relatively high.

Similarly, the lack of a significant difference in
the winter to spring home ranges and summer to early fall home ranges of female hogs during 2006 is also consistent with relatively stable and abundant resources. Increases in winter home ranges are common when food availability declines during these months. For example, Hughes (1985), Saunders and Kay (1991), and Boitani et al. (1994) all found that seasonal home ranges for both male and female hogs were largest in winter when food declined and smallest in autumn when food appeared most abundant. In contrast, winter and summer home ranges of feral hogs did not vary in Tennessee or South Carolina when mast availability was considered high (Wood and Brenneman 1980, Singer et al. 1981). Zengel (2005) also noted that there was little evidence for seasonal patterns of disturbance in long-term monitoring plots within CNP, and this result is also consistent with a similarity in home range size and location between seasons.

Home range studies on hogs in South Carolina have attributed larger home ranges to a lack of food availability (Kurz and Marchinton 1972, Wood and Brenneman 1980, Crouch 1983, Hughes 1985). Similarly, home range size, shifts in home range locations, and extent of home range overlap all tend to vary inversely with resource abundance in feral hogs (Diong 1982, Baber and Coblentz 1986, Saunders and Mcleod 1999, Manfredi et al. 2006, Adkins and Harveson 2007), but see Mersinger and Silvy (2007). These data suggest, therefore, that the small home range sizes we observed may have been due in large part to a relatively high level of habitat quality for feral hogs in the CNP.

Our home range data should be interpreted cautiously, however, and here we briefly describe 3 potential caveats. First, we were not able to relocate hogs during autumn months when mast from oaks and hardwoods would be greatest. It is possible that hogs may shift their home ranges to avail themselves of more mast. Given the extensive availability of oaks and hardwoods throughout CNP, however, it is doubtful such a shift would substantially affect home range sizes. Second, all of our relocations occurred during daylight hours. Hogs are known to move extensively during nocturnal hours (Saunders and Kay 1991, Boitani et al. 1994, Caley 1997, Mersinger and Silvy 2007) and such movements would likely increase home range sizes. This pattern of activity appears, however, to be most common during summer months and in situations where human influence and hunting pressure are substantial (Kurz and Marchinton 1972, Giles 1980, Singer et al. 1981, Massei et al. 1997). We collected data during all seasons and, throughout most of our study area (i.e., within CNP), interactions with humans were limited. Hence, we suggest that our estimates of home range size, while likely to be smaller than what we would have obtained had nocturnal relocation been possible, were not strongly biased downward. We also observed hogs to be foraging and moving during relocations. Lastly, and perhaps most importantly, our study occurred within a drought phase, and flooding was far less common and severe than normal. In the CNP, flood waters may reach several meters in floodplains, and this appears to force hogs to move from bottomland areas to uplands. Such movements would obviously cause shifts in home range locations to occur and also increase home range sizes.

**Habitat use**

Previous studies of habitat use in feral hogs have demonstrated that individuals tend to be habitat generalists and often, but not always, use habitat in proportion to its abundance (Ilse and Hellgern 1995, Gabor et al. 2001, Adkins and Harveson 2007). We observed that male hogs were often found in habitats that were relatively common. The final habitat model for male hogs indicated hog use increased in 3 vegetation classes, which together accounted for approximately 70% of the available habitat in the CNP. In contrast, the final model for female hogs showed that the probability of a cell being used increases as the proportion of bald cypress, green ash, red maple, and swamp oak complex increased. This classic bottomland hardwood complex is relatively rare within the entire park but not uncommon in the northern section of CNP where most of the female hogs were trapped. The selection of the cypress complex by female hogs may be due in part to that habitat's association with more permanent water sources in that section of CNP. Because females travel in large sounder groups, and therefore, require a greater volume of water than do solitary males, a more permanent water...
source might be of greater importance to them compared to males, especially during drought phases that occurred during this study.

In general, habitat selected by hogs during this study was consistent with that of hogs reported in other studies in the southeastern United States, indicating that hog use increased in hardwoods but decreased in pine and shrubby areas (Sweeney 1970, Gaines et al. 2005). Mast crops, such as oaks (Quercus), are important food sources for hogs (Wood and Roark 1980, Singer et al. 1981, Boitani et al. 1994). For both genders, the most commonly used habitats also included some species of oak, and it is likely that mast from the 3 oaks in these classes increased the importance of these vegetation types for hogs.

As with the home range data, the habitat use data may have been affected by lack of relocations during both fall and nocturnal hours, and by drought. It is not unreasonable to suggest that relocations during autumn months may have increased the apparent selection of hardwood habitats and that hogs likely would have shifted to uplands habitat, had the CNP experienced flooding. It does not appear that collecting relocations at night would have substantially affected habitat use models given the relatively homogeneous nature of much of CNP.

Implications of home range and habitat use data for Congaree National Park

Our data indicate that hogs frequently moved between CNP and adjacent private land. During our study, 13 of 23 radio-collared hogs moved onto private lands at some point. Although we confirmed that 8 hogs were shot by hunters (with one likely taken illegally on CNP land), it appears that a greater number were actually harvested. These observations suggest that if control of hogs in CNP were a goal of resource managers, then such control would in large part succeed or fail based on the incorporation of adjacent private lands into the program. Efforts to control populations of feral hogs in Australia and New Zealand suggest it may be necessary to remove >70% of the feral hogs annually to reduce or maintain population numbers (Dziectolowski et al. 1992; Caley 1993; Saunders 1993). It is unclear at this time how the flow of individuals between the park and private lands might affect population dynamics of hogs in CNP and hence the effectiveness of any control program. For example, hunting on lands adjacent to CNP may keep immigration from private lands to CNP low and allow a management of standard yearly hog takes in CNP to be effective. In contrast, high habitat quality and high hog productivity on private lands could support immigration into the park.

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