Management and Conservation Article

Territoriality of Feral Pigs in a Highly Persecuted Population on Fort Benning, Georgia

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ABSTRACT We examined home range behavior of female feral pigs (*Sus scrofa*) in a heavily hunted population on Fort Benning Military Reservation in west-central Georgia, USA. We used Global Positioning System location data from 24 individuals representing 18 sounders (i.e., F social groups) combined with mark–recapture and camera-trap data to evaluate evidence of territorial behavior at the individual and sounder levels. Through a manipulative experiment, we examined evidence for an inverse relationship between population density and home range size that would be expected for territorial animals. Pigs from the same sounder had extensive home range overlap and did not have exclusive core areas. Sounders had nearly exclusive home ranges and had completely exclusive core areas, suggesting that female feral pigs on Fort Benning were territorial at the sounder level but not at the individual level. Lethal removal maintained stable densities of pigs in our treatment area, whereas density increased in our control area; territory size in the 2 areas was weakly and inversely related to density of pigs. Territorial behavior in feral pigs could influence population density by limiting access to reproductive space. Removal strategies that 1) match distribution of removal efforts to distribution of territories, 2) remove entire sounders instead of individuals, and 3) focus efforts where high-quality food resources strongly influence territorial behaviors may be best for long-term control of feral pigs. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):497–502; 2009)

Feral pigs (*Sus scrofa*) are abundant and widespread and are of management concern due to their negative environmental and economic impacts (Choquenot et al. 1996, Gibson et al. 1998, Roemer et al. 2002). Management for feral pigs often includes control or eradication programs, and the spatial behavior of feral pigs can influence effectiveness of these strategies. Territoriality (i.e., exclusive use of an area and its resources through active and passive defense or mutual avoidance; Brown and Orians 1970, Powell 2000) can affect population dynamics, such as population density and dispersal, and can influence management outcomes. Female territoriality can limit offspring rearing space and lead to reproductive declines as population density increases (Wolff 1997, Adams 2001). Territoriality often leads to an inverse relationship between population density and dispersal by limiting opportunities for juveniles to disperse and establish territories (Wolff 1997). Territorial behavior also has direct implications for management aimed at reducing population densities or complete eradication. Removal of animals from territories creates opportunities for immigration. Incomplete removal of social groups occupying a territory may reduce territory size or increase reproductive capacity within the group through increased availability of per capita resources. Thus, changes in density of territorial animals following removals could be short-lived if immigrants rapidly occupy vacated territories or space vacated by shrinking territories or if reproduction within existing territories increases.

Although resource defense and group territories have been predicted for pigs (Geist 1977), most studies of feral pigs have shown that female home ranges overlap (Baber and Coblentz 1986, Boitani et al. 1994), and some have concluded that female pigs are not territorial (Barret 1978, Graves 1984). Because few studies evaluated use of space by sounders, they may have missed evidence for territoriality. Female sounders are matrilineal groups, containing several generations of related females and their dependent offspring (Gabor et al. 1999, Kaminski et al. 2005). Sounders are generally stable social units, with most female offspring remaining with the sounder after weaning (Boitani et al. 1994, Kaminski et al. 2005). In several previous studies (Kurt and Marchington 1972, Singer et al. 1981, Diong 1982, Baber and Coblentz 1986), individual females were the unit of study, and the authors found nonexclusive, overlapping home ranges, suggesting absence of territoriality. Three more recent studies examined pig home-range behavior at the sounder level (Boitani et al. 1994, Ilse and Hellgren 1995, Gabor et al. 1999) and one reported sounders had nonexclusive, overlapping home ranges (Boitani et al. 1994), whereas two (Ilse and Hellgren 1995, Gabor et al. 1999) reported sounders had exclusive, nonoverlapping home ranges. Given the social organization of female feral pigs, examination of spatial behavior at the sounder level should provide a robust test of the evidence for territoriality.

Territories have been defined in many ways, but most definitions include exclusivity of use maintained through

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behavior (Brown and Orians 1970, Kaufman 1983, Maher and Lott 1995). Territories can be defended through physical interaction but are usually defended through scent-marking, calls, or displays and can also be maintained through mutual avoidance (Peters and Mech 1975, Kaufman 1983). Animals are expected to be territorial only when they have a limiting resource that is in short supply and limits population growth (Brown 1969). Across the wide range of habitats that feral pigs occupy, resources are probably not always at levels of productivity that support or necessitate female territorial behavior. But, in seasonally variable, semitropical climates, moderate levels of food productivity may result in territoriality.

For nocturnal or secretive creatures such as pigs, territoriality may have to be inferred indirectly through degree of home range overlap because direct territorial interactions may be infrequent or difficult to observe (Maher and Lott 1995). Territorial animals generally have little home range overlap with conspecifics and maintain exclusive home range core areas. This pattern of spatial behavior has been found in other territorial group-living mammals, such as Eurasian beaver (*Castor fiber*; Herr and Rosell 2004) and capybaras (*Hydrochaeris hydrochaeris*; Herrera and Macdonald 1989). Further, an inverse relationship between home range size and population density is expected where territorial behavior occurs (Huxley 1934). If female pigs are not territorial, a direct relationship between population density and home range size is logical, as seen for other nonterritorial ungulates (Kjellander et al. 2004). Our objective was to test our hypothesis that female feral pigs on Fort Benning were territorial at the sounder level by examining home range use and made the following predictions: 1) female pigs would have extensive home range overlap among individuals within sounders but little or no overlap of home ranges among sounders; 2) individuals within sounders would have overlapping core areas, but sounders would have mutually exclusive core areas; and 3) an inverse relationship would exist between population density and home range size among sounders.

STUDY AREA

We conducted our study between May 2004 and August 2006 on the Fort Benning Military Reservation. The reservation consisted of 735 km^2 on the Coastal Plain–Piedmont fall line in eastern Alabama and western Georgia (USA). The climate was semitropical with an average rainfall of 132 cm (Dilustro et al. 2002). Longleaf pine (*Pinus palustris*), scrub oak (*Quercus* sp.), and loblolly pine (*P. taeda*) dominated ridge tops, whereas slopes graded into upland hardwood forests dominated by oak and hickory (*Carya* spp.) species. Hardwood bottoms were mixtures of sweet gum (*Liquidambar styraciflua*), yellow poplar (*Liriodendron tulipifera*), hickory, and oak. The pig population was hunted year-round, and annual survival for adult and juvenile feral pigs on Fort Benning was low (0.319 ± 0.040 and 0.311 ± 0.047, respectively); hunters removed 2.6 pigs/km^2/year (Hanson 2006). We used control and removal

areas that were approximately 50 km^2 and approximately 10 km apart to reduce the possibility of individuals moving between areas.

METHODS

Capture and Handling

We conducted capture–mark–recapture sessions during summers 2004, 2005, and 2006 to estimate density and to tag feral pigs for survival estimation. We trapped feral pigs in cage-traps capable of catching multiple pigs with 20 trap locations spaced 1–2 km apart across each study area. We prebaited traps with shelled and fermented corn for 2 weeks prior to each trapping session. We checked traps each morning of the 18-day trapping sessions.

We tagged all captured feral pigs with uniquely numbered ear tags in both ears using different colored tags to indicate study area (National Band and Tag, Newport, KY). We measured head and body length to estimate age (Boreham 1981). We recorded sex and estimated weight. We photographed each feral pig before its initial release to aid in identifying tagged feral pigs resighted with the game cameras.

We fitted captured females >30 kg with a G2000 Large Mammal 12-channel Garmin receiver Global Positioning System (GPS)–very high frequency collar (Advanced Telemetry Systems, Isanti, MN). We chose females of this size because of constraints on collar adjustment and because this size is considered minimal for first reproduction (Fernandez-Llario and Mateos-Quesada 1998). We anesthetized females using Telazol at 1 cm^3/30 kg using a jab-stick. We programmed our collars to attempt fixes every 5 hours, with fix attempts lasting 2 minutes. When a collar failed to obtain a fix, it reinitiated an attempt after 1 hour. As collared individuals died or lost their collars, we trapped and fitted new individuals with collars.

Our experimental removal consisted of lethal trapping and shooting in the treatment study area from August 2004 through May 2006 excluding mark–recapture sessions. We excluded collared females from lethal removal. All capture and handling of pigs was approved by the Auburn University Institutional Animal Care and Use Committee (permit no. 2003-0531).

We used digital game cameras (infrared Digital-Scout 3.2 megapixel; Penn's Woods, Export, PA) to resight ear-tagged feral pigs passively in both study areas between August 2004 and May 2006. We baited 15 cameras with fermented corn and moved them every 2–3 weeks in each study area to fully sample the study area several times. We set cameras with a 2-minute delay to acquire multiple photographs of feral pigs to assist with identification.

Home Range Analysis

We identified sounder membership by a combination of direct observations, telemetry, trapping, and camera resightings. We considered ≥2 females of reproductive size captured or observed together, with or without juveniles, ≥3 times as members of the same sounder. In sounders where we collared multiple females simultaneously, we used

only the data for the female with the greatest number of locations to estimate home range for the sounder because we almost always found females from the same sounder together. Where we collared multiple females sequentially with no overlap in timing of locations, we combined data across all collared females to estimate the home range for the sounder. In sounders where we collared only one female, we assumed its locations were representative of the sounder during that time period. We estimated kernel home ranges from GPS location data in ArcView 3.3 using the Animal Movement Extension (Hooge and Eichenlaub 1997) and least-square cross-validation (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001). We used only sounders with ≥ 60 locations over ≥ 30 days in the analysis. We defined the sounder home range as the 95% probability utilization distribution and the core area as the 50% probability utilization distribution (Gabor et al. 1999).

We compared overlap between simultaneously collared sounders that had telemetry locations within 500 m of each other. We used this distance because it approximated half the average distance traveled by a sounder in a day based on telemetry and it encompassed the area likely to include "occasional sallies" where possible interactions between sounders might occur (Burt 1943:351). We quantified home range overlap used Cole's (1949) index,

$$O = 2 \times a_1 / (A_1 + A_2)$$

where a_1 = area of home range A_1 overlapped by the home range of another animal A_2 (Kenward 2001, Wronski and Apio 2006). To test our prediction that there would be an inverse relationship between population density and home range size, we used a one-way analysis of variance (S-PLUS 7.0 Insightful Corp., Seattle, WA) to test for a difference between the 95% kernel home ranges of sounders within the removal and control areas before and after treatment.

RESULTS

Trapping and Removal

During 3 summer mark–recapture sessions, we caught 310 individuals 600 times over 2,160 trap nights. During summer of 2004, we caught 55 feral pigs 134 times in the control area and 35 feral pigs 73 times in the treatment area. During the following summer of 2005, we caught 51 pigs 117 times in the control area and 39 pigs 53 times in the treatment area. During the summer of 2006, we caught 77 pigs 144 times in the control area and 53 pigs 79 times in the treatment area.

Between August 2004 and May 2006, we recorded approximately 2,600 lethal trap nights, primarily during October to March of each year, resulting in removal of 182 feral pigs from the treatment area. Of 182 pigs killed, 51% were male, 49% were female, 65% were <1 year old, and 35% were adult. We removed 2.2 pigs/km^2 from the treatment area per year, reducing adult survival from 32% to 22% and juvenile survival from 31% to 21% relative to the control area (Hanson 2006). Removal kept density in the

Table 1. Number of sounders, number of Global Positioning System locations, and mean home-range sizes for sounders of feral pigs within control and removal areas, before (yr 1) and following (yr 2) removal treatment, Fort Benning, Georgia, USA, 2004–2006.

Study area	No. of sounders	No. of locations		Home range size (km²)	
		$\bar{x}$	SE	$\bar{x}$	SE
Control yr 1	5	389	103.5	3.66	0.77
Control yr 2	4	177	33.7	1.95	0.63
Removal yr 1	4	412	86.4	3.49	1.06
Removal yr 2	5	327	106.1	2.95	0.74

treatment area relatively constant, whereas density in the control area increased.

We collected >4,200 photographs from game cameras over the 10-month sampling period; we captured feral pigs in 35% of photographs with 116 sightings of sounders. Camera sightings corrected for detection probability indicated the average sounder on Fort Benning had 2.59 (95% CI = 2.09–3.45) adult females and 6.76 (95% CI = 5.45–9.00) piglets, for an average sounder size of 9.35 (95% CI = 7.54–12.45) pigs (Hanson 2006).

Home Range Analysis

We retrieved data from 24 individuals representing 18 sounders within the removal and control areas (Table 1). We found no evidence through trapping, camera sightings, or direct observation that any uncollared sounders were present within home ranges of collared sounders. We did not detect subgroups within sounders as seen in other studies (Boitani et al. 1994, Gabor et al. 1999) through telemetry while we had multiple females from individual sounders collared, but we did observe females leaving their sounders and using a small portion of their home range immediately before and approximately 2 weeks after giving birth.

Home range size did not vary with population density in the removal area ($F_{1,8} = 0.185$, $P = 0.680$). Home range size in the control area suggested an inverse relationship with population density but these results had little statistical support ($F_{1,8} = 2.76$, $P = 0.141$).

Our estimated home ranges had well-defined core areas located in dense thickets in pine uplands and hardwood bottoms. Pairs of individuals within sounders ($n = 6$ dyads, mean no. of locations/individual = 368, SD = 128; mean days of overlap = 137, SD = 62) had extensive overlap at the 95% and 75% kernel home ranges (84.0% ± 5.9% and 76.5% ± 13.1%, respectively) and 50% kernel core area (69.4% ± 12.7%). We found little overlap among pairs of sounders ($n = 9$ dyads, mean no. of locations/sounder = 330, SD = 130; mean days of overlap = 97, SD = 42) at the 95% kernel home range (5.6% ± 5.9%), little overlap at the 75% kernel home range (0.4 % ± 1.1%), and no overlap at the 50% kernel core area. We never witnessed territorial interactions between sounders directly, but location data revealed one instance of home range expansion for one sounder (B) after a hunter killed 2 adult females from the
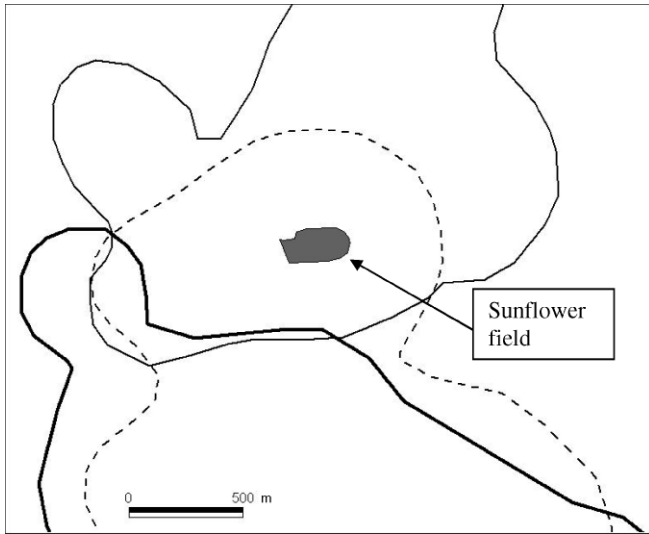
Figure 1. Territories of feral pig sounder A (thin line) and sounder B (thick line) and the sunflower field used by sounder A between June and August of 2005, Fort Benning, Georgia, USA. Dashed line shows expansion of sounder B's home range to include the sunflower field after the collared female and another adult female from sounder A were killed by a hunter.

Figure 2. Territories of 2 sounders adjacent to the same sunflower field the previous year during a 4-month period between July and October 2004, Fort Benning, Georgia, USA. We recorded 56 locations from sounder X (thin line) from the field during a 45-day period between 21 July and 3 September 2004. We recorded 2 locations from sounder Y from this area during these 4 months, one location 55 m from the field on 6 June and one location from the field on 13 September 2004.

neighboring sounder (A). Sounder A's territory included a sunflower field, and it used this field almost daily when sunflowers were mature, exclusive of sounder (B) that maintained an adjacent territory (Fig. 1). Within 10 days of the hunter harvesting the collared female and another mature female from sounder A, sounder B expanded its home range to include the field (Fig. 1). There was a similar relationship between 2 sounders adjacent to the same field the previous year during a 4-month period between July and October 2004. We recorded 56 locations from sounder X (Fig. 2, thin line) from the field during a 45-day period between 21 July and 3 September 2004. We recorded 2 locations from sounder Y from this area during these 4 months, one location 55 m from the field on 6 June and one location from the field on 13 September 2004.

DISCUSSION

Resource defense and group territories have been predicted for Suids in reviews of ungulate ecology because of their unique reproductive and dietary habits that distinguish them from other ungulates (Geist 1977). We found female feral pigs on Fort Benning were territorial at the sounder level but not at the individual level. Although we did not observe direct territorial interactions among sounders, this does not preclude a conclusion of territoriality. Previous reviews on the definition of territoriality vary on how much exclusion and defense is necessary to distinguish territories from home ranges but tend to agree that these behaviors exist along a continuum of intensity (Kaufmann 1983, Maher and Lott 1995). Sounders in our study showed little or no overlap in home ranges and had mutually exclusive core areas, and this type of mutual avoidance between neighboring groups has been used as evidence of territoriality in other species (Chamberlain and Leopold 2000). Further, we observed a
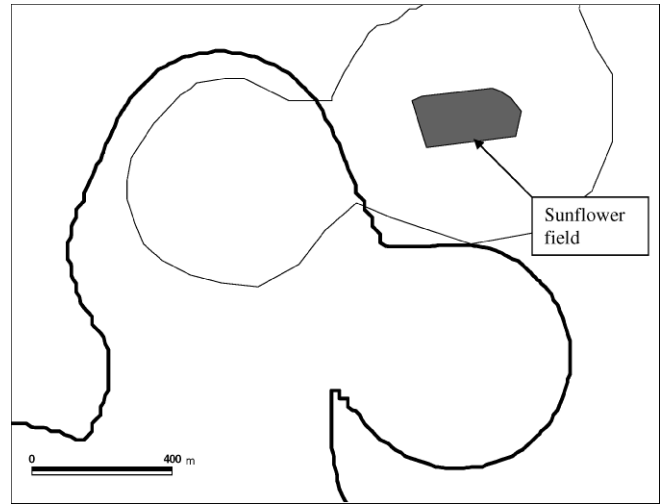
sounder seize exclusive and immediate control of a high-quality food resource (sunflower field) used by another sounder where adult females were removed (Fig. 1), consistent with territorial behavior. This same food resource was used exclusively by a different sounder the previous year, whereas a neighboring sounder that lived in close proximity to the sunflower field did not use it. Given the high nutritional value of the sunflower field, and that the excluded sounders did not have a similar resource elsewhere within their home ranges, some form of resource defense to maintain exclusive use of the field is implied, although we were unable to document this behavior. We did not test for direct interactions (e.g., proximity of sounders near territory boundaries or in areas of home range overlap) between sounders because overlap took place in areas with low probabilities of use and the interval between locations (5 hr) was too long to detect short-term interactions such as inter-sounder strife. Future studies using a shorter time interval between locations could examine such interactions between sounders.

Mean sizes of sounders and home ranges we observed in the treatment and control areas for both years were similar to those reported elsewhere for female pigs in the southeastern United States (Barret 1978, Kurz and Marchington 1972, Wood and Brenneman 1980, Singer et al. 1981, Ilse and Helgren 1995). Contrary to our prediction, we did not find an inverse relationship between population density and home range size. Mean home range size declined for both the control and treatment areas over the 2 years of our study, but it appeared to decline less in the control area, whereas density increased in the control area and remained stable in the treatment area. This pattern, though supported weakly in our analyses, is consistent with the hypothesis that

reduction of group size could result in compensatory, density-dependent responses in immigration and reproduction. We hypothesize this result would have had more statistical support if we 1) had a larger sample size of collared sounders in the treatment and control areas, or 2) were able to remove more pigs from the treatment area.

We assumed that the number of adult females in each sounder was similar enough throughout the study to have had a minimal effect on territory size. This assumption may have been violated if sounder composition varied across those we sampled and if the number of individuals within sounders played a role in interactions between neighboring sounders. Finally, our removal was focused on individual pigs, reducing the size of sounders but not eliminating them. Our results suggest removal of entire sounders would have been better suited to testing hypotheses about territoriality of feral pigs, given our sample sizes. Future studies should test our results by controlling for sounder size and manipulating entire sounders.

Previous studies on home range behavior of feral pigs have been inconclusive or have found female feral pigs to be nonterritorial with overlapping home ranges. Focus on individuals instead of sounders as the unit of study could account for most of these discrepancies. Two studies conducted at the sounder level, however, found evidence for territorial behavior in pigs. Gabor et al. (1999) found that marked sounders showed mostly exclusive, nonoverlapping home ranges and suspected territoriality, but the sample was small (3 sounders), whereas Ilse and Hellgren (1995) suspected unmarked sounders overlapped with marked sounders that appeared to have exclusive home ranges. In a third study using sounder-level data, Boitani et al. (1994) showed sounders had overlapping, nonexclusive home ranges, and territorial behavior was absent; this conclusion was drawn from overlap between 2 sounders that may have been dependent on an artificial food source. Further, Boitani et al. (1994) differentiated between sounders with juveniles present and sounders composed of only adult females (Gabor et al. 1999), which could confound comparisons with other studies that did not.

Observed variation in degrees of territoriality for feral pigs across the wide range of habitats they occupy world-wide could also be explained by the variable nature of territorial behavior. Territoriality of sounders could be a function of food productivity (Powell et al. 1997), where territoriality is intermediate on a continuum of behavior from nomadism (low food productivity) to nonexclusive home ranges (high food productivity). Given the unproductive, arid habitats that feral pigs often occupy (Dexter 1999), food productivity arguably could be low enough that sounders inhabiting these areas would show nomadic, nonterritorial behavior because the benefits of maintaining exclusive use of resources do not balance the costs (Powell et al. 1997). Gabor et al. (1999), however, showed that sounders on the Chaparral Wildlife Management Area in southwestern Texas, USA (an area that is characterized by semiarid vegetation and mean rainfall of 64 cm/yr) maintained exclusive home ranges. By contrast, spatial behavior of feral pigs in highly productive, tropical environments, suggests the inverse relationship between home range size and population density indicative of territoriality (Diong 1982, McIlroy 1989). Unfortunately, home range data in these environments were collected only at the individual level, with no information on sounder-level behavior. Because of the high reproductive potential of feral pigs (Dzieciolowski et al. 1992), we question whether food productivity in any environment is likely to be high enough that resource defense would not provide fitness benefits, and sounders would thus maintain the nonexclusive home ranges predicted by Powell et al. (1997) for high food productivity.

MANAGEMENT IMPLICATIONS

Our findings suggest territorial behavior in feral pigs, which can have a strong influence on management for population control because removal efforts in any location will have limited access to the local population. Pigs from the sounder in the vicinity of removal efforts will exclude conspecifics until enough have been removed that neighboring pigs have the opportunity to invade. This dynamic suggests 2 potential approaches to controlling density of feral pigs, dictated by the spatial and temporal extents of removal efforts. Short-term efforts (i.e., those that will not last longer than the time it takes for sounders to invade vacated territories) should be spatially extensive and designed so that geographic spacing of removal efforts matches the spacing of sounder territories. Where spatially extensive efforts are not feasible, removal from a limited number of locations should 1) focus on removing entire sounders (e.g., using large, corral traps capable of capturing an entire sounder), and 2) last long enough for reinvasions of vacated territories to take place, facilitating removal of pigs other than those in the original sounder. Control efforts located near key resources structuring territories (e.g., the sunflower field in Figs. 1, 2) may be able to draw and remove sounders over a large area and could be more effective than efforts that attempt to lure animals into temporarily baited sites. Control efforts of limited duration and geographic scope are unlikely to affect pig densities. Complete eradication of all feral pigs from an area is likely to require both the temporally and geographically extensive efforts we describe above. Our results further suggest that reinvasion of emptied territories is likely to confound eradication unless removal efforts are combined with barriers to reinvasion (e.g., fencing; Katahira et al. 1993, Cowled et al. 2006).

ACKNOWLEDGMENTS

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