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Territoriality and habitat selection of feral pigs on Fort Benning, Georgia, USA.
By

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Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

The University of Montana
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Territoriality and habitat selection of feral pigs on Fort Benning, Georgia, USA.

Chairperson: Mike Mitchell

Feral pigs are one of the most successful, widespread, economically and environmentally damaging invasive mammalian species worldwide. I conducted a study of feral pig sounders (female social groups) on Fort Benning, Georgia to test our hypotheses that feral pigs were territorial at the sounder level and that territoriality was a key factor influencing habitat selection of feral pigs. I used Global Positioning System (GPS) location data from 24 individuals representing 18 sounders combined with mark-recapture and camera trap data to evaluate evidence of territorial behavior at the individual and sounder levels by comparing the degree of overlap between home ranges. I categorized the landscape into five land cover types (open grassy areas, upland hardwood forest, pine forest, pine-hardwood forest, and hardwood bottomland forest) based on differences in the food and cover resources they provided feral pigs and used Ivlev's index to evaluate habitat use within sounder home ranges.

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. Sounders used the majority of forested cover types in proportion to availability and this supports our hypothesis that territorial behavior is a key factor influencing habitat selection by feral pigs on Fort Benning. Furthermore, the need for territory maintenance (patrolling, scent-marking) may mask changes in habitat selection based solely on resource availability. 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. Since feral pigs use the majority of forest cover types in proportion to availability, feral pig management actions need to address potential impacts across Fort Benning instead of limiting management actions to hardwood bottoms where pig activity is more apparent.

DEDICATION

I dedicate this body of work to all those people who at one time or another said "screw it", and just went fishing.

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CHAPTER ONE

INTRODUCTION

Invasive species are one of the primary causes of ecological damage, second only to habitat loss (Vitousek et al. 1997). They compete with native species, become agricultural pests, spread disease, and lead to extinctions. This can have a large economic impact through loss of agricultural production, reductions in biodiversity, and the high cost of control and eradication programs. Scientifically sound management strategies are needed to reduce negative ecological and economic impact of invasive species. Natural resource managers need information on the type and location of damage and the potential economic and ecological impact of the damage to justify control and eradication programs. In addition, they need basic biological information on invasive species to ensure management actions are as successful and efficient as possible and do not result in unintended consequences. Information describing home ranges and habitat selection of invasive species is important in developing management strategies because it determines where actions take place and the geographic extent of activities necessary to achieve objectives. Natural resource managers often try to manipulate habitat to increase the fitness of a particular species. In the case of invasive species, it might be possible to manipulate the habitat to decrease their fitness while simultaneously minimizing negative effects on native species.

Feral pigs are one of the most destructive mammalian invaders worldwide. Native to Eurasia, feral pigs have spread to every continent except Antarctica and many island chains throughout the world. They compete with native species, alter habitat structure, and spread or facilitate the spread of disease to livestock and wildlife

(Choquenot et al. 1996, Mountainspring 1987, Singer et al. 1984.) The species also has an economic impact on agriculture through losses in production of crops and livestock (Choquenot et al. 1996). To combat these problems, methods are needed to both predict where these impacts are likely to occur and to reduce or eliminate both the detrimental effects and the pigs. Studies have shown that feral pigs can heavily affect native species in many different ecosystems. In Hawaiian rainforests, rooting by feral pigs destroys understory vegetation used by the Maui Parrotbill (*Pseudonestor xanthophrys*), an endangered forest bird (Mountainspring 1987). In the Smoky Mountains of the Southeastern United States, the rooting of feral pigs has nearly eliminated the red-backed vole (*Clethrionomys gapperi*) and short-tailed shrew (*Blarina brevicauda*; Singer et al. 1984). In the California Channel Islands, the introduction of feral pigs has disrupted island food chains and allowed golden eagles (*Aquila chrysaetos*) to colonize the islands; this in turn has led to the near extinction of the island fox (*Urocyon littoralis*; Roemer et al. 2002). Feral pigs also cause economic losses. Pigs damage and destroy agricultural crops and property through foraging and movements. They can affect livestock production through competition, depredation, and the spread of disease. Predation rates on newborn sheep by feral pigs can be as high as 38% (Pavlov et al. 1981). Forestry losses occur through the reduced recruitment of valuable timber species such as longleaf pine (*Pinus palustris*) and oaks (*Quercus spp.*; Lipscomb 1989, Sweitzer and Van Vuren 2002). Feral pigs carry several diseases transmittable to livestock or humans (Romero and Meade 1999, Taft 1999, Gibson et al. 1998) and can cause serious financial losses for hog producers.

Management strategies for feral pigs generally consist of doing nothing, culling, or eradication. Culling and eradication programs in the United States are limited to a combination of trapping or shooting, and often involve dangerous techniques such as hunting with dogs or aerial shooting. These strategies are expensive both politically and economically, and therefore subject to public scrutiny. To develop scientifically sound and effective feral pig management plans, basic biological information is needed for the population to be managed. Information on home ranges, behavior, and habitat use allows natural resource managers to create scientifically sound management strategies that identify the need for control or eradication programs by evaluating their economic and ecological impacts.

In my thesis I link the spatial ecology of feral pigs to potential management strategies. In my first chapter, I examine the home range patterns of feral pigs for evidence of territoriality. Territoriality is a special case of home range use, and it can influence aspects feral pig ecology important to management such as population density, re-colonization rates, and habitat selection. Territoriality directly impacts control or eradication efforts by affecting trap encounter rates and novel techniques such as using Judas animals to locate sounders. I examine habitat selection of feral pigs in my third chapter, and evaluate the relative importance of territoriality, resources, and avoidance of human activity in structuring home range use. Territorial animals have to maintain their territories, and time spent patrolling, scent-marking, and evicting intruders will influence the results of use-availability studies based on resources. This is important to the management of feral pigs, because we generally assume the time spent in an area by feral pigs is proportional to the amount of damage caused by feral pigs. In my fourth chapter I

summarize the results of chapters 2 and 3 in regards to feral pig ecology and the management of feral pigs.

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CHAPTER 2

HOME RANGES AND TERRITORIALITY OF FERAL PIGS ON FORT BENNING, GEORGIA.

Abstract

I examined home range behavior of female feral pigs (*Sus scrofa*) in a heavily hunted population on Fort Benning Military Reservation in west-central Georgia. I used Global Positioning System (GPS) location data from 24 individuals representing 18 sounders (i.e., Female 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, I 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.

Introduction

Feral pigs 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 Coblenz 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 Coblenz 1986), individual females were the unit of study, and the authors found non-exclusive, 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 non-exclusive, overlapping home ranges (Boitani et al. 1994), whereas 2 (Ilse and Hellgren 1995, Gabor et al. 1999) reported sounders had exclusive, non-overlapping 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 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, semi-tropical 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 (*Hydrochoerus hydrochoerus*; 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 non-territorial 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

I conducted our study between May 2004 and August 2006 on the Fort Benning Military Reservation. The reservation consisted of 735 km² on the Coastal Plain – Piedmont fall line in eastern Alabama and western Georgia. The climate was semi-tropical 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/km² per year (Hanson 2006). I used control and removal areas that were approximately 50 km² and approximately 10 km apart to reduce the possibility of individuals moving between areas.

Methods

Capture and Handling

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

I 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). I measured head and body length to estimate age (Boreham 1981). I recorded sex and estimated weight. I photographed each feral pig before its initial release to aid in identifying tagged feral pigs re-sighted with the game cameras.

I fitted captured females >30 kg with a G2000 Large Mammal 12-channel Garmin receiver Global Positioning System (GPS)–very high frequency (VHF) collar (Advanced Telemetry Systems, Isanti, MN). I 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). I anesthetized sows using Telazol at 3.3 mg/kg using a jab stick. I 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, I 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. I 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).

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

Home Range Analysis

I identified sounder membership by a combination of direct observations, telemetry, trapping, and camera resightings. I 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 I collared multiple females simultaneously, I used only the data for the female with the greatest number of locations to estimate home range for the sounder because I almost always found females from the same sounder together. Where I collared multiple females sequentially with no overlap in timing of locations, I combined data across all collared females to estimate the home range for the sounder. In sounders where I collared only one female, I assumed its locations were representative of the sounder during that time period. I 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). I used only sounders with ≥ 60 locations over ≥ 30 days in the analysis. I 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).

I compared overlap between simultaneously collared sounders that had telemetry locations within 500 m of each other. I 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). I quantified home range overlap using 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 (Wronski and Apio 2006, Kenward 2001). To test our prediction that there would be an inverse relationship between population density and home range size, I used a 1-way analysis of variance (ANOVA; 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, I caught 310 individuals 600 times over 2,160 trap nights. During summer of 2004, I 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, I caught 51 pigs 117 times in the control area and 39 pigs 53 times in the treatment area. During the summer of 2006, I caught 77 pigs 144 times in the control area and 53 pigs 79 times in the treatment area.

Between August 2004 and May 2006, I 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. I removed 2.2 pigs/km² 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 treatment area relatively constant, whereas density in the control area increased.

I collected >4,200 photographs from game cameras over the 10-month sampling period; I captured feral pigs in 35% of photographs with 116 sightings of sounders.

Camera sightings corrected for detection probability (Program MARK; Hanson 2006) 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

I retrieved data from 24 individuals representing 18 sounders within the removal and control areas (Table 1). I found no evidence through trapping, camera sightings, or direct observation that any un-collared sounders were present within home ranges of collared sounders. I did not detect sub-groups within sounders as seen in other studies (Boitani et al. 1994, Gabor et al. 1999) through telemetry while I had multiple females from individuals sounders collared, but I 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 locations/individual = 368, SD = 128, mean days of overlap = 137, SD = 62) had extensive overlap at the 95% and 75% kernel home ranges ($84.0\% \pm 5.9\%$ and $76.5\% \pm 13.1\%$, respectively) and 50% kernel core area ($69.4\% \pm 12.7\%$). I found little overlap among pairs of sounders ($n = 9$ dyads, mean locations/sounder = 330, SD = 130, mean days of overlap = 97, SD = 42) at the 95% kernel home range ($5.6\% \pm 5.9\%$), little

overlap at the 75% kernel home range ($0.4 \% \pm 1.1\%$), and no overlap at the 50% kernel core area. I 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 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. I 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. I 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). I found female feral pigs on Fort Benning were territorial at the sounder level but not at the individual level. Although I 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, I 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. 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 I was unable to document this behavior. I 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 I 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, Kurt and Marchington 1972, Wood and Brenneman 1980, Singer et al. 1984, Ilse and Helgren 1995). Contrary to our prediction, I 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. I 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.

I 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 I 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 non-territorial 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, non-overlapping 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 wild male sounders had overlapping, non-exclusive 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 non-exclusive 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, non-territorial 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 (an area that is characterized by semi-arid 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), I 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 non-exclusive 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 I 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).

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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, 2004-2006.

Study area	No. of sounders	No. of locations		Home range size (km ²)	
		\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

Figure 1.-- Map showing 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. The dashed line shows the expansion of sounder B's home range to include the sunflower field after the collared sow and another adult sow from sounder A were killed by a hunter.

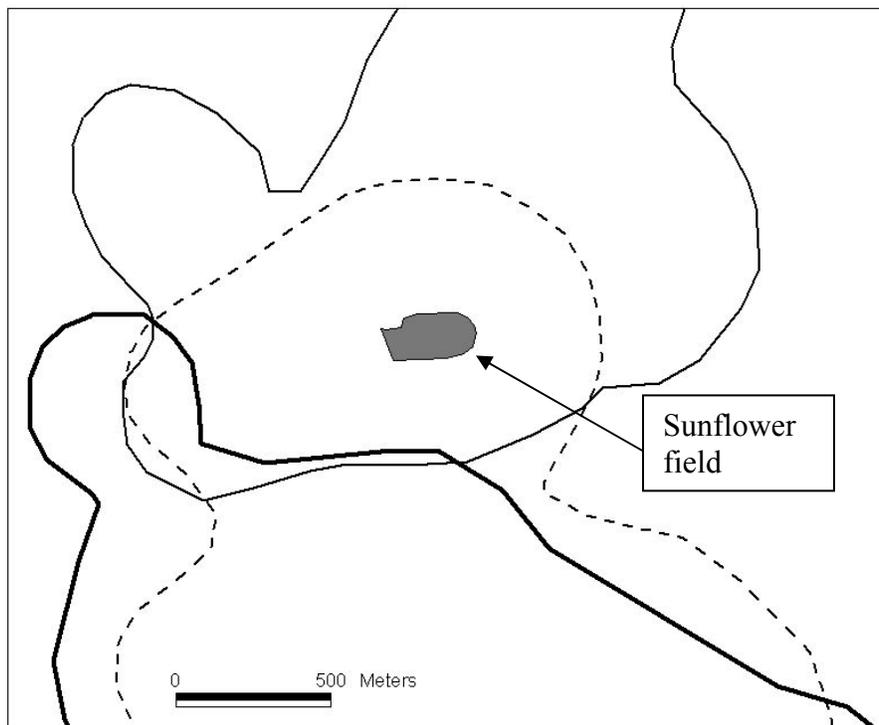
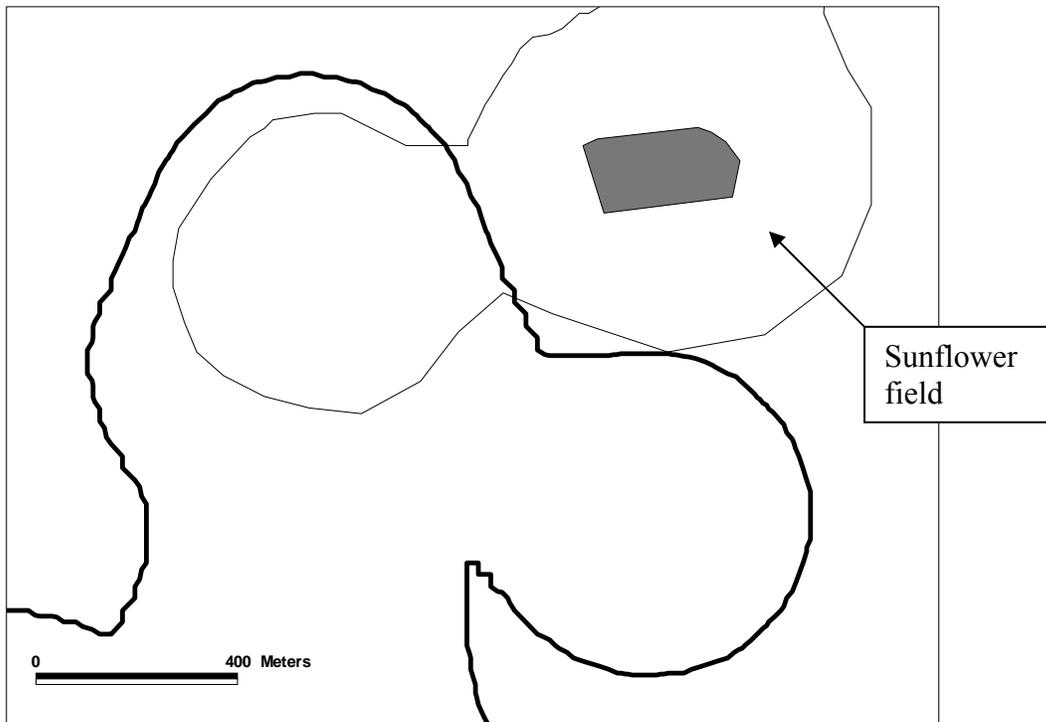


Figure 2.--Map showing territories of two sounders adjacent to the same field the previous year during a four month period between July and October 2004. Fifty-six locations from sounder X (thin line) were recorded from the field during a 45 day period between July 21st and September 3rd, 2004. Two locations from sounder Y were recorded from this area during these four months, one location 55 m from the field on June 6th and one location from the field on September 13th 2004.



CHAPTER THREE

HABITAT SELECTION OF FERAL PIGS ON FORT BENNING, GEORGIA

Abstract

I examined how territoriality, resources, and human activity affected third order selection of habitat by sounders (female groups) of feral pigs using Global Positioning System (GPS) telemetry on the Fort Benning military installation in Eastern Alabama and Western Georgia. I hypothesized that territoriality was a key factor influencing habitat selection and predicted that the need for territory maintenance (patrolling, scent-marking) would result in use of land cover types proportional to their availability overall, but variation in hard mast availability and avoidance of human activity would cause seasonal and daily variation in habitat selection. I categorized the landscape into five land cover types (open grassy areas, upland hardwood forest, pine forest, pine-hardwood forest, and hardwood bottomland forest) based on differences in the food and cover resources they provided feral pigs. In general, pigs avoided upland hardwood forest, and used pine forest, pine-hardwood forest, and hardwood bottomland forest in proportion to availability. Habitat use of forested cover types did not vary with the availability of hard mast, which was surprising given the importance of hard mast in the breeding biology of this species. Pigs avoided open grassy areas during the day and when mast was available, indicating a preference for areas that provide cover when food resources allow it. Even use of forested cover types supports our hypothesis that territorial behavior is a key factor influencing habitat selection by feral pigs on Fort Benning. Since feral pigs use the majority of forest cover types in proportion to availability, feral pig management actions need to address potential impacts across Fort Benning instead of limiting management

actions to hardwood bottoms where pig activity may be more apparent. I also recommend locating large-coral style traps used to capture pigs close to water and away from major roads. Allowing hunters to use centerfire rifles to hunt pigs when mast is unavailable and are more likely to use open grassy areas may increase hunter success.

Introduction

Native to Eurasia, feral pigs (*Sus scrofa*) have spread to every continent except Antarctica and many island chains throughout the world. Where they have been introduced, feral pigs compete with native species, alter habitat structure, and spread or facilitate the spread of disease to livestock and wildlife (Singer et al. 1984, Mountainspring 1987, Choquenot et al. 1996). Feral pigs frequent riparian areas and are associated with issues of water quality such as water-borne illnesses and erosion (Atwill et al. 1997, Kaller et al. 2007). Feral pigs also have a negative economic effect on agriculture and forestry due to losses of crops and livestock and reduced recruitment of valuable timber species (Lipscomb 1989, Choquenot et al. 1996, Sweitzer and Van Vuren 2002). Feral pigs are thus often considered a serious pest species requiring intensive management.

Management strategies to reduce or eliminate the negative impacts of feral pigs are generally limited to either eradication or culling, and these efforts are expensive, costing millions of dollars in U.S. currency (Katahira et al. 1993, Schuyler et al. 2002, Mccann and Garcelon 2008). Studying the habitat use of feral pigs allows land managers to identify areas affected by feral pigs and justify the expense of management actions. It can also guide management actions by identifying areas for exclusionary fencing, placing traps, and detecting evidence of feral pig activity.

On the Fort Benning Military Post located on the Georgia-Alabama border, natural resource managers were concerned with an increasing pig population (Hanson et al. 2006) and its impact on plant and animal communities on Fort Benning. Relict trilliums (*Trillium reliquum*) are a federally endangered plant species found in hardwood bottomland forest on Fort Benning that require exclusionary fencing to prevent pigs from injuring or consuming them while foraging. Feral pigs could negatively affect longleaf pine (*P. palustris*) restoration efforts intended to protect other threatened and endangered species on Fort Benning. Species of concern such as Gopher tortoises (*Gopherus polyphemus*) and Gopher frogs (*Rana capito*) occupy the upland pine and mixed pine-hardwood areas of the base and may be eaten by feral pigs (Macfarland et al. 1974, Coblenz and Baber 1987), because heavy depredation of reptiles and amphibians by feral pigs has been reported on Fort Benning (Jolley 2007). Rooting and wallowing by feral pigs in riparian areas was a concern because of increased erosion, impacts on aquatic communities, and reduction of water quality.

Natural resource personnel commonly found pig sign (rooting, tracks, feces) in hardwood bottomland forest and open grassy areas such as training fields and wildlife openings, but infrequently found sign in upland pine or pine-hardwood forest types (Mark Thornton, Fort Benning Natural Resources, personal communication). Natural resource managers believed this might be evidence of limited use of upland forest types by feral pigs on Fort Benning. If true, pig management might be limited to bottomland hardwood areas and fencing might be the only action needed to exclude pigs from known relict trillium populations. Equal use of all forest types would require additional

management to protect endangered species such as gopher turtles and gopher frogs within the longleaf pine ecosystem.

Pigs are highly social and sociality can influence habitat selection. Feral pig 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 (Boitani et al. 1994), with most female offspring remaining with the sounder after weaning (Kaminski et al. 2005). Sounders on Fort Benning are territorial (Sparklin et al. 2009) and the need to maintain these territories by active or passive defense could result in homogeneous use of home ranges and lead to an apparent lack of habitat selection based on resources (Lewis et al. 1997). Two previous studies of feral pig sounders that appeared to be territorial found they used habitat types in proportion to availability and support this hypothesis (Gabor et al 2001, Ilse and Hellgren 1995). Because sounders form the basic social unit in feral pigs, I designed our study to examine habitat selection of feral pig sounders (rather than individual pigs) at Johnson's (1980) third order of habitat selection (i.e., selection of resources within the home range).

Fort Benning provides many resources exploited by feral pigs. Upland and bottomland hardwood forests on Fort Benning produce hard mast and have moist soils that provide favorable rooting substrates for invertebrates. Hard mast is probably the single most important food resource for feral pigs (Henry and Conley 1972, Singer et al. 1984, Sweitzer and Van Vuren 2002) and is important in maintaining breeding condition (Matschke 1967). The availability of hard mast is also an important determinant of juvenile fecundity in pigs which has been shown to drive population growth (Bieber and Ruf 2005). When hard mast was unavailable, pine and pine-hardwood mixed forests on

Fort Benning provided food resources for pigs in the form of grasses, roots, and soft mast such as hawthorn (*Crataegus* spp.) and persimmon (*Diospyros virginiana*). In the absence of territoriality, these dietary changes should result in pigs reducing selection for upland hardwoods and hardwood bottomlands and increasing use of pine and pine-hardwood mixed forest cover types. Feral pigs eat the roots of longleaf pine, negatively affecting longleaf pine trees and reducing the regeneration of longleaf pine seedlings (Graves 1984, Lipscomb 1989). Feral pigs use upland pine stands (Wood and Brenneman 1980) and mixed oak-pine stands (Singer et al 1984) for bedding areas. Prescribed burning in these areas may initially reduce food and cover resources available but increase the amount and nutritional value of herbaceous plants eaten by feral pigs as vegetation recovers (Harlow and Beiling 1961, Crawford 1984, Brockway and Lewis 1997). Military training fields and wildlife plantings also provide important food resources for feral pigs such as grasses, roots, tubers, and earthworms (Henry and Conley 1972, Graves 1984, Belden and Frankenberger 1990), but they offer little escape cover which may lead to avoidance of these areas.

Because pigs lack sweat glands, they depend on water to thermoregulate (Barret 1978, Caley 1997). In studies occurring in arid climates, the availability of water and thermal refugia are thought to be limiting factors influencing home ranges and movements (Barrett 1978, Choquenot 2003). However, in temperate climates, these factors have little effect (Boitani et al 1994.) Modeling by Choquenot (2003) showed that in Australia the need to access riverine woodlands can compromise the foraging efficiency of feral pigs, and they cannot exist in areas more than 10 km from extensive riverine woodlands without periodic recolonization. The Chattahoochee River and

several major tributaries flow across Fort Benning, and the abundance of water may allow feral pigs to utilize all portions of the installation.

Feral pigs are sensitive to disturbance and avoidance of areas with human activity can influence habitat selection. Hunting was the primary cause of mortality for pigs on Fort Benning, and annual survival for adult and juvenile feral pigs was low (0.319 ± 0.040 and 0.311 ± 0.047 , respectively Hanson 2006). Saunders and Kay (1996) showed feral pigs became almost completely nocturnal as a result of hunting pressure, spending the daytime hiding in bedding areas that provide thick cover. In addition to hunting pressure, human activity associated with roads can lead to changes in habitat selection (Frid and Dill 2002). Wild boars are known to avoid areas near roads (Theuerkauf and Rouys 2008) and feral pigs may also exhibit this behavior. The combined affect of hunting pressure and use of roads during military training exercises on Fort Benning should result in a pig population that shows nocturnal behavior and avoids roads.

Study Area

I conducted our study between May 2004 and August 2006 on the Fort Benning Military Reservation. The reservation consisted of 735 km² on the Coastal Plain – Piedmont fall line in eastern Alabama and western Georgia. The climate was semi-tropical with an average rainfall of 132 cm (Dilustro et al. 2002). Longleaf pine, scrub oak (*Quercus* sp.), and loblolly pine (*P. taeda*) dominated ridge tops, whereas slopes transitioned into upland hardwood forests dominated by oak and hickory (*Carya* spp.) species. Hardwood bottomland forest was a mixture of sweet gum (*Liquidambar styraciflua*), yellow poplar (*Liriodendron tulipifera*), hickory, and oak. Most training compartments were undeveloped forest, but some contained semi-developed sites such as firing ranges,

obstacle courses, and wildlife openings that were mostly open grassy areas. Training compartments were accessed by perimeter roads and one or more interior roads. Logging trails and 4x4 trails were also common in training compartments but were used infrequently by the military allowing for the retention of vegetation. Perimeter roads were heavily traveled during the day but nighttime military activity was infrequent.

Methods

Land Cover Classification

I used existing GIS data of land cover from the Georgia GAP classification (Kramer et al. 2003), validated by natural resource personnel from Fort Benning. Based on previous feral pig habitat selection studies in the Southeastern United States (Gaines et al. 2005), I merged the 30 cover classes present into five habitat classes. I merged the 11 pine categories into a single pine forest class and eight mixed pine-hardwood categories into a pine-hardwood mixed forest class. I merged the 10 hardwood categories into two hardwood classes, upland hardwood forest and hardwood bottomland forest. I merged wildlife openings and military training areas into a single open grassy area category. Because forested stands recovered rapidly from prescribed burns, I examined effects of prescribed burning on habitat selection using 3 burn classes, first year after burning, second year after burning, and third year after burning. I assumed understory vegetation responded similarly to fire across all cover types, and combined them for analysis.

To assess the use of riparian areas by feral pigs, I categorized the landscape into six categories based on distance to streams, 0 to 50 m, 51 to 100 m, 101 to 150 m, 151 to 200 m, 201 to 250 m, and areas greater than 250 m from the nearest stream. I assumed

the effects of human activity declined with distance from the nearest road and used the same distance categories used for the analysis of distance from streams.

Trapping

I used walk-in box traps baited with corn and corn mash to capture pigs. I pre-baited for 5-14 days with trap doors tied open to allow pigs to become accustomed to the traps. All captured pigs were ear-tagged, measured, and photographed to aid in identification.

Captured sows larger than 30 kg were fitted with a G2000 Large Mammal 12-channel Garmin receiver GPS/VHF collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). I chose sows of this size because of constraints on collar adjustment and because this size is considered the minimum size for first reproduction (Fernandez-Llario and Mateos-Quesada 1998). I anaesthetized sows to be collared with Telazol at 1 cc/30 kg using a jab stick. I programmed collars to attempt self-location for two minutes every five hours. When a collar failed to obtain a location, it re-tried self location after one hour. All capture and handling of pigs was done in accordance to Auburn University Institutional Animal Care and Use Committee, permit number 2003-0531.

Identifying sounder membership and home ranges

I identified sounder membership by a combination of direct observations, telemetry, trapping, and camera re-sightings. I considered ≥ 2 females of reproductive size captured or observed together ≥ 3 times as members of the same sounder. In sounders where I collared multiple females simultaneously, I used only the data for the female with the greatest number of locations to estimate home range for the sounder because I almost always found females from the same sounder together. Where I collared multiple females sequentially with no overlap in timing of locations, I combined data across all

collared females to estimate the home range for the sounder. In sounders where I collared only one female, I assumed its locations were representative of the sounder during that time period.

I 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 (Seaman and Powell 1996, Kernohan et. al. 2001). I defined the sounder home range as the 99% probability utilization distribution (Gabor et al. 1999). I generated all home range estimates using a minimum of 60 locations over a period of at least 30 days with KERNELHR software (Seaman et al 1998) using a 50 m grid size and least squares cross validation to determine the smoothing factor. I generated daytime home ranges using locations that were collected between 60 minutes after sunrise and 60 minutes before sunset, whereas nighttime home ranges were generated using locations collected 60 minutes after sunset and 60 minutes before sunrise. Based on stomach content analysis at Fort Benning (Jolley 2007) hard mast was available between October and March and unavailable between April and September. Therefore, I generated home range estimates for these two periods. For the analysis of the affect of mast availability on home range size, I only used sounders that met our data requirements for both the mast available and mast unavailable periods and compared estimates using repeated-measures ANOVA.

Habitat Selection

To measure habitat selection, I used Ivlev's electivity index (1961) to estimate selection of habitat components. Ivlev's index is a simple measure of habitat selection where for each habitat type $1 \dots k$ use, standardized for availability, is calculated

$$(U-A) / (U+A),$$

where U is (summed kernel densities in habitat k) / (summed kernel densities in all habitats), and A is defined as (area of habitat k) / (total area of all habitats). Values of electivity index can range from -1.0 to 1.0. A positive value in Ivlev's index indicates a use greater than expected by chance (preference), and a negative value indicates less use than expected by chance (avoidance).

For each sounder, I considered availability of habitats to be that the proportion found within each 99% kernel home range, and I calculated use of habitat k as sum of total kernel density probabilities that were located within habitat k . I generated kernel density probabilities and cover type data in raster format using the same 50 m grid of the study area.

Results

Trapping

During 3 summer mark-recapture sessions, I caught 310 individuals 600 times over 2,160 trap nights. During summer of 2004, I caught 55 feral pigs 134 times in the control area and 35 feral pigs 73 times in the treatment area. During the summer of 2005, I caught 51 pigs 117 times in the control area and 39 pigs 53 times in the treatment area. During the summer of 2006, I caught 77 pigs 144 times in the control area and 53 pigs 79 times in the treatment area. I collected >4,200 photographs from game cameras; I 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).

Identifying sounder membership and home ranges

I collared 32 female pigs and retrieved data from 24 individuals which I used to generate home range estimates for 18 different sounders. Each sounder was followed for an average of 146 days (SE = 21) with 330 locations (SE = 48) collected per sounder. The average annual home range size using all locations was 3.05 km² (SE = 0.80). Nine sounders met our data requirements for generation of home range estimates for both the mast available and mast unavailable periods. The average home range size when mast was available was 2.41 km² (SE = 0.55), when mast was unavailable the average home range size was 3.68 km² (SE = 0.70). Eight of the 9 sounders decreased their home range size when mast was available, while the remaining sounder increased its home range size (from 5.20 km² to 6.39 km²), but appeared to shift its home range into an adjacent area. Home ranges did not decrease strongly in size when mast was available using all 9 sounders ($F_{1,8} = 2.84, P = 0.131$), but when the sounder that shifted its home range was removed from the analysis, the decrease in home range size was more pronounced ($F_{1,7} = 5.80, P = 0.047$).

Habitat selection

Pigs used pine, pine-hardwood, and hardwood bottomland forest in proportion to availability with a weak trend towards avoidance of pine and pine-hardwood forest and a weak trend towards preference of hardwood bottomland forest (Figure 1). Pigs strongly avoided upland hardwood forest (Figure 1). Mast availability did not significantly influence habitat use of any forested cover type (Figure 1). Pigs used open grassy areas in proportion to availability overall, at night, and when mast was unavailable. Pigs avoided grassy areas during the day and when mast was available (Figure 1). Pigs

avoided or tended to avoid areas subjected to prescribed burns regardless of years since burning (Figure 2).

Pigs preferred areas within 50m of streams, used areas between 50 and 200m from streams in proportion to availability, and avoided areas greater than 200m (Figure 3). Pigs appeared to also show a higher level of avoidance of areas greater than 200m from streams during the daytime (Figure 3). Pigs avoided areas less than 100m to roads, and used areas greater than 100m from roads in proportion to availability (Figure 4). When only daytime locations were used, pigs strongly avoided areas less than 150 m from roads, and used areas greater than 150 m from roads in proportion to availability (Figure 4). There was still a trend towards avoidance of areas near roads at night, but all distance categories were used in proportion to availability (Figure 4).

Discussion

Management of feral pigs is expensive, with options available to land managers in the U.S. limited to exclusion by fencing, or attempting to cull or eradicate feral pigs through a combination of trapping and shooting. Because of the cost and contentious nature of feral pig management (McCann and Garcelon 2008, Witmer et al. 2003), land managers need to be able to identify where and when pigs are damaging natural resources to determine if management actions are necessary. I was interested in how territoriality, resources, and human activity influenced habitat selection by feral pigs, and if this information could provide insight into the potential impact of feral pigs on plant and animal communities on Fort Benning. I hypothesized that territoriality (Sparklin et al. 2009) would have a large influence on habitat selection at the third order of selection, resulting in homogenous use of the four forested cover types overall with seasonal

changes in habitat use and home range size related to hard mast availability. Prescribed burning within the three upland forest types could initially reduce the amount of food and cover, but then increase the amount and quality of food and cover resources as vegetation recovers. I also hypothesized that hunting and military training would result in pigs avoiding areas with high potential for contact with humans and as a result pigs would avoid open grassy areas and areas near roads.

Pigs used pine, pine-hardwood, and hardwood bottomland forest in proportion to availability. Contrary to our prediction, pigs consistently avoided upland hardwood forest. Upland hardwood forest on Fort Benning had an open understory, and the lack of cover within this forest type combined with the high level of human activity on Fort Benning might explain why upland hardwood forest was avoided by pigs in this study but preferred by feral pigs in previous studies (Gaines et al. 2005). Contrary to our predictions, availability of hard mast did not influence selection among forest types. These results are unexpected because 1) the importance of hard mast in the breeding biology of this species (Matschke 1967, Bieber and Ruf 2005), 2) stomach content analysis of feral pigs on Fort Benning showed hard mast was the primary dietary component when available (Jolley 2007), and 3) observed sizes of home ranges changed with mast availability, suggesting resource limitation (Powell 2000). However, sufficient amounts of hard mast may have been produced in pine forest to attract pigs when mast was available, and other food resources may have been exploited by pigs in bottomland hardwood forest when hard mast was unavailable. It is also possible and consistent with our predictions that the need to maintain territories (i.e. patrolling and scent-marking) masked seasonal variation in habitat selection based on changes in mast availability

within these forest types. The need for territory maintenance would also explain why use of pine, pine-hardwood, and hardwood bottomland forests was in close proportion to availability. These results also support our prediction that the absence of pig sign does not necessarily indicate the absence of feral pig activity, and that feral pigs are active within the upland pine and pine-hardwood mixed forest cover types on Fort Benning.

Contrary to our prediction, pigs used open grassy areas in proportion to availability, although there was a trend towards avoidance. The increased use of grassy areas when mast was unavailable is likely due to the change in diet from hard mast to one primarily of grasses, roots, and tubers which increased the value of resources provided by this cover type. Open grassy areas provided little or no cover, and pigs foraging in these areas were highly vulnerable to being harvested by hunters. Pigs appeared to reduce the risk of foraging in these areas by using them at night, and avoided open grassy areas within their home ranges when mast was available. Seasonal and nocturnal use of similar cover types has been reported in heavily hunted wild boar populations (Boitani et al. 1994). Given the territorial nature of feral pig sounders on Fort Benning (Sparklin et al. 2009), I hypothesize that pigs increased the use of these areas out of necessity when adequate food resources were not available in other cover types within their territory. The overall trend of avoidance of areas subjected to prescribed burns reflects the trend towards avoidance of pine and pine-hardwood forest and avoidance of upland hardwood forest. Pigs showed a weak trend of preferring those burned areas in the second year following a burn, and this could be related to the recovery of vegetation providing better food resources or cover.

The strongest habitat selection responses shown by feral pigs on Fort Benning were not responses to cover type, but responses to distance from streams and roads. Pigs preferred areas in close proximity to streams. Riparian areas were likely used by pigs to aid in thermoregulation during warm weather, but on several occasions I also observed pig rooting in shallow or exposed stream beds and around the receding edges of vernal ponds which indicated they were feeding in these areas as well. Reptiles and amphibians that breed in these areas are vulnerable to depredation by feral pigs, especially those species that occur temporarily in large concentrated breeding aggregations (Jolley 2007). Pigs avoided areas close to roads as predicted, and the diurnal response to roads supports our hypothesis that feral pigs attempt to avoid human contact.

Management Implications

Management of feral pigs on Fort Benning needs to address the impacts of feral pigs within upland pine forest and mixed pine-hardwood forest as well as bottomland hardwood forest. Feral pigs preferred areas near water, and given the evidence for high levels of depredation on reptiles and amphibians on Fort Benning (Jolley 2007), I recommend using fencing to exclude feral pigs from vernal ponds used for breeding by gopher frogs. I also suggest that selecting areas close to water and removed from major roads may be more important than choosing a specific cover type when selecting trap locations. Although pig sign (rooting in particular) is a clear indicator of pig activity, care should be taken in interpreting its absence. Pig sign on Fort Benning indicated that hardwood bottomland forest and open grassy areas were used most frequently by pigs, but our results indicate that pine and pine-hardwood mixed forest were used just as frequently. Dietary analysis may provide more useful insights into the affects of feral

pigs on plant and animal communities than habitat selection studies because they are not as likely to be confounded by territorial behavior. Future research into habitat selection of feral pigs should address if the population was territorial, because of the potential for territoriality to confound the results.

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Figure 1.--Ivlev's index values and 95% confidence intervals showing selection by feral pigs for pine, hardwood bottomland, pine-hardwood, upland hardwood, and open grass cover types on Fort Benning between May 2004 and August 2006 using (●) all locations, (◆) nighttime locations, (◇) daytime locations, (■) locations when mast was available, and (□) locations when mast was not available at the third order of selection.

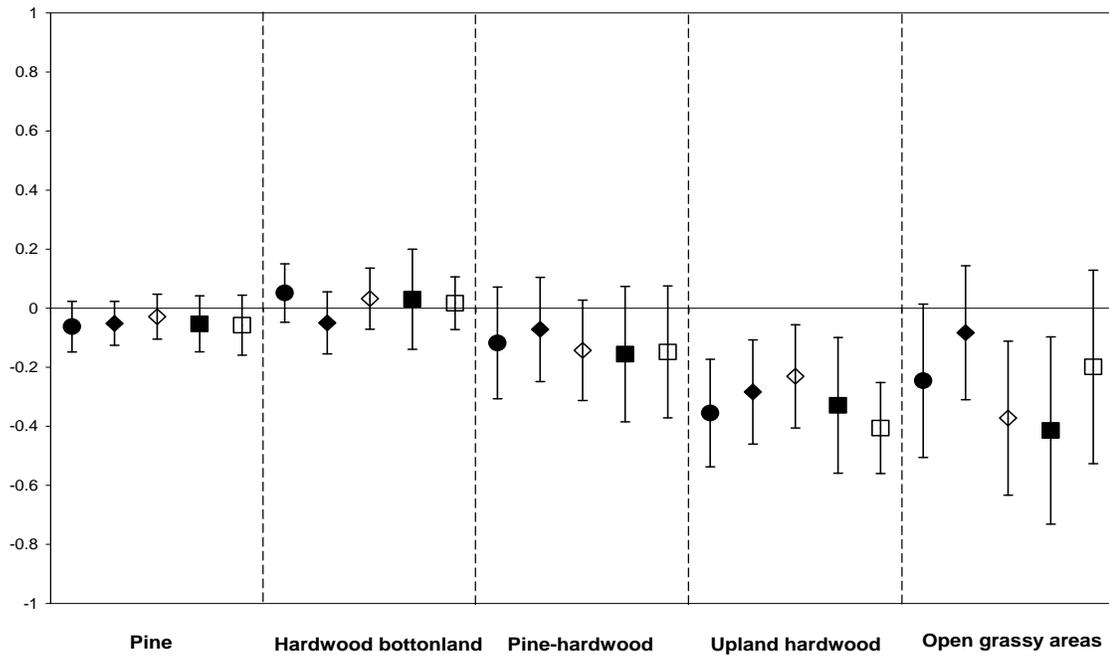


Figure 2.--Ivlev's index values and 95% confidence intervals showing selection of areas subjected to prescribed burns by feral pigs on Fort Benning between May 2004 and August 2006 during the (◆) first year, (■) second year, and (□) third year after burning at the third order of habitat selection.

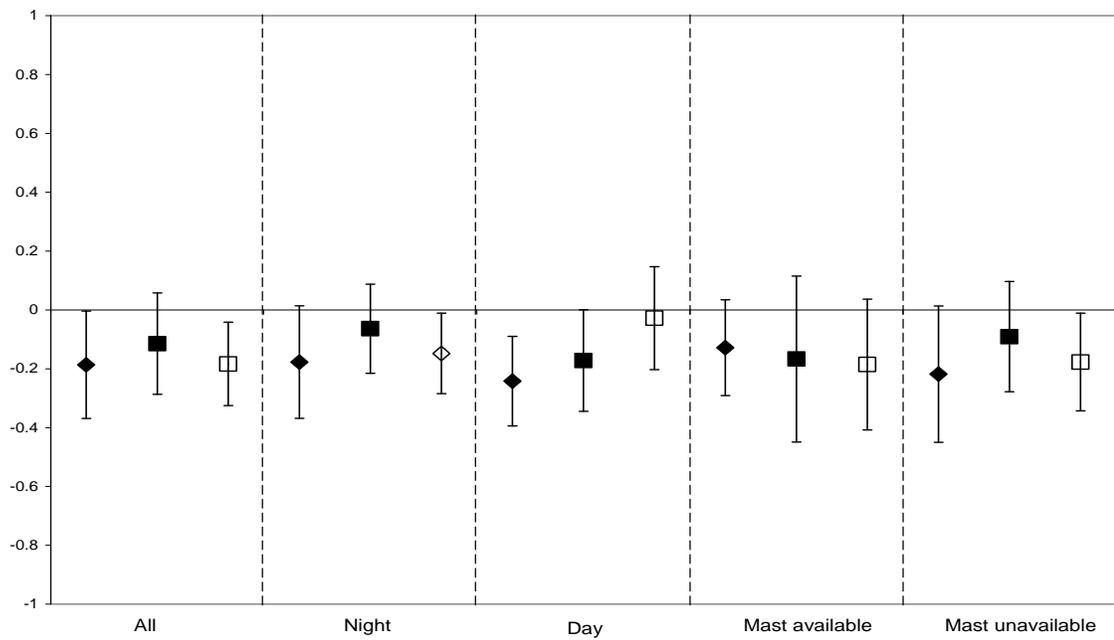


Figure 3.--Ivlev's index values and 95% confidence intervals showing selection of areas by feral pigs on Fort Benning based on distance to the nearest stream between May 2004 and August 2006 using (●) all locations, (◆) nighttime locations, (◇) daytime locations, (■) locations when mast was available, and (□) locations when mast was not available at the third order of selection.

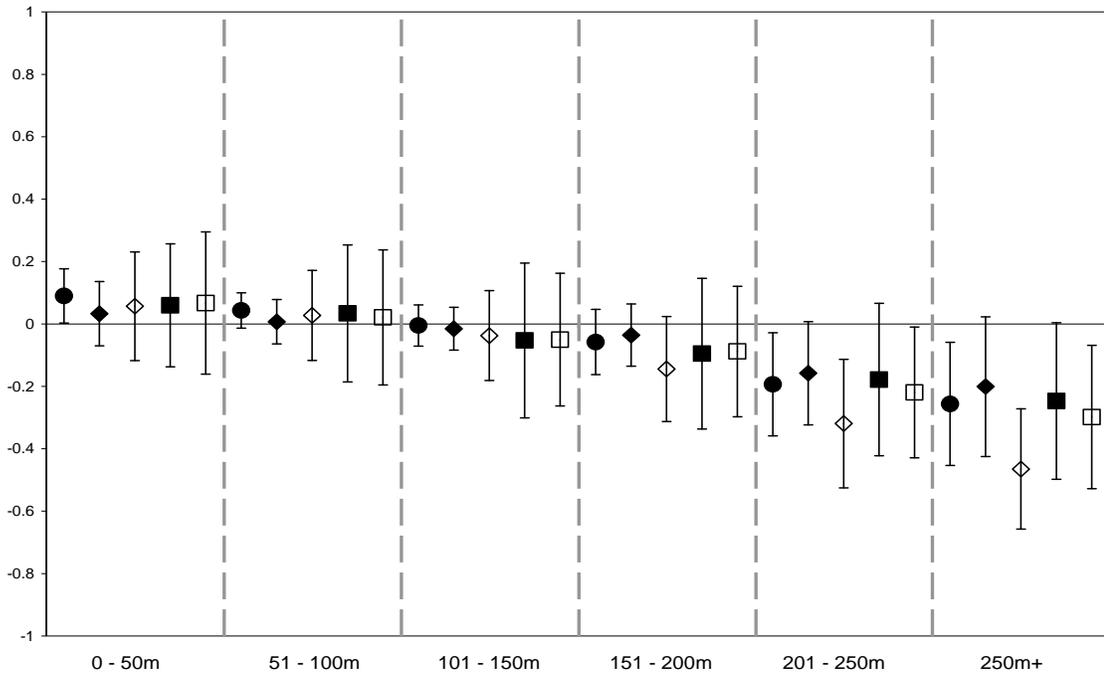
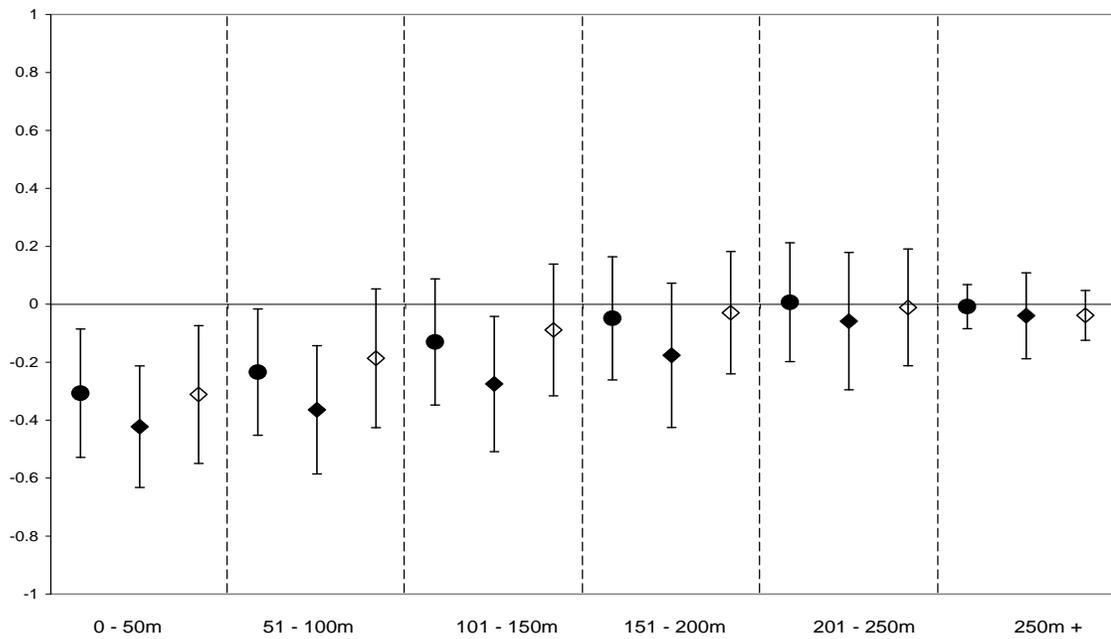


Figure 4.— Ivlev's index values and 95% confidence intervals showing selection of areas by feral pigs on Fort Benning based on the distance to the nearest road between May 2004 and August 2006 for (●) all locations, (◆) nighttime locations, (◇) daytime locations at the third order of selection.



CHAPTER 4

CONCLUSIONS

Feral pigs are one of the most successful, widespread, and destructive mammalian invaders known. They cause widespread ecological and economic damage making them to one of the greatest concerns to wildlife biologists and managers today (Ditchkoff and West 2007). They directly or indirectly imperil many threatened and endangered species and cause heavy losses to agriculture (Singer et al. 1984, Mountainspring 1987, Choquenot et al. 1996). Because management options are often contentious as well as expensive (McCann and Garcelon 2008, Witmer et al. 2003), land managers need basic biological information describing home ranges and habitat selection to predict the response of feral pigs to management actions and determine the geographic extent of management actions necessary to achieve management objectives. Understanding habitat use of feral pigs helps land managers to document the ecological and economic impacts of feral pigs and justify the need for feral pig management. Because of their worldwide geographic distribution, feral pigs have adapted to many different environments. Each environment where feral pigs occur provides its own combination of resources that influences habitat selection and dictates which spacing pattern is the most efficient use of those resources, be it nomadism, an undefended home range, or territoriality.

To my knowledge this study was the first to specifically test for territoriality in feral pig sounders. I examined the home ranges and habitat selection of feral pig sounders on Fort Benning and found that they were territorial. This contributes to our basic biological understanding of feral pigs as a species because territorial behavior has been predicted,

but previous information at the sounder level had been inconclusive (Boitani et al. 1994, Ilse and Hellgren 1995, Gabor et al. 1999.) It also demonstrates the need to understand the social biology of the species in question. Many previous studies may have failed to observe evidence for territoriality because they were using the home ranges of individual sows and not sounders as the sample unit. If I had done this, I would have concluded that feral pigs had overlapping home ranges and were not territorial, which would have confounded the results of our habitat selection analysis.

Territoriality influenced habitat selection, with feral pig sounders using most cover types in proportion to availability and changes in habitat selection based on resources being masked by the need to maintain their territories (i.e., patrolling and scent-marking). This has important implications for future research and management of feral pigs on Fort Benning and in other territorial pig populations because territoriality will not only influence how and where pigs utilize the landscape and subsequently cause environmental and economic damage, but also define the spatial and temporal extent of management actions needed to reduce the negative affects of feral pigs. Future research into the habitat selection of feral pigs needs to begin by identifying if sounders are territorial; because territoriality is likely to confound use-availability habitat selection studies at Johnson's (1980) second and third orders of selection. When feral pigs are territorial, dietary analysis may provide better insights than habitat selection studies into food resources utilized by feral pigs. Natural resources managers need to be aware that in territorial populations of feral pigs, new sounders will quickly occupy vacant territories, and that attempts to reduce feral pigs densities through culling may prove

fruitless unless steps are taken to prevent reinvasion. Some highly valuable resources (such as the sunflower field in Chapter 2) will structure home ranges. Incorporating them into management activities such as trapping programs can increase effectiveness because as sounders are removed, nearby sounders will quickly incorporate them into their territories and become susceptible to trapping efforts without the need to move traps.

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