Contract No:

This document was prepared in conjunction with work accomplished under Contract No. DE-AC09-08SR22470 with the U.S. Department of Energy (DOE) Office of Environmental Management (EM).

Disclaimer:

SOCIAL UNIT ORGANIZATION IN THREE WILD PIG POPULATIONS

J. J. Mayer

February 2021

SRNL-STI-2021-00074, Revision 0

DISCLAIMER

Printed in the United States of America

Prepared for
U.S. Department of Energy

SRNL-STI-2021-00074
Revision 0

Keywords: Group, herd, Invasive species, social organization, *Sus scrofa, wild pig*

Retention: *Permanent*

SOCIAL UNIT ORGANIZATION IN THREE WILD PIG POPULATIONS

J. J. Mayer

February 2021

Prepared for the U.S. Department of Energy under contract number DE-AC09-08SR22470.

Savannah River National Laboratory®
OPERATED BY SAVANNAH RIVER NUCLEAR SOLUTIONS

PREFACE OR ACKNOWLEDGEMENTS

We thank the Collier Companies, the Ossabaw Island Foundation, and the U. S. Department of Energy's Savannah River Site for access to lands under their controls. We are especially grateful for the assistance of E. T. West, A. W. Conger, the late J. W. Reiner, P. E. Johns, H. O. Hillestad, R. W. Whiteside, J. R. Fudge, J. T. Vermont, D. B. Land, M. R. Ramsey, D. B. Pylant, J. C. Kilgo, R. E. Parker, D. L. Stallnecht, and J. L. Corn. The Southeastern Cooperative Wildlife Disease Study generously provided specimens and data from Ossabaw Island for use in this study. Funding for this study was provided by Collier Enterprises, Inc. under the auspices of Project No. 55-7608 of Law Environmental, Inc., the Ossabaw Island Foundation, and by the U. S. Department of Energy to the University of Georgia under financial assistance award no. DE-SC09-96SR18546, and Contract DE-AC09-08SR22470 to Savannah River Nuclear Solutions LLC.

EXECUTIVE SUMMARY

Wild pig (*Sus scrofa*) social unit organization was compared in three introduced populations in the southeastern United States. Group size, age and sex composition and types of social unit were recorded from field observations. Groups of two or more individuals were significantly more frequent than solitary animals in all three populations. Mixed adult/immature groups were the largest social unit of two or more individuals, followed by groups of immature animals and the various types of adult groups. In two of the populations, this same trend among these groups types was seen for the frequency of occurrence (i.e., with the adult/immature group being the most common). In the third population, the frequency of the adult/immature and immature-only groups were reversed. Size variation within all except the mixed-sex adult group type was similar among the three field sites. Adult males were the most frequently observed solitary category. Increased percentage of hardwood forest was significantly correlated with a decrease in the percent frequency of immature-only groups and an increase in adult/immature groups. Increasing annual harvest by man was significantly correlated with an increase in the frequency of immature-only groups and a decrease in those of adults/immatures. The biased removal of females through trapping would be consistent with the apparent shift from adult/immature groups to immature-only groups among the three field sites.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1.0 Introduction

Wild pigs (*Sus scrofa*) have the simplest type of social organization within the Artiodactyla (Mammalia: Ungulata) (Ewer 1968). The basic social unit documented for this species is composed of mature females and their offspring; mature males are largely solitary (Barrett 1978; Conley et al. 1972; Diong 1973; Eisenberg and Lockhart 1972; Frädrich 1974; Kurz and Marchinton 1972; Martys 1991a, 1991b; Sweeney et al. 2003). Groups consisting of only adults or unaccompanied immatures, solitary adult females, and solitary immatures are also known to exist (Baber 1977; Dardaillon 1988; Diong 1982; Mansfield 1978; Nichols 1962). However, only limited data are available on the size variation, specific sex and age composition, or frequencies of such social units, and the differences among these parameters due to varying environmental conditions or management regimes.

Social unit size in wild pigs has been reported to vary depending on season, habitat and predation (Dardaillon 1988; Eisenberg and McKay 1974). Throughout both the native and introduced portions of its global range, this species is known to occupy a wide variety of habitats, and be subjected to varying levels of predation, most importantly in the form of harvest by man (Frädrich 1974; Mayer and Brisbin 2008; Sweeney et al. 2003; Tisdell 1982). However, the effects of differing percentages of general habitat types and levels of harvest by man on the social unit size, composition and frequency have not been assessed in wild pigs. In addition, seasonal effects on social unit organization in this species have not been adequately addressed. Further, there are no studies that have compared the effects of these environmental parameters on two or more populations of wild pigs. This type of comparative information would be important to have for the effective management of this controversial species in the various environments where these animals occur, especially when they represent introduced or invasive populations.

The purpose of this study was to: (1) characterize and compare the size, age and sex structure and frequency variation in the social unit organization among three introduced populations of *Sus scrofa*; and (2) assess the potential effects of seasonal change, habitat composition and levels of harvest by man upon this organizational structure.

2.0 Field Site Descriptions

The study was conducted in three locations in the southeastern United States: (1) Immokalee Ranch, Collier and Hendry Counties, Florida; (2) Ossabaw Island, Chatham County, Georgia; and (3) Savannah River Site, Aiken, Barnwell and Allendale Counties, South Carolina. All three sites had greatly limited public access with only minimal disturbance from human activities during the course of this study aside from annual harvest efforts. Based on either historical or morphological data, all three of these populations were composed of animals with varying degrees of wild boar/feral pig hybrid ancestry (Law Environmental 1989; Mayer and Brisbin 2008; J. J. Mayer unpubl. data). Mean population size estimates for the three sites during the course of this study were 1,250 for Immokalee Ranch (Law Environmental 1989), 1,675 for Ossabaw Island (R. E. Parker pers. comm.; SCWDS pers. comm.), and 1,370 for Savannah River Site (J. J. Mayer unpublished data).

The Immokalee Ranch was a 312 km^2 privately-owned multiple-use ranch with a mosaic of improved rangeland and irrigated cropland and citrus groves interspersed with corridors and patches of forested and herbaceous wetlands, pine forest, and hardwood hammocks dominated by *Quercus* spp. Land-use varied from essentially unimpacted habitats (31.1 percent) to intensive agricultural management (56.4 percent) (Law Environmental 1989).

Ossabaw Island, a 110 km^2 coastal barrier island, included salt marsh and open forested habitats. Upland areas were composed of interspersed pine and hardwood forests with the latter dominated by live oak (*Q. virginiana*), laurel oak (*Q. laurifolia*), and southern magnolia (*Magnolia grandiflora*). Upland areas were surrounded by tidal marsh with extensive stands of *Spartina* spp. (LaGory et al. 1991).

Savannah River Site, a 780 km^2 federal nuclear facility, contained 93 percent forested habitats. The land use was dominated by managed pine plantations consisting primarily of loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and slash pine (*P. elliotti*). The site was transected by several stream drainage corridors occupied by bottomland hardwood forest and forested swamp. Pockets of upland hardwood forest and mixed pine/hardwood forest were scattered throughout the site (Workman and McLeod 1990).

3.0 Methods

Data were collected during both vehicular and pedestrian diurnal surveys conducted in the three field sites. Any observations with either questionable counts or identifications of animals were not used in this study. Data were collected in a number of sampling efforts during all seasons at each location between 1982 and 2001. Wild pig sightings were classified into one of ten categories including: groups of adult males; groups of adults females; groups of adult males and females; groups of adult animals of unknown sex; groups of unaccompanied immatures; groups of both adult and immature animals; solitary adult males; solitary adult females; solitary adults of unknown sex; and solitary immatures. Groups were defined as social units composed of two or more individuals of either sex and any age (i.e., adults or immatures). Groups of adults for which only a portion of the animals could be sexed were classified as groups of adults of unknown sex. Immature animals (i.e., piglets or shoats) included individuals less than approximately 25-30 kg in total body mass. No attempt was made to determine the sex of immature animals.

The social unit size and composition was analyzed both collectively and among the three field sites. The percent frequency was compared for grouped versus solitary sightings, and for the specific social unit types within and between the field sites. Grouped observations were analyzed for size, sex and age class variation within and between group types. Overall sex and age ratios at each of the sites were also compared.

Seasonal variation in the size, composition and frequency of the ten social unit types were compared collectively and among the three field sites. The frequency difference between collective group versus solitary sightings were also analyzed. Because of the seasonal variation in social groupings previously reported for this species (Dardaillon 1988), comparisons were also made between social unit variation and that of the seasonal fluctuations in recruitment. Farrowing season data for the three field sites were determined from the following sources: Immokalee Ranch – Belden et al (1985); Ossabaw Island – J. J. Mayer (unpubl. data); and Savannah River Site – J. J. Mayer (unpubl. data). The site (i.e., Fisheating Creek Wildlife Management Area) addressed in Belden et al (1985) was located just north of the Immokalee Ranch, and the farrowing seasonal variation was therefore assumed to be comparable to that of the field site included in the present study. Analyses at the latter two sites entailed the aging of harvested animals (Matschke 1967) and fetuses (Henry 1968) to determine the farrowing dates.

Because of the unique habitat compositions of the three study areas, comparisons of correlations between social unit parameters and specific habitats were not possible at each site. Habitats from the three field sites were therefore collectively categorized into five non-exclusive general categories as follows: forested habitat (both pine and hardwood), open habitat (no standing timber or dense shrub/scrub present), pine forest, hardwood forest habitat (including upland, bottomland and swamp habitats), and wetland habitat (including both forested and non-forested freshwater wetlands) (Table 3-1). Correlations between the percentages of social unit frequency (i.e., percent of total observations for each study area) and the percent of habitat types (Table 3-1) were tested for significance. With one exception, subsequent analyses determined that social unit size did not vary significantly among the study areas. Therefore, no comparisons were made between social unit size and general habitat categories.

In contrast to the minor impacts of natural predation on wild pigs, harvest by man (including both hunting and trapping) is the single-most important mortality factor for this species (Sweeney et al. 2003). The average annual harvest by man for each of the three field sites was based on the mean annual known number of animals removed through hunting and corral trapping. As percentages of the mean estimated population size during the period of time when data were collected, annual harvest estimates were as follows: Immokalee Ranch - 5 %, Ossabaw Island - 40 %, and, Savannah River Site - 25 %. All animals harvested

at Immokalee Ranch were shot by hunters (Law Environmental 1989). An average of 87.5 % (range: 85-90 %) of the animals removed from Ossabaw Island were taken by corral trapping. The remainder were removed through shooting (R. E. Parker pers. comm.; SCWDS pers. comm.). On Savannah River Site, an average of 43.6 % (range: 0-69 %) of the animals were removed by means of corral traps with the remainder removed through shooting (J. J. Mayer unpubl. data).

Table 3-1. Comparison of the areas occupied by the five non-exclusive general habitat categories within the three field sites[a].

General Habitat Category	Field Site	Area (km^2)	Percent of Total Area
Forested Habitat	Immokalee Ranch	134	42.9
	Ossabaw Island	48	43.6
	Savannah River Site	725	93.1
Open Habitat	Immokalee Ranch	150	48.1
	Ossabaw Island	61	55.5
	Savannah River Site	55	7.1
Pine Forest Habitat	Immokalee Ranch	37	11.8
	Ossabaw Island	24	21.8
	Savannah River Site	523	67.1
Hardwood Forest Habitat	Immokalee Ranch	97	31.1
	Ossabaw Island	24	21.8
	Savannah River Site	203	26.0
Wetland Habitat	Immokalee Ranch	72	23.1
	Ossabaw Island	1	0.9
	Savannah River Site	117	15.0

[a] Calculated for Immokalee Ranch from Law Environmental (1989), Ossabaw Island from Le Gory et al. (1991), and Savannah River Site from Workman and McLeod (1990)

All statistical analyses were performed using the JMP Pro Version 11.2.1 software package (SAS Institute Inc. 2014). Differences in the ratio of grouped versus solitary animals and in the frequencies of various social units were compared using a Chi square analysis. Social unit size variation was tested for normality using a Shapiro Wilk W test. Paired differences in group size between field sites were compared using Tukey-Kramer HSD mean comparison test. Size variation of the different group types was analyzed with an Analysis of Variance (ANOVA). Statistical significance using these analyses was accepted at $p<0.05$. Correlations between variables were made using linear regressions.

4.0 Results

Social Unit Size and Composition

The total numbers of observations (total number of individual animals observed in parenthesis) were as follows: Immokalee Ranch - 304 (1,109); Ossabaw Island - 399 (1,014); and Savannah River Site - 355 (1,163). The average social unit size at each of the field sites was: Immokalee Ranch – 3.6 (observed range

= 1 to 19; SD = 2.8); Ossabaw Island – 2.5 (observed range = 1 to 19; SD = 2.3); and Savannah River Site – 3.3 (observed range = 1 to 22; SD = 3.1). Based on a Tukey-Kramer HSD for comparison of these means, only the Ossabaw Island sample differed significantly from those of the other two field sites at $p \leq 0.05$. This variation among the three field sites resulted from differences in group size and the overall percentage of group versus solitary sightings.

All ten of the social unit categories were observed at each study area. Overall, groups of two of more animals were more frequent than solitary animals in each of the three study areas. The ratio of grouped to solitary animal observations differ significantly from parity at all three sites (Immokalee Ranch - χ^2=61.15; df=1; $p \leq 0.0001$; Ossabaw Island - χ^2=4.64; df=1; $p \leq 0.0312$; Savannah River Site - χ^2=11.24; df=1; $p \leq 0.0008$). The percentages of all observations of grouped individuals to the total sample at each field site were as follows: Immokalee Ranch - 72.0 %; Ossabaw Island – 55.4 %; and Savannah River Site – 58.9 %.

The size variation and percent frequency of the groups observed are summarized in Table 4-1. The size variation within each group type was similar among all three study areas. The only group types that differed significantly in size among the three field sites were the adult male/adult female group (F=4.30; df=2; $p \leq 0.04$), the mixed adult/immature group (F=3.57; df=2; $p \leq 0.03$), and the immature-only group (F=3.18; df=2; $p \leq 0.04$). Based on the between site comparisons for each group type (i.e., using Tukey-Kramer HSD), the only significant differences were as follows: adult male/adult female group - Immokalee Ranch and Ossabaw Island; mixed adult/immature group – Ossabaw Island and Savannah River Site; and immature-only group - Immokalee Ranch and Savannah River Site. A significant difference probably also exists between these last two sites for the adult male/adult female group type; however, the small sample for that group type at the Savannah River Site was too small to enable a valid statistical comparison. These differences between sites for this group type was primarily attributable to the larger (i.e., as many as 5-7 animals) mixed-sex adult groups observed at the Immokalee Ranch.

The collective size differences among all six group types within the same field site were also significant (i.e., Immokalee Ranch - F=14.44; df=5; $p \leq 0.0001$; Ossabaw Island - F=7.47; df=5; $p \leq 0.0001$; and Savannah River Site - F=11.57; df=5; $p \leq 0.0001$). However, at all three locations, only the mixed adult/immature groups were significantly larger than any of the other group types at $p \leq 0.05$ using the using the Tukey-Kramer HSD comparisons of mean pairs.

The mixed groups of adults and immatures were consistently the largest group type in size, both on average and overall, among the three field sites (Table 4-1). This was also the most common group type in the Immokalee Ranch and Savannah River Site samples, while it was the second most common group type on Ossabaw Island. Within the adult/immature group sample for each location, groups composed of one adult and one or more immatures were the most common (i.e., 55.1 to 73.7 percent). In all of the cases for which a sex could be determined, the single adult in these groups was a female (i.e., these were matriarchal groups). The collective percentage of these groups containing any adult males was low (i.e., 4.2 percent), ranging from 1.3 to 7.7 among the field sites. All of these observations consisted of only one adult male being in the group. At least one adult sow was also present in each of these groups that had the single adult males. The largest groups were composed of several adult sows and immatures, which were presumably the offspring of one or more of the accompanying sows. This was corroborated by the presence of different sized cohorts of immatures in these larger groups. Although the immatures collectively outnumbered the adults by a ratio of 1.7 immatures to every 1.0 adult in all three samples (Figure 4-1), the adult:immature ratio for individual observations within this group type varied, ranging from 1.0:0.1 to 1.0:13.0. The mean and maximum numbers of immature animals consistently increased in all three samples with the increasing number of adults present (Figure 4-1). Therefore, the higher number of immatures with two or more sows is the result of the presence of combined or successive litters of one or more of the sows. The increasing percent of immatures in the Savannah River Site sample (Figure 4-2) is caused by the higher average litter size (i.e., number of immatures observed with one sow) seen in that population (mean = 4.6, observed range = 1-10, SD = 2.3), as compared to the other two populations (Immokalee Ranch – mean = 3.6, observed range = 1-13, SD = 2.0; and Ossabaw Island – mean = 3.4, observed range = 1-7, SD = 2.0).

Table 4-1. Summary of the wild pig group size and percent composition from the three field sites.

Field Site	Group Social Unit Category	N	Mean	Observed Range	SD	Percentage of Total Group Sightings for Field Site
Immokalee Ranch	Adult Males	7	2.1	2-3	0.4	3.2
	Adult Females	6	2.0	2	0.0	2.7
	Adult Males & Females	5	4.0	2-7	2.0	2.3
	Adults of Unknown Sex	11	2.2	2-3	0.4	5.0
	Immature Animals	34	2.7	2-5	0.9	15.5
	Adults/Immatures	156	5.5	2-19	2.7	71.2
	Total Groups	219	4.7	2-19	2.7	100.0
Ossabaw Island	Adult Males	5	2.0	2	0.0	2.3
	Adult Females	13	2.2	2-3	0.4	5.9
	Adult Males & Females	7	2.1	2-3	0.4	3.2
	Adults of Unknown Sex	11	2.3	2-3	0.5	5.0
	Immature Animals	106	3.5	2-15	2.3	48.0
	Adults/Immatures	79	4.9	2-19	2.8	35.7
	Total Groups	208	3.8	2-19	2.5	100.0
Savannah River Site	Adult Males	7	2.0	2	0.0	3.3
	Adult Females	9	2.2	2-3	0.0	4.2
	Adult Males & Females	3	2.0	2	0.0	1.4
	Adults of Unknown Sex	14	2.4	2-3	0.5	6.7
	Immature Animals	51	3.8	2-10	1.9	24.4
	Adults/Immatures	125	6.0	2-22	3.4	59.8
	Total Groups	209	4.9	2-22	3.1	100.0

In general, the next most common type of group observed was composed of only immature animals. These groups were on average and overall smaller than the mixed age groups (Table 4-1). Groups containing only immature animals were almost two times more common compared to all of the adult groups at the three locations. Groups consisting of only immature animals (Table 4-1) were smaller in size compared to the numbers of immatures with one or more sows in the mixed adult/immature groups in both the Immokalee Ranch (mean = 3.82; observed range = 1 to 15; SD = 2.40) and Savannah River Site (mean = 4.62; observed range = 1 to 19; SD = 2.98) samples. However, only the difference at the Immokalee Ranch was significant (F=7.13; df=1; $p \leq 0.008$). The immature group size on Ossabaw Island was slightly larger than the number of immatures in the mixed groups (mean = 3.41; observed range = 1 to 13; SD = 2.10). As with the Savannah River Site, this difference was not significant. Based on the maximum sizes of this group type at the field sites (Table 4-1), a few of the groups of only immatures at Ossabaw Island and Savannah River Site appeared to be composed of multiple litters, while the maximum groups of this type at the Immokalee Ranch would readily fit into the expected size of a single litter. In addition, a few of the larger immature groups observed at the former two sites were composed of two distinctly different size classes of immature animals. In contrast to the previously discussed group type, the immature-only groups were found in the highest frequency on Ossabaw Island, decreasing in abundance at the Savannah River Site and lowest at the Immokalee Ranch (Table 4-1).

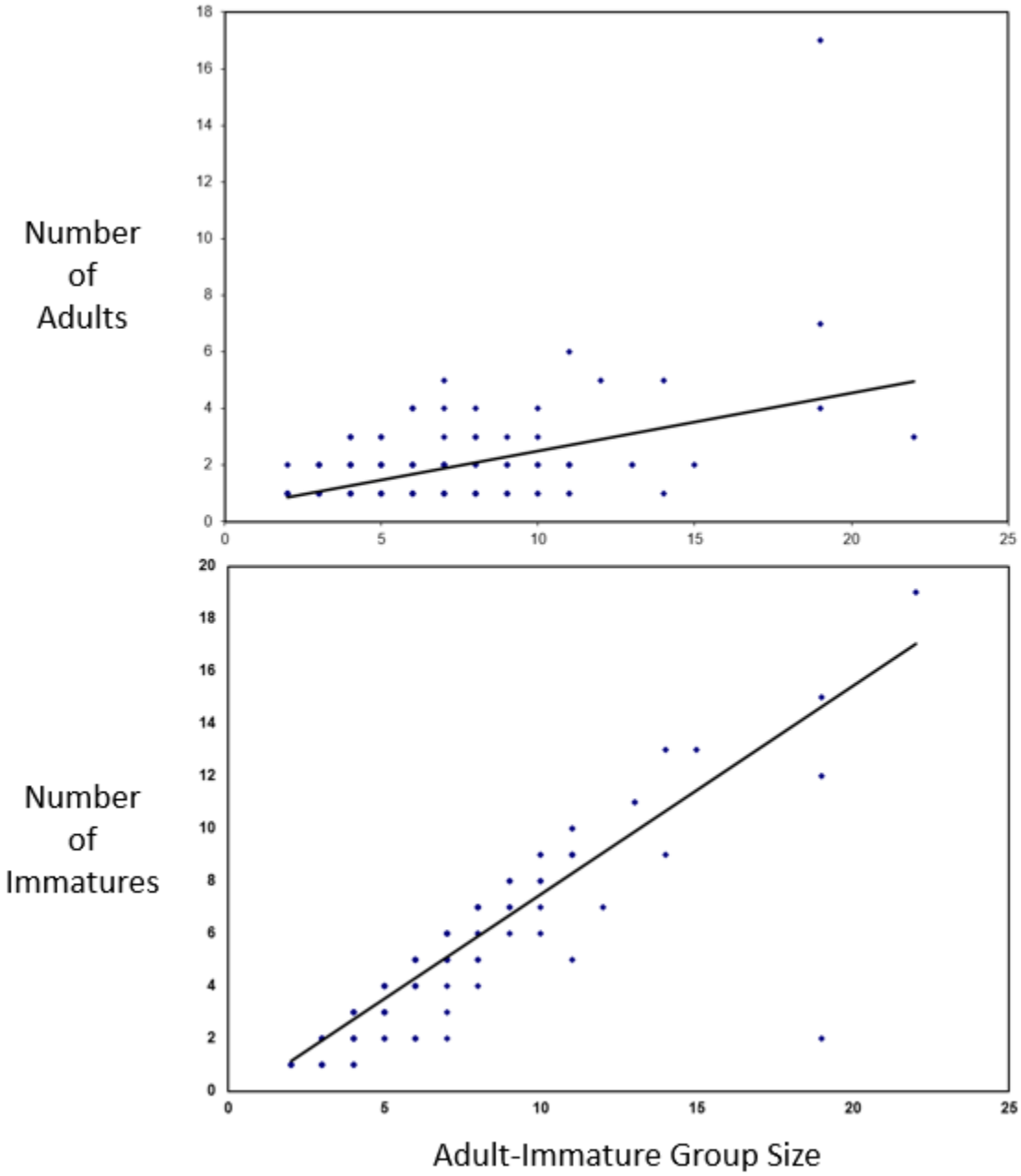

Figure 4-1. Comparison of the different rates of increase of individuals between adults (top) and immatures (bottom) in the mixed groups of adult and immature animals. Trendlines represent collective data from all three field sites.

Groups of adult animals were generally smaller than the overall group mean, with most (i.e., 75.9 to 80.0 percent) of these adult groups consisting of only two individuals (Table 4-1). Collectively among all three samples, the sexual composition of the mixed groups of adult males and females was 1.0 male to 1.2 females. Adult groups of all types were low in frequency, with all comprising less than six percent of the combined total group sighting sample for all three study areas, or less than seven percent of the total group sightings for each location. Aside from the adult groups with unknown sex animals, the frequency of occurrence of specific adult groups was collectively highest for adult female groups, followed by groups of adult males, and then by groups composed of both sexes.

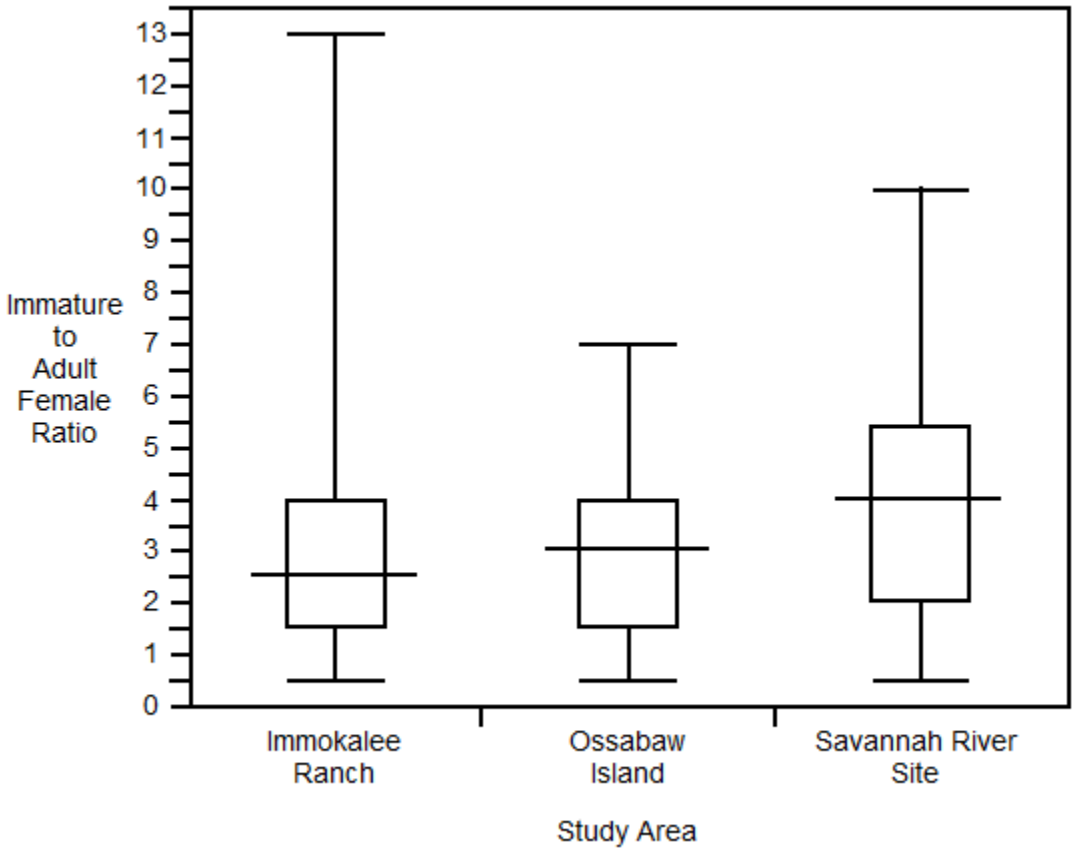

Figure 4-2. Comparison in the variation among the three field sites in the number of adult females to the number of immature animals in the mixed adult/immature groups.

Summaries of the solitary sightings are given in Table 4-2. In each area, adult animals made up most (i.e., 66.9 to 95.2 percent) of the solitary sightings. Males were the most frequent (i.e., 72.5 to 86.7 percent) type of adult sighting for which the sex could be determined. Among all three samples, a collective average of 73.6 percent (range of 56.6 to 81.3 percent) of all adult males sighted were solitary animals, compared to 4.8 to 16.7 percent for adult females. Solitary immature animals were uncommon, occurring in frequencies of 4.8 to 33.1 percent of the total solitary sightings for each area.

The adult male:adult female ratios, adult:immature ratios and adult female:immature ratios listed respectively for the total samples from each of the three field sites were as follows: Immokalee Ranch – 1.00:3.29, 1.00:1.70, and 1.00:2.56; Ossabaw Island - 1.00:1.82, 1.00:2.24, and 1.00:4.58; and Savannah River Site - 1.00:1.59, 1.00:1.81, and 1.00:3.81. Analysis of these indicate that Immokalee Ranch had a significantly lower adult male:female ratio (χ^2=11.02; *df*=1; $p \leq 0.01$ for comparison with Ossabaw Island, and χ^2=18.76; *df*=1; $p \leq 0.01$ for comparison with Savannah River Site). The Immokalee Ranch also had a significantly lower adult female:immature ratio than either Ossabaw Island (χ^2=23.34; *df*=1; $p \leq 0.01$) or Savannah River Site (χ^2=15.31; *df*=1; $p \leq 0.01$). With the adult to immature ratios, Ossabaw Island has significantly lower proportions of adults than either of the other two field sites (Immokalee Ranch - χ^2=17.32; *df*=1; $p \leq 0.01$; and Savannah River Site - χ^2=12.48; *df*=1; $p \leq 0.01$).

Effect of Seasonal Variation

The frequency of grouped to solitary sightings varied significantly with the seasonal change (χ^2=29.6; *df*=3; $p \leq 0.0001$), with the collective grouped sightings being slightly higher than parity for most of the year and increasing to 73 percent in the spring. Among the specific group types, the mixed adult/immature groups were fairly constant in their frequency (i.e., 50 to 61 percent) over the seasons. This general pattern was

consistent among the three field sites. Collectively, the groups of only immature animals are most frequent in the summer, decreasing into the spring. At Immokalee Ranch, this type of group was equally common in the spring (16.6 percent) and summer (16.7 percent), completely absent in the fall and then increased again in the winter (9.1 percent). On Ossabaw Island, the immature-only groups were the most common in the summer (46.5 percent), and least common in the spring (13.1 percent). At the Savannah River Site, this group type was most common in the spring (31.4 percent) and least common in fall (19.6 percent). The groups of adult males only, adult males/adult females, adult females only, and adults of unknown sex were constant and in low frequency throughout the year. Again, this general pattern was repeated at the three sites.

Table 4-2. Composition of solitary sightings of wild pigs from the three field sites.

Field Site	Solitary Social Unit Category	N	Percentage of Total Solitary Sightings for Field Site
Immokalee Ranch	Adult Male	47	55.3
	Adult Female	13	15.2
	Adult of Unknown Sex	15	17.7
	Immature	10	11.8
	Total Solitary Sample	85	100.0
Ossabaw Island	Adult Male	66	37.1
	Adult Female	25	14.0
	Adult of Unknown Sex	27	15.2
	Immature	60	33.7
	Total Solitary Sample	178	100.0
Savannah River Site	Adult Male	104	71.2
	Adult Female	16	11.0
	Adult of Unknown Sex	19	13.0
	Immature	7	4.8
	Total Solitary Sample	146	100.0

Size and composition of the social units appeared to vary with the seasons (Fig. 4-3). The highest immature to adult ratios were in the winter at all of the sites. This ratio decreases, although not consistently, over the rest of the year at the three sites. The mean seasonal group size was also highest in winter, while the maximum group sizes were highest in spring (Fig. 4-3). In all cases, these maximum groups sizes in the spring were composed of groups multiple matriarchal units. At all three field sites, adult males were only seen in the mixed adult/immature groups during the winter, spring and summer. None were seen in these groups during the fall. In contrast, adult male only groups were only seen during spring, summer and fall. Groups of adult males/adult females were observed during all four seasons. The highest numbers of males in these groups (i.e., 2 males) were only seen during winter, spring and summer.

Overall, solitary adult male sightings were highest in the winter. This decreased progressively into the spring and then into the summer. These numbers then suddenly increased in the fall to almost the winter levels. This site-specific pattern was the same for Ossabaw Island and Savannah River Site, but not the Immokalee Ranch. The pattern at this last site was the highest percentage of solitary adult males were in the summer, and then it steadily decreased through the fall through the spring. In contrast to the males, the percentages of solitary adult females appear to be low and constant throughout the year. This pattern was consistent at all three field sites. The highest numbers of solitary immatures were collectively seen in the

spring and summer among the three sites. The lowest numbers of solitary immatures are in the winter. Highest number of solitary immatures at Immokalee Ranch were in the spring, and on Ossabaw Island and at Savannah River Site are in the summer. In addition, there was a major increase in solitary immatures on Ossabaw Island in the summer (i.e., 65.5 percent of the total annual observations).

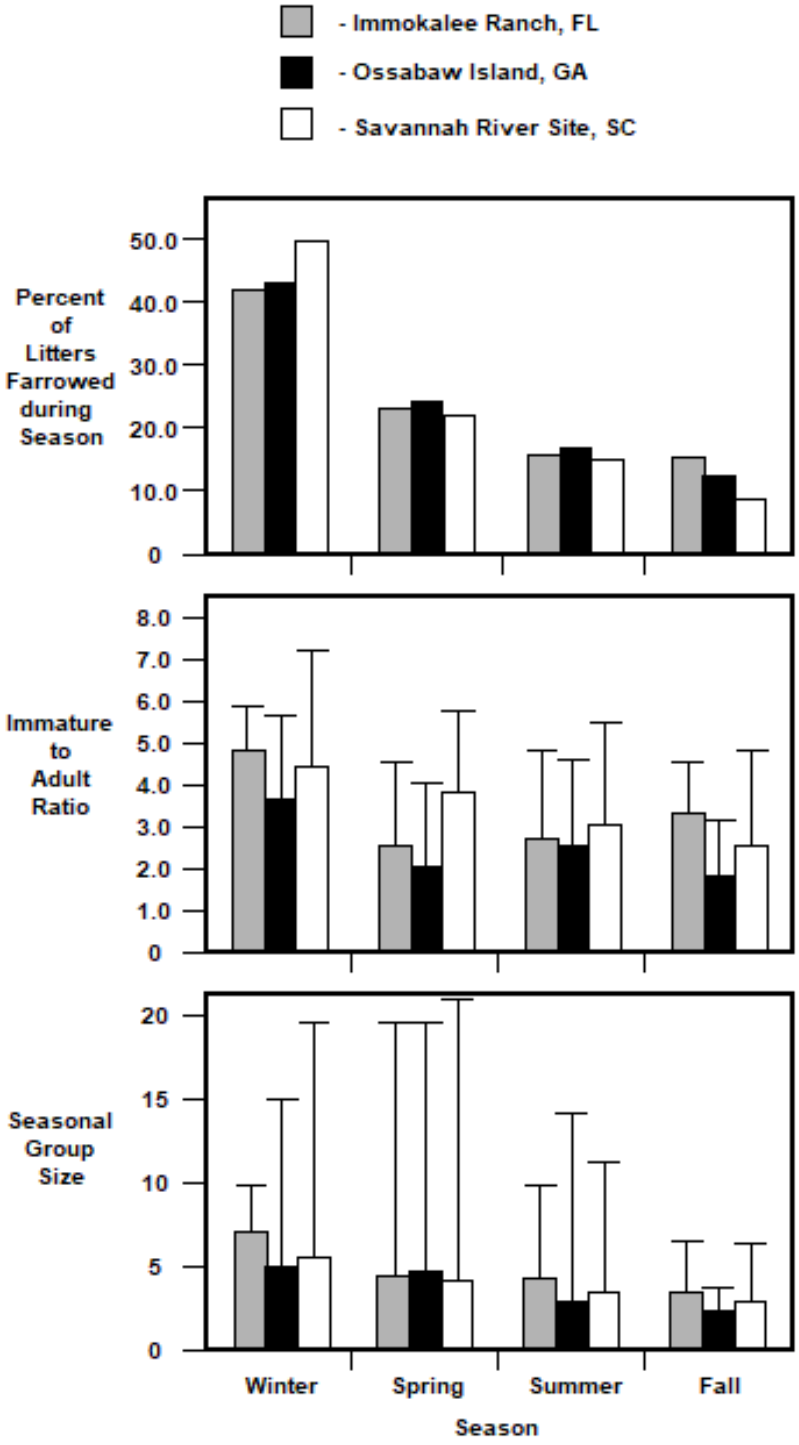

Figure 4-3. Seasonal comparison of the percent of litters farrowed (top), the immature to adult ratio (middle), and the overall group size (bottom) in the three field sites.

Correlation of Habitat Composition and Harvest by Man

Only two of the ten social unit categories (i.e., mixed adult/immature groups and immature-only groups) were significantly correlated with any of the general habitat types or mean annual harvest percentages. The percent frequency of only one general habitat type (i.e., hardwood forest) was significantly correlated with these two social unit types. Specifically, as the percentage of hardwoods increased, the frequency of groups of immature animals decreased (r^2=0.91) and the mixed adult/immature groups increased (r^2=0.94). In the three study areas, mean annual harvest percentages were positively correlated with the frequency of immature groups (r^2=0.90), and negatively correlated with mixed groups of adults and immatures (r^2=0.93).

5.0 Discussion and Conclusions

Social Unit Size and Composition

Overall, the social unit size and frequency for the three study areas were comparable to data from other wild pig populations (Table 5-1). The range of ratios of grouped to solitary animals determined in the present study encompassed most of the ratios observed in these other populations with the exceptions of Barrett (1978) having much a larger proportion and Singer et al. (1977) a much smaller proportion of grouped individuals, respectively. In general, with the exception of the data presented by Singer et al. (1977), the frequency of grouped animals is higher than solitary animals; although, as in the case of Ossabaw Island and Savannah River Site, this difference may not have been significant. The high percentages of grouped sightings in the Immokalee Ranch and Dye Creek Ranch populations may have been due to the fact that these areas are not as heavily harvested as the other locations.

The group size variation of the populations evaluated in the present study was similar to that observed for other populations (Table 5-1). In general, for the samples where the average group size was higher than that observed in the present study, the maximum observed size was also higher. The reverse was also true (Table 5-1). Other anecdotal observations on group size variation in this species corroborate the findings of the present study. Hanson and Karstad (1959) reported that feral pigs in the lower coastal plain of Georgia lived in groups of five to eight individuals. McKnight (1964) stated that groups of these animals typically contained six to 12 individuals. Conley et al. (1972) reported a maximum group size of 12 animals for the Tellico Wildlife Management Area in Tennessee. Jenkins and Provost (1964) reported an earlier maximum group size of 19 individuals for the Savannah River Site, noting that this group represented an "exceptional concentration." Maximum observed group sizes of 50 and "40 or more" were reported for populations of wild pigs found in Louisiana (Lowery 1974) and coastal Texas (Mayer and Brisbin 2008), respectively.

Although not described to the same level of detail as in the present study, sex and age class variation in group composition has been previously reported for this species. Of these, the mixed groups of adult and immature animals have been consistently reported for other wild pig populations, typically in the form of one or more sows with their young (Conley et al. 1972; Kurz 1971; Mansfield 1978; Nichols 1962). Variation is reported in the size of such social groupings from different wild pig populations. Populations with higher reproductive success form larger family units (Diong 1982). Eisenberg (1981) characterized such groups as being composed of females with young of similar age. He further stated that females forming multiple matriarchal groups may be related. Other studies (i.e., Hirotani and Nakatani 1987) did not find any multiple groupings of family units in wild pigs. The increasing number of immature animals with a corresponding increase in the number of sows reported in the present study was also reported by Graves and Graves (1977) in comparing groups with one and two sows. The larger groups (i.e., 10 or more animals) were composed of single or multiple family groups and can contain up to three generations of related animals (Barrett 1978).

Table 5-1. Summary of wild pig social unit size from other populations.

Location	Reference	Group Sightings				Solitary Sightings		
		N	Percent of Total Sightings	Mean	Range	N	Percent of Total Sightings	Adult Male Percent of Total Solitary Sightings
Merritt Island National Wildlife Refuge, FL	Baber, 1977	55	64	3.7[a]	2-9	31	36	70.9
Dye Creek Ranch, CA	Barrett, 1978	1,128	81.5	8.4	2-97	256	18.5	Majority
Donana Reserve, Spain	Braza and Alvarez, 1989	438	61.1	-	2-16	279	38.9	93.6[a]
Auckland Island, New Zealand	Challies, 1975	16	36.4[a]	-	2-5	28	63.6[a]	75.0[a]
Tour du Valat Reserve, Camargue, France	Dardaillon, 1988	583	66.8	4.0	2-23	299	34.2	Mainly
Kipahulu Valley, Maui, HI	Diong, 1982	39	67.2	3.6	2-9	19	32.8	Usually
Great Smoky Mountains National Park, TN and NC	Duncan, 1974	23	47.9	2.8[a]	2-6	25	52.1	-
Wilpattu National Park, Sri Lanka	Eisenberg and Lockhart, 1972	128	64.6[a]	8.9[a]	2-30+	70	35.4[a]	74
Pasoh Forest Reserve, Malaysia	Ickes, 2001	39	47.0[a]	3.6[a]	2-32	44	53.1[a]	Usually seen
Welder Wildlife Refuge, TX	Ilse and Hellgren, 1995	59	58.4[a]	5.3	2-16	42	41.6[a]	Majority
Rokko Mountains, Japan	Nakatani and Ono, 1995	188	69.1[a]	-	-	84	30.9[a]	71.4[a]

Table 5-1. Summary of wild pig social unit size from other populations (Continued).

Location	Reference	Group Sightings				Solitary Sightings		
		N	Percent of Total Sightings	Mean	Range	N	Percent of Total Sightings	Adult Male Percent of Total Solitary Sightings
Somiedo National Park, Spain	Nores et al., 2000	14	34[a]	-	2-13	27	66	-
Girilambone, New South Wales, Australia	Pavlov, 1980	125[a]	41.3[a]	4.8[a]	2-27	88[a]	58.7[a]	-
Ili River Region, Kazakstan	Pfeffer, 1960	157	45.5[a]	6.1[a]	2-35	188	54.5[a]	-
Kosciusko National Park, Australia	Saunders, 1988	93	60.8[a]	6.2[a]	2-22	60	39.2[a]	89.0
Great Smoky Mountains National Park, TN and NC	Shaffer, 1979	21	47.7	3.1	2-8	23	52.3	-
Great Smoky Mountains National Park, TN and NC	Singer et al., 1977	26	41.3[a]	3.1[a]	2-9	37	58.7[a]	13.5[a]

[a] Calculated from reference

The origin of groups composed of only immature animals is not clear. Such defined social groupings of young pigs without sows have been observed in other populations (Baber 1977; Mansfield 1978; Nichols 1962). Loss of the maternal sow to a predator or hunter could produce such situations. Nichols (1962) reported that sows chase off or leave their litters shortly after the piglets are weaned, and that these piglets will join one or two similarly abandoned litters of young to form groups of up to eight or ten individuals. Several of the immature groups observed during this study were composed of two separate litters based on the notable presence of two size classes or the large overall size of these groups. The stability of such immature groups is also unknown. Nichols (1962) stated that these groups may form the basis for long-term associations among some of the group members. The increased potential for predation may also impact the cohesiveness of these groups to probably a minor degree. However, it is also possible that such groups could largely only be a temporal phenomenon, in that the sow might only be separated from her litter at the time of the observation.

Groups made up of only adult animals were both smaller in average size and in the percentage which these made up of the total group sightings. Adult male groups have been reported for other populations (Kurz 1971; Nichols 1962) and are usually composed of only two or three boars. This is consistent with the results of the present study. Such groups of only males are very unstable in nature. They typically form when feeding, and then seldom stay together for more than a few hours (Kurz 1971). Because of the usual

intolerance that mature males display toward one another, Kurz (1971) suggested that litter mates may be at least one source of the adult males that form such groups. Rarely have more than three animals been reported as being observed in adult groups (Graves and Graves 1977; Kurz and Marchinton 1972; Sweeney et al. 2003). The primary exception to this is breeding groups. Such groups are temporary and can be variable in both size and composition. Baber (1977) and Barrett (1978) reported male-biased breeding groups of six males with two females and ten males with one female, respectively. Kurz and Marchinton (1972) reported observing two evenly sexed breeding groups, each consisting of four males and four females. McIlroy (1989) reported two breeding groups consisting of one sow with two and three boars, respectively. No breeding groups were observed during the present study. The largest adult group (i.e., total of seven animals: two males and five females) was observed feeding together as a group on a patch of newly-sprouted bahia grass (*Paspalum notatum*) and coastal Bermuda grass (*Cynodon dactylan*) in an improved rangeland area at the Immokalee Ranch study area.

The apparent existence of very large groups (i.e., more than 20 animals) of wild pigs can occasionally be observed in situations of a concentrated attractant (e.g., food resources such as agricultural crops, waterholes in arid areas or during dry seasons). These groups are typically only a temporary localized phenomenon and do not persist beyond the immediate site of the attraction (Frädrich 1984). Such wild pig groups have been reported to be as large as 97 animals, observed in an irrigated pasture on the Dye Creek Ranch in northern California (Barrett 1978). Anecdotal accounts have the maximum group size as exceeding 100 individuals (Prater 1965, Lekagul and McNeely 1988, Choquenot et al. 1996). The largest groups in all three samples and the group of seventeen adults and two immatures were examples of groups resulting from this type of temporary concentration around a planted forage resource.

Collectively, sightings of solitary individuals have been reported as including adult boars, adult sows, or immature animals. Most of these sightings in the present study were adult animals, primarily boars. Most of the unknown sex solitary adult sightings were also likely males. With the exception of Singer et al.'s (1977) data from the southern Appalachians, adult males constitute most of the solitary observations reported in other studies (Table 5-1). General observations in other studies substantiate this finding (Conley et al. 1972; Graves and Graves 1977; Kurz 1971; Mansfield 1978; Nichols 1962). The reason for the inconsistent finding in Singer et al.'s (1977) study is inexplicable. Both behavioral (e.g., intense shooting pressure) and observational (e.g., data collected in dense forested habitat) factors may have in combination resulted in this finding. Further, most (55 percent) of the solitary adults observed in that study were unclassified as to sex. Therefore, this finding may be an artifact of the data rather than a reality for that population.

Solitary adult sows were uncommon and are thought to usually consist of either pregnant sows about to birth to a litter of piglets or females that were in ill health (Baber 1977; Genov 1981). Observations of solitary immature pigs were also uncommon in occurrence. Such animals are probably either orphaned, temporarily separated from their family group, or in the process of dispersing from their family group.

The ratios of adult male to adult female were lower in all three samples compared to that previously reported for this species, while the ratios of adults to immatures and adult females to immatures were similar (e.g., Baber 1977; Barrett 1978; Shaffer 1979). In the present study, since the immature percent compositions of the overall samples from each study area were similar (i.e., Immokalee Ranch - 63 percent; Ossabaw Island - 69 percent; Savannah River Site - 67 percent), the differences in the ratios of adult females to either adult males or immature animals were due to an increased percentage of females in the Immokalee Ranch sample.

Effect of Seasonal Variation

The social structure of Eurasian wild boar has been reported as being dynamic and changing throughout the year in relation to the farrowing and breeding season (Dardaillon 1988). Frädrich (1974) described the annual cycle social unit organization of wild boar in temperate regions as follows: parturition in the spring (i.e., solitary pregnant sows or mothers with newborn litters); mother family and family groups in the

summer and autumn; temporary formation of pairs or mating units at end of autumn or in wintertime; and then separation of pregnant females at the end of winter. Multiple-family groups are usually thought to form after the offspring are weaned (Eisenberg and Lockhart 1972). In contrast to this, Illmann et al. (2002) stated that wild pigs form multiple family groups during lactation, except for a few days of isolation directly after parturition. Wild boar in the Camargue were found to regroup gradually during the summer and autumn seasons, and consequently live in larger groups during the second half of the year. Groups including at least one piglet increased in April and reached a maximum in May. Maximum group size lagged the peak of farrowing by one to two months (Dardaillon 1988).

The immature to adult ratios in the three field sites correspond very closely to the seasonal farrowing pattern (i.e., highest in winter, decreasing over rest of year). The mean seasonal group is also highest in winter, when most of the piglets are born (Fig. 4-3). The high group sizes in winter would reflect the preponderance of newborn litters before first of the year attrition rates really impact the litter/group size. As time progresses, the attrition of these piglets decreases both litter and group sizes. Diong (1982) also reported that family group size decreased during the lactation period because of piglet postnatal mortality.

At all three field sites, no adult males were seen in the mixed adult/immature groups during the fall, which is also the peak breeding period. In contrast, adult male only groups were not seen during the winter, which is the peak farrowing season. No comparative data about seasonality of the presence of adult males in groups were available elsewhere in the literature.

Overall, the highest numbers of solitary immatures are seen about the time when these piglets are being weaned and are dispersing (i.e., spring and summer). The lowest numbers of solitary immatures are in the winter, when the most litters are being farrowed. Similar changes in seasonal frequency of solitary immatures was reported by Dardaillon (1988).

Overall, solitary adult male sightings are highest in the winter (i.e., post peak breeding period). The same post-breeding increase in the frequency of solitary individuals was exhibited by adult male wild boar in the Camargue (Dardaillon 1988).

Correlation of Habitat and Harvest by Man

Typically, the size of ungulate social groups has been correlated with the openness of the habitat being occupied. In general, the more open the habitat, the larger the group size (Eisenberg and McKay 1974, Estes 1974). Wild pigs, however, tend to be the exception to this phenomenon (Eisenberg and McKay 1974).

In spite of being the exception to this generalization, great variation in the size of wild pig social groupings has been noted between different habitats (Eisenberg and Lockhart 1972). The size of such groups appears to be at least in part a function of the carrying capacity of the different habitats (Eisenberg 1981; Seydack 1991). With respect to social organization as a function of resource availability, in places where food is nonseasonal (i.e., unpredictable) and dispersed, the social groups of wild suids tend to be small and dispersed because of intergroup competition. In areas where foods are seasonal, often concentrated, and temporarily predictable surpluses occur, suids tend to form medium to large multi-female groups (Martys 1991b; Seydack 1991). Changes in group size within the same habitat can also vary over time in response to changing environmental conditions (Martys 1991b).

In general, natural predation is of minor importance as a cause of mortality in wild pig populations (Sweeney et al. 2003). This is particularly true for adult animals (Barrett 1978; Sweeney et al. 2003). The few studies which have evaluated the impact of predation of wild pigs in the three study areas have noted that natural predation was not believed to be an important decimating factor of the resident wild pig populations (Cothran et al. 1991; Kight 1962; Law Environmental 1989; Sweeney 1970). Therefore, natural

predation was assumed to have only a minor impact at best on the social unit organization within the subject populations.

Group formation in suids has also been hypothesized as a mechanism to permit an active group offensive against predators in spite of the fact that it makes the social unit more conspicuous (Eisenberg and McKay 1974). Such a strategy, however, would generally do little to defend against predation efforts by man. Individual behavioral methods appear to be the only effective method for defense against human harvest activities in this species. For example, wild pigs inhabiting areas with heavy hunting pressure have been observed to shift daily activity patterns from diurnal to nocturnal time periods to avoid exposure to hunters (Frädrich 1974; Prater 1965; St. George 1973). It should be noted that individual vigilance for potential predators (i.e., including man) decreases at feeding sites as group size increases (Quenette and Gerard 1992). Therefore, larger group sizes at such locations would benefit the individuals in being able to forage longer.

Although the sample size in the present study was extremely small (i.e., N=3), the high levels of correlation (i.e., r^2 equal to 0.90 to 0.94) would at least indicate a relationship worth considering in future research efforts. The only group types to be correlated with either the habitat parameters or the levels of harvest by man were mixed adult/immature groups and groups composed of only immature animals. Correlations of these two environmental influences were inversely related, such that an increase in one and a decrease in the other were correlated to similar changes in group composition. In addition, concurrent changes in the group types were also inversely related. The collective group types containing immature animals (i.e., both mixed adult immature groups and immature groups) in all three study areas were present in approximately the same percent frequency (i.e., Immokalee Ranch - 87 percent; Ossabaw Island - 84 percent; Savannah River Site - 84 percent). A decrease in the percent of hardwood forest or an increase in the annual harvest would appear to cause a quicker transition from groups composed of sows and their offspring to unaccompanied groups of immature animals. This could result from either an earlier weaning of the young or an increased attrition of the sows.

Oak mast production previously has been shown to strongly influence reproduction in this species (Matschke 1964). Barrett (1978) found that the ratio of adult females to immatures was variable over time depending upon the quality of the mast crop. Fewer immatures produced as a consequence of a poor acorn crop resulted in a higher proportionate presence of adult sows. However, the Immokalee Ranch, the field site with the highest percent frequency of hardwoods also has the lowest percent frequency of immatures. It should be noted that the percent availability of this habitat type is not necessarily indicative of the potential mast crop and, hence, the potential carrying capacity of the subject area.

Increases in harvest level among the three field sites were reflected by increases in the percent trapping that occurred. Studies have reported that trapping may be biased toward the removal of females from the population (Choquenot et al. 1993). An increased attrition of females because of trapping would be consistent with the apparent comparative shift from the adult/immature to immature groups among the three populations.

Since these correlations are of a coincidental and not specifically applied nature, any cause and effect relationships between either the habitat or harvest parameters and the percent frequency of the social unit organization at the study areas would be difficult to specifically resolve. Changes in one or the other would appear to have caused a quicker transition from one group type to the other. Since both the percent frequency of the immature animals and the collective percentage of groups with immature animals did not significantly change among the three areas, a change in the number of adult sows present would apparently explain the difference in the group frequencies. A biased removal of sows through trapping would most consistently appear to corroborate this explanation.

Based on the combined observations in the three field sites, most (i.e., 61.0 percent) of the social unit organization in wild pigs is composed of groups of two or more individuals. However, the frequency difference between this general social unit type and solitary sightings is not always significant. As has been

previously reported, most of these groups are composed of adult sows and their offspring. Most adult males are solitary. Combined observations of adult/immature groups and solitary adult males made up 54.5 percent of the total sightings from all locations. Based on the data for solitary adults of known sex, if 80 percent of the solitary adults of unknown sex are included as males in the total, this estimate would increase to 60 percent. In the order of decreasing frequency, additional social units observed in the remaining approximate one-third of the sightings were groups of only immature animals (18 percent), groups of only adult animals (9 percent), solitary immature animals (7 percent), and solitary adult females (5 percent).

Results of the correlation analyses of habitat percent frequency and percent harvest levels on the variation among the social units were not clear. The data suggest a shift from adult/immature groups to groups of only immature animals. Both increased attrition among of the sows or an earlier weaning/abandonment of the young could explain such a change. Although trapping being biased toward the removal of females from the population would be a consistent explanation with causing such a shift, the potential effect of the hardwood mast crop on these differences cannot be discounted. Specific cause and effect analyses would be required to clarify such results.

6.0 References

Baber, D. W. 1977. Social organization and behavior in the feral hog, *Sus scrofa*, Linnaeus. M.S. Thesis, Florida Institute of Technology, Melbourne, Florida, USA. 66 pp.

Barrett, R. H. 1978. The feral hog on the Dye Creek Ranch, California. Hilgardia, 46(9):283-355.

Belden, R. C., W. B. Frankenberger, and D. H. Austin. 1985. A simulated harvest study of feral hogs in Florida. Final performance report, P-R Project W-41-R, Study No. XIII-FEC. Florida Fresh Water Fish and Game Commission Wildlife Research Laboratory, Gainesville, Florida, USA. 83 pp.

Braza, F., and F. Alvarez. 1989. Utilisation de l'habitat et organisation sociale du sanglier (*Sus scrofa* L.) a Donana (Sud-Ouest de l'Espagne). Canadian Journal of Zoology, 67(8):2047-2051.

Challies, C. N. 1975. Feral pigs (*Sus scrofa*) on Auckland Island: Status and effects on vegetation and nesting sea birds. New Zealand Journal of Zoology, 2(4):479-490.

Choquenot, D., R. J. Kilgour, and B. S. Lukins. 1993. An evaluation of feral pig trapping. Wildlife Research, 20:15-22.

Choquenot, D., J. McIlroy, and T. Korn. 1996. Managing vertebrate pests: feral pigs. Bureau of Rural Sciences, Australian Government Publishing Service, Canberra, Australia. 163 pp.

Conley, R. H., V. G. Henry, and G. H. Matschke. 1972. European hog research, Project W-34. Tennessee Game and Fish Commission, Knoxville, Tennessee, USA. 259 pp.

Cothran, E. G., M. H. Smith, J. O. Wolff, and J. B. Gentry. 1991. Mammals of the Savannah River Site. SRO-NERP-21. Savannah River Ecology Laboratory, Aiken, South Carolina, USA. 191 pp.

Dardaillon, M. 1988. Wild boar social groupings and their seasonal changes in the Camargue, southern France. Zeitschrift für Saugetierkunde, 53:22-30.

Diong, C. H. 1973. Studies of the Malayan wild pig in Perak and Johore. Malayan Nature Journal, 26(1973):120-151.

Diong, C. H. 1982. Population biology and management of the feral pig (*Sus scrofa* L.) in Kipahulu Valley, Maui. Ph.D. Dissertation, Univ. Hawaii, Honolulu, Hawaii, USA. 408 pp.

Duncan, R. W. 1974. Reproductive biology of the European wild hog (*Sus scrofa*) in the Great Smoky Mountains National Park. M.S. Thesis, University of Tennessee, Knoxville, Tennessee, USA. 95 pp.

Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, Adaptation, and Behavior. The University of Chicago Press, Chicago, Illinois, USA. 610 pp.

Eisenberg, J. F., and M. C. Lockhart. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. Smithsonian Contributions to Zoology, 101:1-118.

Eisenberg, J. F., and G. M. McKay. 1974. Comparison of ungulate adaptations in the New World and Old World Tropical Forests with special reference to Ceylon and the rainforests of Central America. Pages 585-602 in V. Geist and F. R. Walther (eds.). The behaviour of ungulates and its relation to management. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland. 940 pp.

Estes, R. D. 1974. Social organization in the African Bovidae. Pages 166-205 in V. Geist and F. R. Walther (eds.). The behaviour of ungulates and its relation to management. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland. 940 pp.

Ewer, R. F. 1968. Ethology of mammals. Logos Press, London, United Kingdom. 418 pp.

Frädrich, H. 1974. A comparison of behaviour in the Suidae. Pages 133-143 in V. Geist and F. R. Walther (eds.). The behaviour of ungulates and its relation to management. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland. 940 pp.

Frädrich, H. 1984. Swine and peccaries. Pages 76-108 in B. Grzimek (ed.). Grzimek's animal life encyclopedia. Vol. 13. Mammals IV. Van Nostrand, New York, New York, USA. 566 pp.

Genov, P. 1981. Significance of natural biocenoses and agrocenoses as the source of food for wild boar (*Sus scrofa* L.). Ekologia Polska, 29(1):117-136.

Graves, H. B., and K. L. Graves. 1977. Some observations of biobehavioral adaptations of swine. Pages 103-110 in G. W. Wood (ed.). Research and management of wild hog populations. Belle Baruch Forest Science Inst. of Clemson Univ., Georgetown, South Carolina, USA. 113 pp.

Hanson, R. P., and L. Karstad. 1959. Feral swine in the southeastern United States. Journal of Wildlife Management, 23(1):64-75.

Henry, V. G. 1968. Fetal development in European wild hogs. Journal of Wildlife Management, 32(4):966 970.

Hirotani, A., and J. Nakatani. 1987. Grouping-patterns and inter-group relationships of Japanese wild boars (*Sus scrofa leucomystax*) in Rokko Mountain area. Ecological Research, 2:77-84.

Ickes, K. 2001. Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of peninsular Malaysia. Biotropica, 33(4):682-690.

Illmann, G., L. Schrader, M. Spinka, and P. Sustr. 2002. Acoustical mother offspring recognition in pigs (*Sus scrofa domestica*). Behaviour, 139(4):487 505.

Ilse, L. M., and E. C. Hellgren. 1995. Spatial use and group dynamics of sympatric collared peccaries and feral hogs in southern Texas. Journal of Mammalogy, 76(4):993-1002.

Jenkins, J. H., and E. E. Provost. 1964. The population status of the larger vertebrates on the Atomic Energy Commission Savannah River Plant Site. Off. Tech. Serv., Dept. Comm., Washington, DC, USA. 45 pp.

Kight, J. 1962. An ecological study of the bobcat, *Lynx rufus* (Shreber), in west-central South Carolina. M.S. Thesis, Univ. Georgia, Athens, Georgia, USA. 52 pp.

Kurz, J. C. 1971. A study of feral hog movements and ecology on the Savannah River Plant, South Carolina. M.S. Thesis, Univ. Georgia, Athens, Georgia, USA. 97 pp.

Kurz, J. C., and R. L. Marchinton. 1972. Radiotelemetry studies of feral hogs in South Carolina. Journal of Wildlife Management, 36(4):1240-1248.

Law Environmental. 1989. Wildlife assessment for citrus grove conversion. Project No. 55-7608.01. Law Environmental, Inc., Kennesaw, Georgia, USA. 12 sections; pagination by section.

LaGory, K. E., C. Bagshaw, III, and I. L. Brisbin, Jr. 1991. Niche differences between male and female white-tailed deer on Ossabaw Island, Georgia. Applied Animal Behaviour Science, 29(1991):205-214.

Lekagul, B., and J. A. McNeely. 1988. Mammals of Thailand. 2nd Edition. Saha Karn Bhaet Co., Bangkok, Thailand. 758 pp.

Lowery, G. H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge, Louisiana, USA. 565 pp.

Mansfield, T. M. 1978. Wild pig management on a California public hunting area. Transactions of the California-Nevada Section of the Wildlife Society, 25:187-201.

Martys, M. F. 1991a. Monographie des eurasiatischen Wildschweines (*Sus scrofa*). Bongo, 18:8-20.

Martys, M. F. 1991b. Social organization and behavior in the Suidae and Tayassuidae. Pages 65-77 in R. H. Barrett and F. Spitz (eds.). Biology of Suidae. Imprimerie des Escartons, Briancon, France. 170 pp.

Matschke, G. H. 1964. The influence of oak mast on European wild hog reproduction. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners, 18:35-39.

Matschke, G. H. 1967. Aging European wild hogs by dentition. Journal of Wildlife Management, 31(1):109-113.

Mayer, J. J., and I. L. Brisbin, Jr. 2008. Wild pigs in the United States: their history, comparative morphology, and current status. 2nd Edition. The University of Georgia Press, Athens, Georgia, USA. 313 pp.

McIlroy, J. C. 1989. Aspects of the ecology of feral pigs (*Sus scrofa*) in the Murchison area, New Zealand. New Zealand Journal of Ecology, 12:11-22.

McKnight, T. 1964. Feral livestock in Anglo-America. University of California Publications in Geography, 16:1-104.

Nakatani, J., and Y. Ono. 1995. Grouping pattern of Japanese wild boar (*Sus scrofa leucomystax*). Journal of Mountain Ecology (Ibex), 3:128-129.

Nichols, L., Jr. 1962. Ecology of the wild pig. Federal Aid to Wildlife Restoration, Final Report Project W-5-R-13. Hawaii Department of Land and Natural Resources, Division of Fish and Game, Honolulu, Hawaii, USA. 20 pp.

Nores, C., A. Fernández Gil, and N. Corral. 2000. Estimating wild boar (*Sus scrofa*) population by counting family herds (in Spanish with English summary). Naturalia Cantabricae, 1:53-59.

Pavlov, P. M. 1980. The diet and general ecology of the feral pig (*Sus scrofa*) at Girilambone, N. S. W. M.S. Thesis, Monash University, Melbourne, Australia. 117 pp.

Pfeffer, P. 1960. L'ecologie du sanglier in Asie Central d'apres les researches d'A. A. Sloudsky. Revue d'Ecologie (La Terre et la Vie), 108:368-372.

Prater, S. H. 1965. The book of Indian animals. Bombay Natural History Society, Bombay, India. 323 pp.

Quenette, P. Y., and J. F. Gerard. 1992. From individual to collective vigilance in wild boar (*Sus scrofa*). Canadian Journal of Zoology, 70(8):1632-1635.

SAS Institute Inc. 2014. JMP Pro Version 11.2.1. SAS Institute Inc., Cary, North Carolina, USA.

Saunders, G. R. 1988. The ecology and management of feral pigs in NSW. M.S. Thesis, Macquarie University, Ryde, Australia. 190 pp.

Seydack, A. H. W. 1991. Aspects of a study of bushpig ecology. Pages 130-140 in R. H. Barrett and F. Spitz (eds.). Biology of Suidae. Imprimerie des Escartons, Briancon, France. 170 pp.

Shaffer, M. L. 1979. Behavior of the European wild boar in the Great Smoky Mountains National Park. Proceedings of the Conference on Scientific Research in National Parks, 1:357-363.

Singer, F. J., B. B. Ackerman, M. E. Harmon, and A. R. Tipton. 1977. Studies of European wild boar in the Great Smoky Mountains National Park. Part I.: census, trapping, and population biology of European wild boar. National Park Service, Dept. Interior, Gatlinburg, Tennessee, USA. 137 pp.

St. George, G. 1973. Shovel nose: Hungary's pugnacious wild boar. International Wildlife, 3(2):32-35.

Sweeney, J. M. 1970. Preliminary investigation of a feral hog (*Sus scrofa*) population on the Savannah River Plant, SC. M.S. Thesis, Univ. Georgia, Athens, Georgia, USA. 58 pp.

Sweeney, J. M., J. R. Sweeney, and S. W. Sweeney. 2003. Feral hog, *Sus scrofa*. Pages 1164-1179 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman (eds.). Wild mammals of North America: biology, management, and conservation. The Johns Hopkins Univ. Press, Baltimore, Maryland, USA. 1368 pp.

Tisdell, C. A. 1982. Wild pigs: environmental pest or economic resource. Pergamon Press, New York, New York, USA. 445 pp.

Workman, S. W., and K. W. McLeod. 1990. Vegetation of the Savannah River Site. SRO-NERP-19. Savannah River Ecology Laboratory, Aiken, South Carolina, USA. 137 pp.