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).

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BODY MASS VARIATION IN AN INTRODUCED WILD PIG POPULATION WITH CHANGING ANCESTRY

J. J. Mayer

April 2021

SRNL-STI-2021-00110, Revision 0

SRNL.DOE.GOV

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Printed in the United States of America

Prepared for
U.S. Department of Energy

SRNL-STI-2021-00110
Revision 0

Keywords: *Body mass, feral hog, invasive species, Sus scrofa, wild pig*

Retention: *Permanent*

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PREFACE OR ACKNOWLEDGEMENTS

The following were most helpful with the collection of data for this study: J. C. Agostine, C. Bagshaw, J. F. Bergan, F. Bridges, I. L. Brisbin, Jr., F. A. Brooks, M. B. Caudell, A. W. Conger, R. E. Dubos, D. T. Elliott, T. E. Fox, R. E. Hamilton, G. Hogsed, R. T. Hoppe, T. W. Hughes, W. L. Jarvis, P. E. Johns, T. Jones, J. C. Kilgo, the late J. C. Kurz, E. T. LeMaster, B. H. Miller, L. A. Moore-Barnwell, D. A. Napier, the late J. W. Reiner, Sr., O. E. Rhodes, Jr., B. Schwartz, J. C. Segar, T. B. Segar, L. M. Smith, W. Stephens, G. L. Sullivan, J. M. Sweeney, L. D. Vangilder, M. J. Vargo, and D. W. Wilson. B. C. Marcy, Jr., and L. D. Wike critically read earlier drafts of the manuscript. Funding for this study was provided by the U. S. Department of Energy under Contract DE-AC09-08SR22470 to Savannah River Nuclear Solutions LLC.

EXECUTIVE SUMMARY

Total body mass variation was studied in a single wild pig (*Sus scrofa*) population that originated from three introductions of varying ancestry. Body mass data from 12,257 wild pigs collected over more than five decades were analyzed for differences due to the effects of sex, age class, reproductive status, season, and historic subpopulation groupings. Total body mass data from this population averaged 38 kg and ranged from 0.511 to 189 kg. The overall observed range of body mass data was consistent with previous studies. Very heavy individuals (i.e., >150 kg) made up only a small percentage of the overall population. Males were significantly larger than females, being on average 1.09 times heavier. This significant sexual dimorphic difference was seen in all but the piglet age class. This percent dimorphic difference increased with age. Body mass variation and overlap between the age classes also increased with age. Males were more variable than females within the same age class. The study area's wild pigs were on average born at slightly less than one percent of their adult body mass. Percent weight gain toward the adult body mass increased with age and was slightly greater in females than in males. In contrast, absolute weight gain between age classes was greater in males. Pregnant sows were significantly heavier than non-pregnant females in all age class comparisons; however, this difference decreased with age. There was a seasonal shift in body mass with age, with younger age classes being heaviest in the fall-winter period and the older age classes being heaviest in spring-summer. Having originated from different ancestral stocks, two major subpopulations of wild pigs on the study area differed significantly in body mass in all sex and age class comparisons. The SRS wild pig population showed a decrease in body mass during the 1990s that was significant. This change may have been the result of both ancestral and population density variation, as well as unspecified environmental factors.

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1.0 Introduction

Body mass (i.e., weight) is one of the most basic sources of data concerning an animal's life history. Variation in this parameter can stem from different sources, and is also strongly related to physiological, ecological, evolutionary, and other characteristics of the organism (Silva and Downing 1995). Within wild pigs (*Sus scrofa*), both genetic and environmental factors have been shown to affect the body mass variation (Gallo Orsi et al. 1992; Saunders and McLeod 1999; Spitz et al. 1998). Body mass data in this species is variously used for studies of taxonomic/morphological variation, reproductive potential/performance, prey base characterization, food chain/trophic level studies, contaminant uptake studies, and human health risk assessments associated with the consumption of wild pig meat (e.g., following a contaminant release, such as after the Chernobyl and Fukushima nuclear disasters).

Body mass variation in both native and introduced populations of wild pigs has been the subject of numerous studies (Spitz et al. 1998). Although the analysis of large sets of body mass data in this species (i.e., 2,000+ specimens) have been published (e.g., Spitz et al. 1998), these studies have used data from regional or widely scattered geographic areas. Other studies with large samples have analyzed wild pig carcass or gutted weights rather than intact weights or total body mass (e.g., Dzieciolowski et al. 1990; Milkowski and Wojcik 1984). No previous studies have analyzed a large set of total body mass (i.e., intact/ungutted body weight) data compiled from one population. In addition, there are also minimal published data on neonatal total body mass for this species. Lastly, no studies have looked at the variation in this parameter from a single population over an extended period of time or as a result of changing ancestry (i.e., new introductions of other types of wild pigs) within that population.

Introduced wild pig populations in the United States are present in three morphologically identifiable ancestral types including Eurasian wild boar, feral hogs (wild pigs solely of domestic ancestry), and hybrids between these two (Mayer and Brisbin 1993, 2008). In addition, there are populations of long-term and short-term feral hogs, long-term ferals being those in populations that became wild prior to 1800. After that date, intensive swine breed improvement began in the United States that forever changed the appearance of American domestic swine. Therefore, short-term feral hogs, in populations established from domestic stock after 1800, are physically different from their long-term counterparts. Both early colonial domestic swine and long-term feral hogs are physically smaller, with proportionately longer snouts, legs, and hair, higher shoulders, and shorter bodies. The diverse origins of these populations have resulted in animals that can exhibit a wide spectrum of physical variation (Mayer and Brisbin 1993, 2008). As such, the ancestral makeup of a population would be expected to have an impact on body mass variation among those animals.

A large data set of body mass data from an introduced wild pig population in western South Carolina was compiled over a 52-year period. The size and complexity of this data set would permit addressing the previously stated deficiencies or shortfalls with respect to this species. The purpose of the present study was to use this large data set to characterize total body mass variation within this single wild pig population, and to determine to what extent, if any, changes in body mass over time may be attributed to changes in ancestry.

2.0 History of Study Population

The wild pig population used in the present study inhabits the Savannah River Site (SRS), an 803 km^2 federal nuclear facility located in Aiken, Barnwell and Allendale counties in the upper coastal plain of western South Carolina, USA (Fig. 2-1). This site and its resident wild pig population have been isolated from public contact for over seven decades. The history of this population is complex (Mayer and Brisbin 2012). When the lands presently included in the SRS were purchased by the federal government in 1950, the resident farmers were given one year to capture and remove all of their free ranging domestic swine. Large numbers could not be recovered by the end of 1951 and were left behind by their owners when the farmers were finally prohibited further access to the land in 1952 (Jenkins and Provost 1964). By 1970, the distribution of the SRS wild pig population had expanded to include most of the hardwood bottomland forest and swamps along the Savannah River and the adjacent upland pine plantations in the southwestern portion of the site (Sweeney 1970; Kurz 1971) (hereafter called the "riverswamp" or RS subpopulation). Historically and morphologically, these animals were short-term feral hogs.

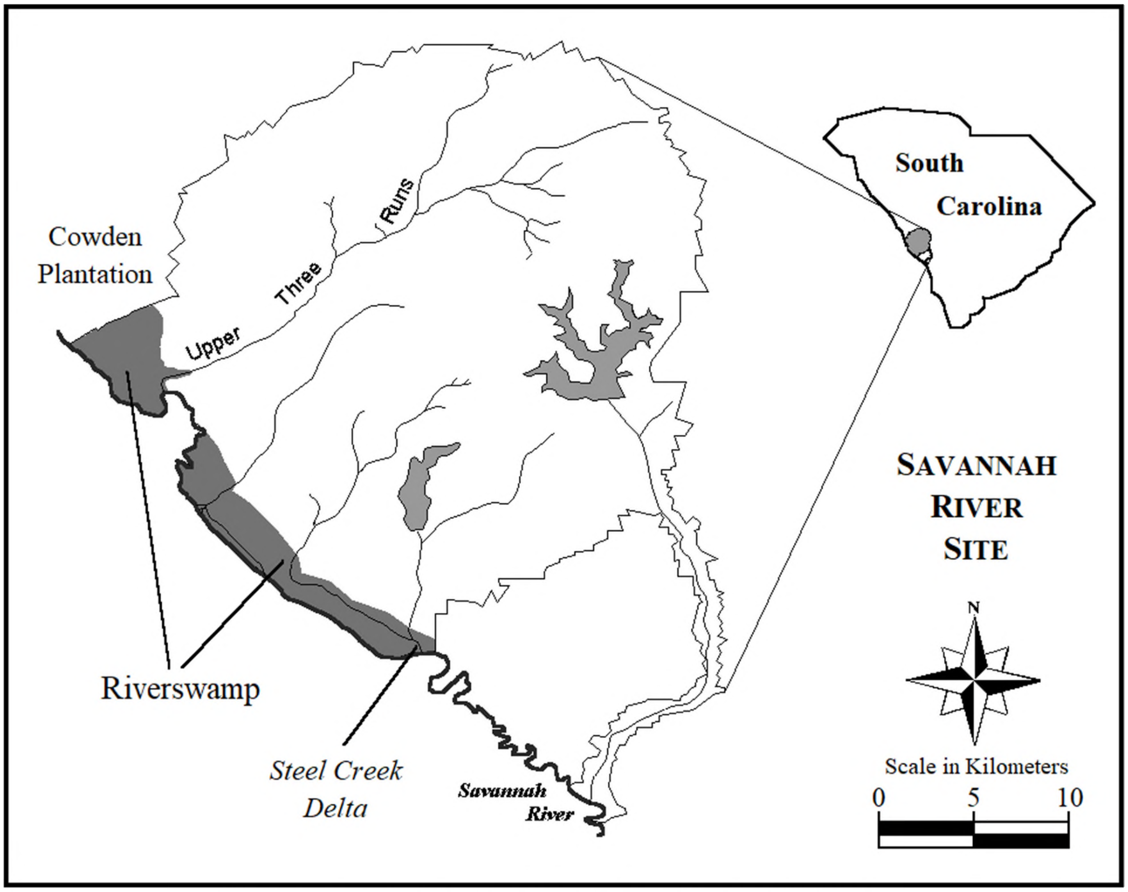

Fig. 2-1. - Map of the Savannah River Site, South Carolina.

In the mid-1970s, a small second subpopulation of wild pigs was discovered along the Upper Three Runs drainage in the central northern portion of the site (hereafter called the "upland" or UP subpopulation). Several theories have been posed as to the origin of these animals, but none have been verified (Mayer and Brisbin 2012). However, based on their morphology (i.e., that of long-term feral hog/Eurasian wild boar hybrids), it was evident that this second subpopulation was not derived from the RS subpopulation (Mayer and Brisbin 2008, 2012). In the years subsequent to their initial discovery, the UP pigs expanded their distribution toward the Savannah River. In 1986, the two subpopulations became sympatric in their distributions with the expansion of the UP subpopulation. Beginning in the late 1980s, animals exhibiting the UP phenotype were collected in the area of the site adjacent to the riverswamp (Mayer and Brisbin 2012).

During the fall of 1983, nine wild pigs were collected near the central western boundary of the site that were found to exhibit characteristics typical of short-term feral hog/Eurasian wild boar hybrids (Mayer and Brisbin 2012). The origin of these animals was traced to a release of this type of hybrid wild pig onto private property, Cowden Plantation, which is adjacent to the SRS (Fig. 2-1) (Mayer and Brisbin 2008, 2012). By the fall of 1987, animals showing these hybrid characteristics were found throughout the riverswamp from the border with Cowden Plantation southeast to the Steel Creek delta (Mayer and Brisbin 2012).

At present, the SRS wild pig population phenotype appears to be a widespread mosaic of all three ancestral sources, with the UP phenotype still being dominant in the northern half of the site. However, wild pigs in the area of the riverswamp now exhibit mixed characteristics from all three ancestral stocks.

3.0 Methods

Total body mass (i.e., intact body weight with no organs removed) was measured for wild pigs taken on the SRS between 1968 and 2020 (Fig. 3-1). Animals were harvested through a variety of methods (shooting, trapping, and dogging), and were categorized by sex and into one of six age classes. Age classes, which included neonates, piglets, juveniles, yearlings, subadults and adults, were based on either the presence of a drying umbilicus and fetal membranes (for neonates vs. the remaining five age classes) or dental characteristics (for piglets through adults; assigned as per Mayer and Brisbin 2008, 2012). Harvested animals were weighed ± 0.5 kg for the piglet through adult age classes, and ± 1.0 g for neonates. Of the complete sample of piglet through adult females, a subset was examined for reproductive status (pregnant or not pregnant).

Fig. 3-1. Collection of wild pig total body mass data at the SRS public deer hunt.

Data were compared for significant differences due to sex, age class, reproductive status, season, historic subpopulation grouping, and decade. Variation of the entire data set was analyzed for comparisons of total body mass for sex, age class, and reproductive status. Differences in total body mass were also analyzed between the sexes for each age class, and between age classes for each sex. The growth rate toward adult body mass (expressed as average percent of the adult body mass for each age class) was compared between the sexes. Reproductive status was compared (pregnant vs. not pregnant) overall and within age classes. Pregnant females were also compared to males overall (i.e., juveniles through adults) and within age class. Seasonal differences were analyzed between and within both sex and age class. Seasons were defined as: winter – Dec-Feb; spring – Mar-May; summer – Jun-Aug; and Fall – Sep-Nov. Combined age groupings of younger (i.e., piglet and juvenile) and older (i.e., yearling through adult) animals of either sex were used for seasonal comparisons. In addition, the monthly variation of adult body mass was compared by sex. The SRS is divided into 50 hunt units. The breakdown into the two subpopulations by hunt units was as follows: riverswamp subpopulation – Hunt Units 9, 10, 12, 19, 20, 24, 28, 29, 30, 32, 35, 36, 37, 38, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49 and 50; upland subpopulation – Hunt Units – 2, 3, 4, 5, 6, 7, 8, 13, 14, 15, 16, 17, 18, 23, 25, 26, 27, 33 and 34. Based on the known introduction history of the SRS wild pig population, the two subpopulations were analyzed for differences overall and by decade (i.e., starting in the 1970s).

All statistical analyses were performed using the JMP Pro Version 11.2.1 software package (SAS Institute Inc. 2014). The total body mass data were tested for normality using a Shapiro Wilk W test. An Analysis of Variance was used to determine significant differences among three or more groups. A *t* Test was used to evaluate variables between two groups. A Tukey-Kramer HSD was employed to evaluate differences between specific pairs of three or more groups. Statistical significance was accepted at $p = 0.05$.

4.0 Results

The mean body mass for the total SRS wild pig sample (N = 12,257) was 38.4 kg and varied from 0.511 up to 189 kg (SD = 33.3). With all age classes combined, males (mean = 40.1 kg; range = 0.511 to 189; SD = 35.4) were significantly heavier ($t = -5.583$, $df = 12{,}255$, $p \leq 0.0001$) than females (mean = 36.7 kg; range = 0.519 to 170; SD = 30.9), being on average 1.09 times greater in total body mass within the entire sample. The heaviest animal overall was an adult male. The heaviest female was a non-pregnant adult.

A breakdown of the body mass data by age class and sex is presented in Table 4-1. Although range overlap occurred in all age classes, males consistently averaged heavier than females. The overall ranges were heavier in males than in females for all except the piglet age class. Sexual dimorphism was also significant in all but the piglet age class (Table 4-1). The variation within and overlap between age classes increased with age. With the exception of the adult age class, males were more variable than females within the same age class. Differences between the sexes also increased with age, indicating that males achieve absolute weight gain faster than females (Table 4-1, Fig. 4-1). On average, SRS wild pigs (sexes combined) were born at approximately 0.9 percent of their adult weight. This growth rate progressed toward the adult body mass at an average rate of: 8 percent (piglets), 31 percent (juveniles), 55 percent (yearlings), 75 percent (subadults), and 100 percent (adults). Females showed a consistent and slightly faster percent growth rate toward the adult body mass than males on an individual age class basis (Fig. 4-1); however, this difference was not significant. Within each sex, comparisons of body mass between each pair of age classes consistently indicated significant differences ($p = 0.05$ using Tukey-Kramer HSD). The average weight gain between age class means was 15.8 kg for females and 18.1 for males. For both sexes, the rate of weight gain was initially fast, and then leveled-out over the older age classes. Weight gain was the same for each sex in the neonate-piglet age class interval and then increased in the piglet-juvenile interval. This increased slightly for the juvenile-yearling interval, decreased for the yearling-subadult, and then increased again for the subadult-adult interval (Fig. 4-1).

Within the subset of pregnant to non-pregnant females (N = 3,019), pregnant females were significantly heavier than non-pregnant females in the juvenile through adult age classes (Table 4-2). Because of the small sample size, the single pregnant piglet sow was not compared to the rest of the non-pregnant sows in that age class. For all age classes combined, pregnant sows averaged 66.5 kg. The smallest was a juvenile that weighed 11.5 kg and had a fetal litter of 4 embryos, while the largest was the adult that weighed 170 kg, which had a fetal litter of 13. The overall increase of the pregnant over the non-pregnant animals was by 1.32 times, which generally decreased with increasing age. Comparing pregnant females to males in the same collective age range (i.e., combined juveniles through adults), the pregnant sows were significantly larger in body mass ($t = 5.38$, $df = 4{,}716$, $p \leq 0.0001$). Within each specific age class (juveniles through adults), pregnant sows were on average heavier than the boars in the juvenile and yearling age classes but were then lighter in the two oldest age classes. These differences were significant in the juvenile ($t = 3.72$, $df = 978$, $p \leq 0.0002$) and adult ($t = -6.59$, $df = 1{,}537$, $p \leq 0.0001$) age classes.

Table 4-1. Summary of total body mass data (in kg) of 12,257 wild pigs from the Savannah River Site, South Carolina. These data, collected between 1968 and 2020, were separated by age class and sex. Differences between the sexes within each age class were analyzed using a *t* Test. The body mass data for neonates were originally taken to the nearest gram, and to the nearest 0.5 kg in the remainder of the age classes.

Age Class	Sex	N	Total Body Mass (in kg)			*t* Test $p \leq$ [a]	Times that males are larger than females on average
			Mean	Range	SD		
Neonate	F	243	0.754	0.519-1.375	0.176	0.002	1.08
	M	203	0.818	0.511-1.614	0.246		
Piglet	F	1,963	6.5	0.5-38.5	5.3	0.144	1.03
	M	2,182	6.7	0.5-32.5	5.6		
Juvenile	F	819	26.4	10.0-55.5	8.5	0.003	1.05
	M	930	27.6	8.0-59.0	9.1		
Yearling	F	1,000	46.0	9.5-99.0	12.6	0.0001	1.07
	M	928	49.1	20.0-109.0	14.2		
Subadult	F	1,024	62.7	12.5-122.5	16.2	0.0001	1.07
	M	802	66.9	12.5-150.0	18.6		
Adult	F	941	80.0	31.0-175.0	21.4	0.0001	1.14
	M	1,223	91.1	16.5-189.0	21.0		

[a] Differences are considered to be significant at $p \leq 0.05$

Significant seasonal differences were found in all of the sex and age class combinations except for juvenile females, subadult females and adult females. In general, there was a shift with age from being heaviest in the fall-winter period (younger animals) to being heaviest in the spring-summer timeframe (older animals). Within the neonate age class, the heaviest animals were born in the winter and the lightest ones in the spring. This pattern held for both sexes, and the seasonal differences within each sex were significant (females – *F*

= 2.94, $df = 3$, $p \leq 0.03$; males - $F = 2.98$, $df = 3$, $p \leq 0.03$). For both sexes in the piglet age class, the heaviest seasonal mean weights were in the fall, while the lightest were in the summer. These differences were significant for both sexes at $p \leq 0.0001$. Juvenile males had the heaviest seasonal mean in winter and the lightest in spring ($F = 4.83$, $df = 3$, $p \leq 0.002$). Except for the subadult females, beginning with the yearling and continuing through the adult age class for both sexes, the lowest seasonal mean weight was in the fall, and the heaviest were in either spring or summer. The seasonal differences for these older age classes were significant at $p \leq 0.0006$ for all of the males, and significant at $p \leq 0.0046$ for yearling females. In all cases, the fall mean weights of these older groups were significantly lower than the other seasonal means.

Table 4-2. Comparison of differences in body mass between pregnant and non-pregnant female wild pigs from the Savannah River Site, South Carolina.

Age Class	Pregnancy Status	N	Total Body Mass (in kg)			*t* Test Results – $p \leq$ [a]	Times that pregnant females are larger than non-pregnant females on average
			Mean	Range	SD		
Piglet	Not Pregnant	98	14.1	10.0-55.5	8.1	-[b]	-[b]
	Pregnant	1	12.5	12.5	-		
Juvenile	Not Pregnant	478	25.7	10.0-55.5	8.0	0.0001	1.26
	Pregnant	55	32.4	11.5-51.5	10.6		
Yearling	Not Pregnant	545	44.9	9.5-99.0	12.8	0.0001	1.12
	Pregnant	204	50.2	24.0-93.0	11.7		
Subadult	Not Pregnant	559	60.2	12.5-120.0	15.4	0.0001	1.11
	Pregnant	273	66.8	32.0-122.5	17.2		
Adult	Not Pregnant	486	77.5	35.0-175.0	21.4	0.0008	1.06
	Pregnant	320	81.5	40.0-170.0	19.7		

[a] Differences are considered to be significant at $p \leq 0.05$
[b] Sample size too small to analyze

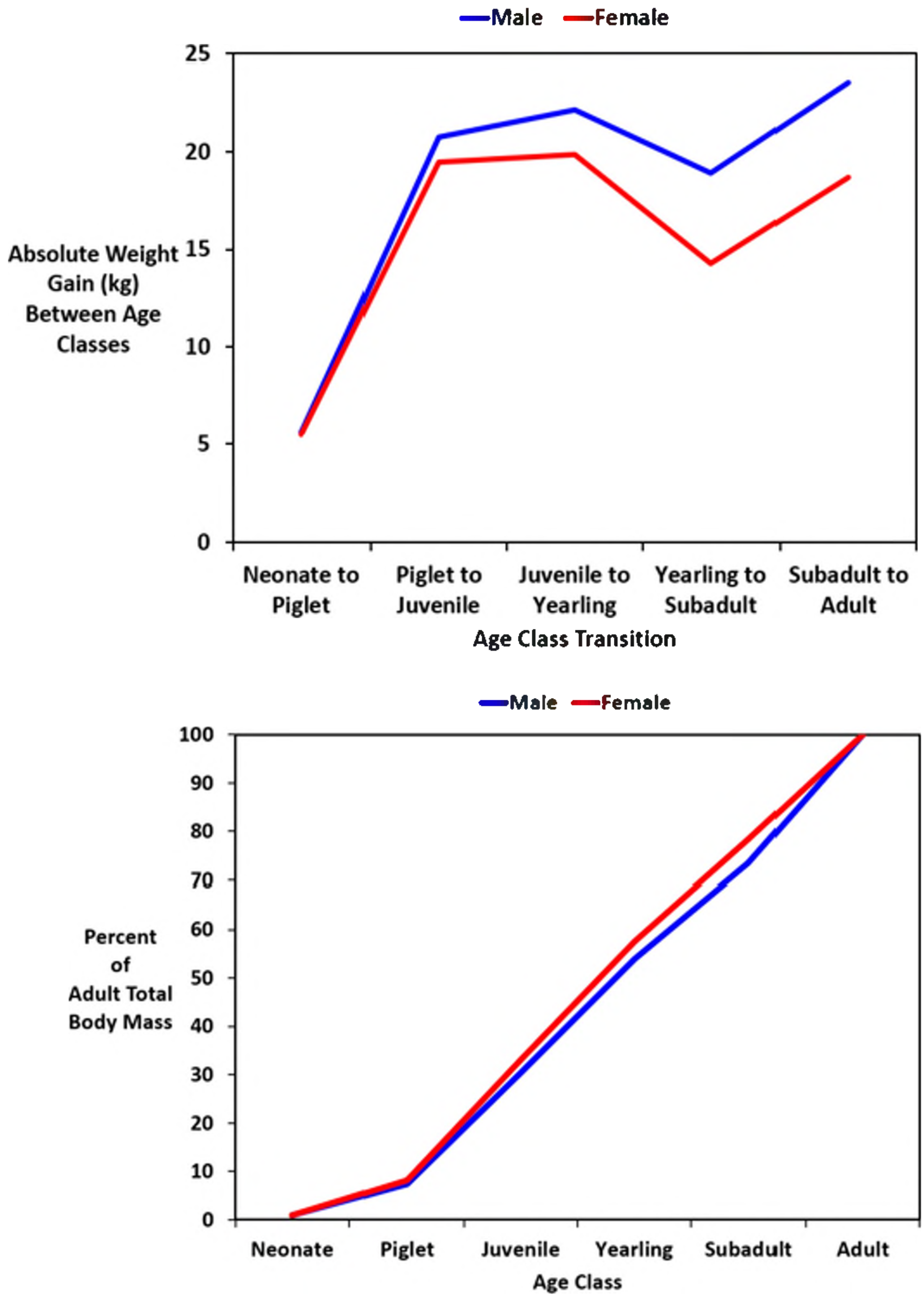

Fig. 4-1. Top graph: changes in absolute weight gain (kg) among age class intervals for female versus male SRS wild pigs. Bottom graph: percent growth rate toward the adult body mass in males and females on an individual age class basis.

Similar to the seasonal fluctuations, most sex and age class combinations had significant monthly differences except for subadult females and adult females. Again, there a general age-related shift from being heaviest in the fall-winter months (younger animals) to being heaviest in the spring-summer months (older animals). Differences were seen in the monthly fluctuations of mean total body mass of each sex of adult animals. However, only those of the males were significantly different ($F = 4.60$, $df = 11$, $p \leq 0.0001$). Both females and males had a major peak in April and a low in November. In all cases, these average monthly fluctuations entailed deviations of less than 10 kg from the annual adult mean. On an annual basis, variation in the mean total body mass (i.e., minimum to maximum) for adults of each sex was 12.0 and 11.8 kg for females and males, respectively.

In general, the RS subpopulation (mean = 42.2 kg; range = 0.517 to 189; SD = 34.1) was significantly heavier ($t = 16.22$, $df = 12{,}255$, $p \leq 0.0001$) than the UP subpopulation (mean = 32.3 kg; range = 0.511 to 178; SD = 31.0). All sex and age class comparisons between the two SRS subpopulations resulted in the RS subset consistently averaging and ranging larger than the UP sample. All of these differences were significant at $p \leq 0.05$ except for both neonate sexes, female piglets, female juveniles and female subadults. The weight difference was overall the same between the sexes. For both sexes, this difference increased with age up through the yearlings, and then decreased with each successive age class.

The overall SRS wild pig population showed a significant drop in total body mass reaching a low in the 1990s (Fig. 4-2; $F = 195.09$, $df = 5$ $p \leq 0.0001$). This same decrease in total body mass during the 1990s was seen for each sex and age class grouping except for the neonatal age classes, which had insufficient data to make this comparison. All of the remaining sex-age class groupings were significant at $p \leq 0.0001$. A similar significant decrease in the 1990s was also seen in the overall RS subpopulation ($F = 86.75$, $df = 5$ $p \leq 0.0001$). This pattern was consistent for all sex and age class groupings within the RS subpopulation except for the subadult and adult male age classes. The subadult males showed a significant decrease in the 2000s, which then increased. In contrast to the rest of the RS sample, the adult males showed a significant and steady decrease from the 1960s through the 2010s with a mean decrease of 14 kg. Overall, from the 1970s through the 2010s, the UP subpopulation also showed a significant similar decrease in the 1990s ($F = 154.56$, $df = 4$ $p \leq 0.0001$). However, the 1970s UP subpopulation sample only had 3 data points (i.e., one juvenile male, one yearling female, and one adult male). In contrast to this overall pattern for the UP subpopulation, if the 1970s UP sample is excluded, most of the specific sex-age class groupings show a significant increase from the 1980s through the 2010s, with the exception of the subadult and adult male age classes. Both of those male age class groupings were unchanged (i.e., flat lined) and not significant for any change.

5.0 Discussion

The overall variation observed in the present study generally agrees with that published previously for this species. Most significantly, males are almost always reported as being larger or heavier than females in total body mass. The basis for this pervasive sexual dimorphism of body mass in this species is male-male competition for breeding opportunities with estrus females (Herring 1972). It follows, then, that this difference is typically reported to be most often statistically significant in mature or more dominant-breeding animals. In addition to averaging heavier than females, males also typically exhibit a larger maximum observation. However, in some samples (e.g., Barrett 1971; Belden et al. 1985; Briedermann 1986; Wood and Brenneman 1977), females were the heaviest animals weighed. In contrast to this relationship between the sexes, variation due to other factors (e.g., age class, pregnancy status and season) are often not consistent among either populations of this species or the three ancestral types of wild pigs.

The percent difference between the sexes in the present study was similar to but at the lower end of the spectrum reported for other populations (Fig. 5-1). The highest sexual dimorphism in mass (2.44) was for adult Eurasian wild boar from the Caucasus Mountains (calculated from Heptner et al. 1966). In comparing the percentage by which males are larger than females for the three morphotypes, the mean of various percent differences from the literature resulted in Eurasian wild boar (n=36) having an average percent difference of 1.44, feral hogs (n=15) having a ratio of 1.27, and hybrids (n=4) having a mean percent difference of 1.31. In studies with comparable data (e.g., Gallo Orsi et al. 1992), the percent difference between the sexes increased from younger to older age groupings, as was generally found in the present study.

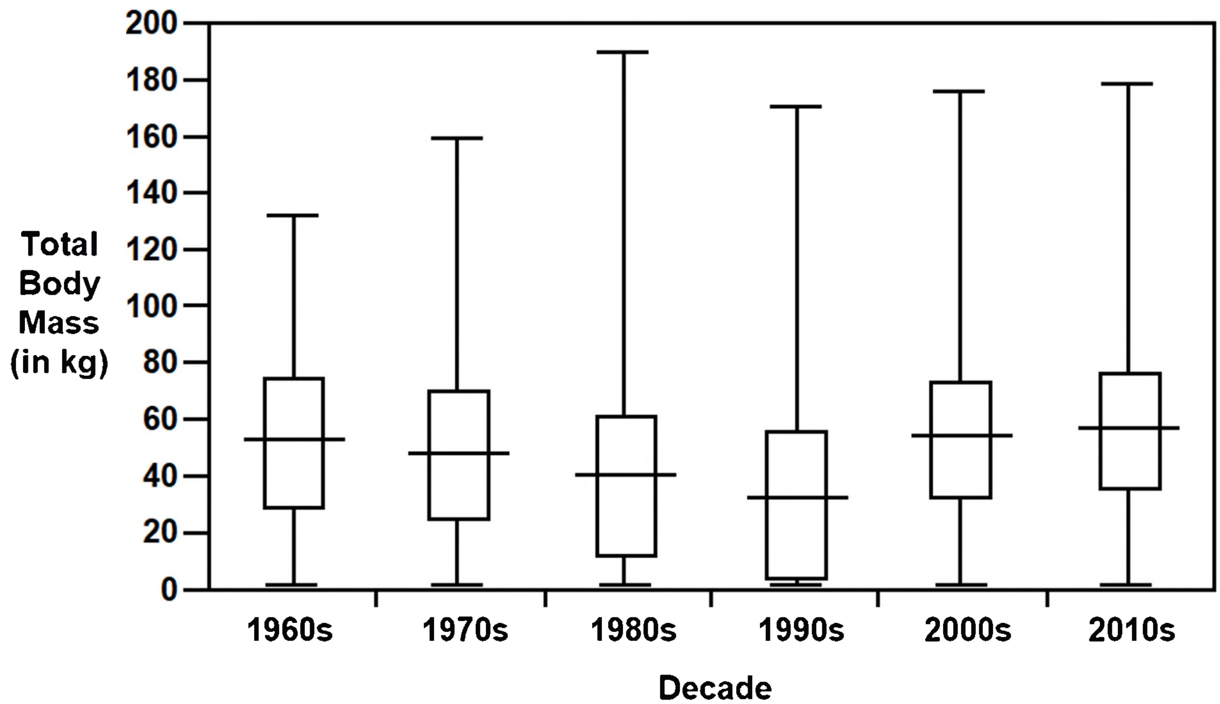

Fig. 4-2. Change in the total body mass (in kg) of the SRS wild pigs over the decades from the 1960s to the 2010s. Combined data includes both sexes and all age classes.

Environmental factors can also affect the sexual dimorphism of body mass in this species. Dexter (2003) found that during periods of drought, the difference in body mass between the sexes of adult feral hogs in semi-arid New South Wales was not significant. He theorized that this lack of a significant difference could have been due to a disproportionately higher mortality among smaller females, which would have had less resistance to starvation under these harsh conditions.

Similar to the present study, the range of body mass data between age classes has generally been extremely variable, with a great deal of overlap existing between adjacent age classes. This is usually true for all comparisons within and between the sexes. Although some studies have considered body mass as a means of age estimation (e.g., Klein et al 1990; Nehring 1888; Stethem 1977), this morphological parameter has been too variable to enable accurate age determinations.

The age at which sexually dimorphic differences in body mass becomes significant varies among the studies. Typically, this difference becomes significant during the second year of life (about 13-21 months of age; e.g., Brooks and Ahmad 1993; Conley et al. 1972; Dzieciolowski et al. 1990; Gallo Orsi et al. 1992; Giles 1980; Henry 1970; Pedone et al. 1995; Romic 1975; Saunders 1993; Spitz et al. 1998). Other studies (Hell and Paule 1983; Wood and Brenneman 1977) reported this difference to only be significant in animals three years and older in age. In the present study however, significant sexual dimorphism in total body mass was found in age class samples as young as the neonates. This difference was then not significant in the next oldest age class but was again significant in the rest of the age classes. In contrast, some studies with samples including only individuals less than one year of age (e.g., Zurowski et al. 1970) have shown no significant difference between the sexes. Other studies, reporting on weight comparisons between the sexes in younger samples, have even found that in some cases females averaged larger than males (e.g., Briedermann 1970; Gallo Orsi et al. 1992). However, these atypical sexual dimorphic differences did not prove to be significant.

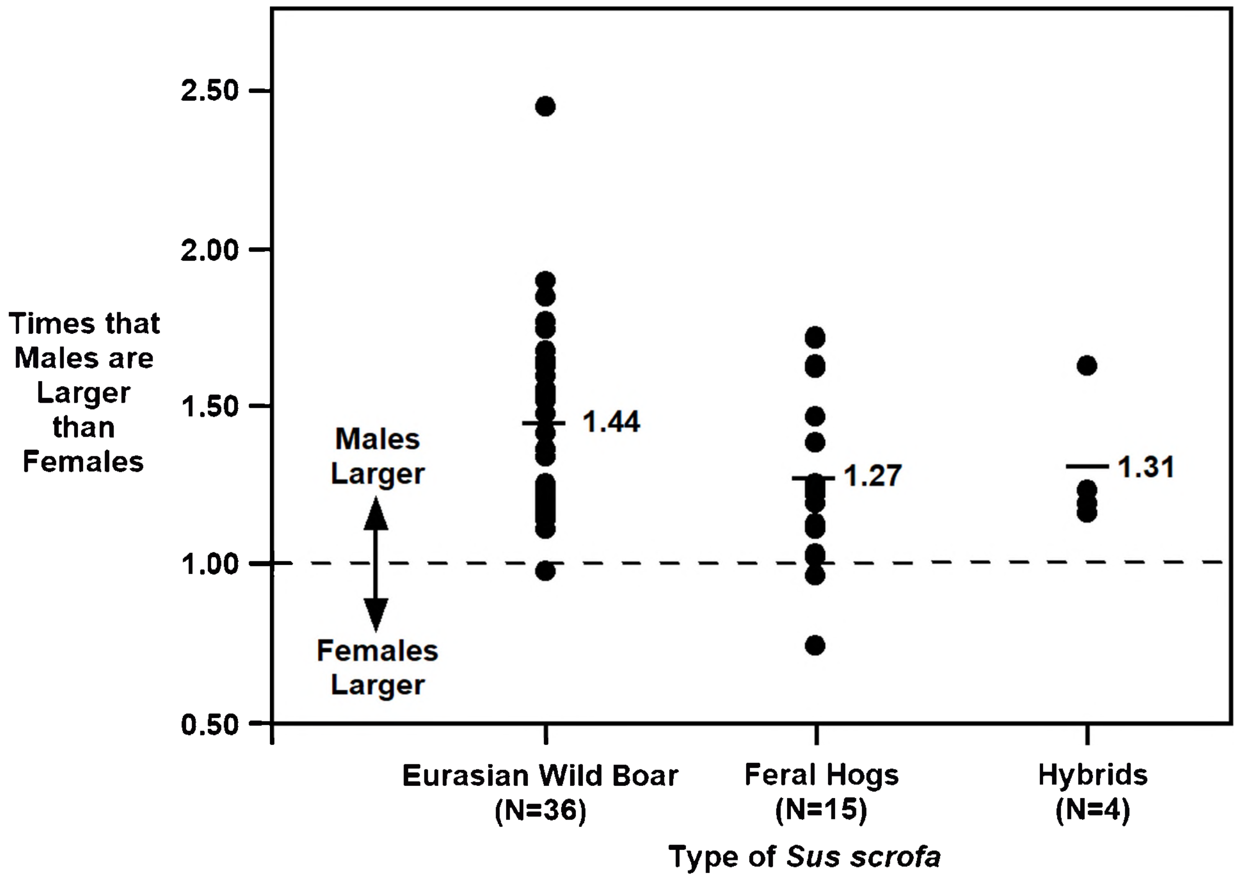

Fig. 5-1. Comparison of the percent difference between the sexes in the three major types of wild pigs.

Wild pig studies with comparable mean data (e.g., Belden and Frankenberger 1979; Belden et al. 1985; Brooks and Ahmad 1993; Conley et al. 1972; Gallo Orsi et al. 1992) show similar growth patterns with females, at least in the younger age classes, gaining weight more rapidly as a percentage of the mean adult total body mass. The increased absolute weight gain in males was also consistent in these same studies. In all cases, absolute male weight increased with age as in the present study.

The total body mass increase in wild pigs is reported to continue until approximately 3 5 years of age (Briedermann 1970; Dzieciolowski et al. 1990; Hell and Paule 1983; Romic 1975). Dzieciolowski et al. (1990) found that physical growth in boars continues after it has ceased in sows. Hell and Paule (1983) reported that body growth was completed in this species by the ninth year of life. In contrast, Wood and Brenneman (1977) reported that animals more than 5 years of age tended to decrease in body condition. Examples of such decreased body masses of very old adult sows and boars in that study were 18 kg and 36 kg, respectively. An older adult male in the present study weighed only 16.5 kg. Dzieciolowski et al. (1990)

noted that wild pigs of both sexes were past their prime by the age of 6 years, probably because tooth wear and loss would have affected their ability to feed.

The variation in total body mass in females of this species due to pregnancy has been addressed in several studies. Dzieciolowski et al. (1992) found that breeding females up to 17 months of age were significantly heavier than nonbreeding females, but the difference ceased to be significant for older animals. Gaillard et al. (1993) determined that a positive correlation existed between body mass and reproductive performance (i.e., females that were either ovulating or pregnant) for female wild boar less than one year of age. However, it should be noted that both of these studies were based on either carcass or gutted body mass data. Barrett (1971) found that linear regressions predicting total body mass from gutted body mass of pregnant sows differed from those for nonpregant females, males, and castrated males. This difference was attributed to the increased weight of the reproductive tract in pregnant sows. Pépin et al. (1987) noted a step by step change in the body mass of wild sows with an increase in age. This was reportedly a consequence of their annual investment in breeding. Fernández-Llario and Mateos-Quesada (1998) found that sows that were reproductively active (i.e., pregnant or lactating) were significantly heavier than sows that were not. They also found that as the body mass increased incrementally, the percentage of reproductively active sows in the sample increased.

Seasonal differences in the total body mass of wild pigs have been reported previously in the literature; however, no common pattern appears to exist. Barrett (1971) reported that adult wild pigs increase their live weight rapidly in the fall, which then decreases through the summer. Conley et al. (1972) described seasonal weight fluctuations in this species with similar peaks in May and November, and lows in February and August. Those authors attributed this pattern to food availability, with body mass peaks reportedly coinciding with the availability of the spring/summer foods and mast crop, respectively. Lows occurred after mast had been consumed and before the spring thaw and then after the spring/summer foods had been consumed and before mast had fallen. Dzieciolowski et al. (1990) found that seasonal weight changes were significant for males but not for females. Males reached a peak in fall, lost weight during the winter through spring, and then begin gaining mass back during the summer. Females had a similar pattern, although their peak weight was spread over both fall and winter. Saunders (1993) found, using a length/weight relationship, that significant differences occurred between summer/fall and spring periods. The animals were in poorer condition (i.e., weighed less for a given length) in the summer/fall sample. Although a winter sample was not collected, the author speculated that this deteriorating condition would continue through that season also. These reported seasonal effects were most pronounced for younger pigs. The present study found age related patterns, with younger animals being heaviest in the fall-winter, and older animals being heaviest in the spring-summer.

Changes in body mass among wild pigs can also reflect the availability of important foods (e.g., acorn mast). Massei et al. (1996) found that the availability of primary forage resources (acorns and olives) directly influenced body weights in Mediterranean populations of wild boar. Higher body weights were exhibited following high production of these foods. Pépin et al (1987) reported that adult wild boar were heavier following a large mast crop. Pedone et al. (1995) found that yearly changes in body mass due to the abundance in the mast crop were even more extreme in the younger animals.

Reproductive activity can also affect weights in wild pigs. The body mass of mature male Eurasian wild boar has been reported to drop during the breeding season (due to testosterone production and resultant reduced foraging), with some individuals losing up to 20-25 percent of their body weight (Frädrich 1984; Goulding 2003). A similar drop was seen in the total body mass of adult males on the SRS in the October through December timeframe. Although the wild pigs at the SRS breed year-round, this observed drop immediately followed the peak-breeding season, which is from August through October in this population (Mayer and Brisbin 2012). In addition, the adult females showed monthly lows in body mass coinciding with the annual peak post-farrowing periods for this population (Mayer and Brisbin 2012). In spite of this observation being an expected annual change, comparable drops in adult females have not been reported previously.

The neonatal data from the present study are similar to the sparse total body mass data for this age class that has been previously published. The previously reported neonatal range for wild specimens of this species is from 590 to 1620 grams, and averages around 900 to 1000 grams (Briedermann 1970; Conley et al. 1972; Heptner et al. 1966; Pilz 1966). Both the minimum observation and mean from the present study (i.e., 511 and 783 grams, respectively) were lower than previously reported figures, while the maximum observation (i.e., 1614 grams) was close. Further, the sample sizes reported in the present study were larger than any other published study.

Published total body mass data for adult wild pigs (both sexes combined) generally average around 85 kg (based on the mean of means from 55 published data sets). The comparable averages for the sexes from these same sources are approximately 73 and 97 kg, for adult females and males respectively. The adult mean in the present study was 86 kg. The sex-specific adult means from the SRS (i.e., 80.0 kg for females, and 91.1 kg for males) were also similar to general averages for wild pigs. The lesser amount of difference in body mass between the sexes at the SRS compared to the overall sample likely reflects the lower degree of sexual dimorphism in the SRS wild pigs compared Eurasian wild boar, which made of most of the 55 data sets analyzed. Barrett (1978) also noted that Eurasian wild boar show greater sexual dimorphism than do feral hogs in body mass.

As a species (including both wild and domestic forms), *Sus scrofa* has the potential to attain large body mass. The heaviest record for this species was a domestic boar that weighed 865 kg (Mayer and Brisbin 2008). In contrast to this record, the maximum observations of total body mass data typically reported for wild pigs are between 140-145 kg. In almost all instances, these observations are composed of males within these populations.

Exceptional wild pig specimens exceeding 300 kg have also been reported, but these animals are rare. Heck (1950) reported on a 350-kg wild boar taken in the Caucasus Mountains. Beginning in 2009, several large male wild pigs were killed in various locations in the United States including the following: 2009 - Mobile County, Alabama - 354 kg (Dute 2009); 2012 - Sonoma County, California – 333 kg (Orth 2012); 2015 – Transylvania County, North Carolina – 321 kg (Fox News 2015); 2015 – Comanche County, Texas – 358 kg (Huffman 2015); and 2017 - Samson, Alabama - 372 kg (Songer 2017). In 1995, a large feral boar weighing 404 kg was taken near the towns of Coward and Scranton in South Carolina (O'Connell 1995). Earlier, Rutledge (1965) anecdotally reported the weight of a large feral boar taken from the Santee River delta in South Carolina as 405 kg. In all of these instances, the animals were males. Recent reports of harvested wild pigs exceeding 450 kg (e.g., "Hogzilla," "Hog Kong," and "Monster Pig") have turned out to be capture-reared or domestic males that either were released or escaped into the wild before being killed (Mayer and Brisbin 2009).

Anecdotal accounts exist of adult boars from the SRS wild pig population weighing in the range of 225-275 kg. However, none of these animals have ever been either actually weighed or had measurable body parts brought in that would indicate an animal being that heavy (see Mayer 2003, for that methodology). Although not included in the present study, the heaviest body mass ever reported for a wild pig at SRS was a male that anecdotally weighed in at 204 kg (Mayer et al. 2021). This animal was harvested in 2017 on a portion of SRS that is public wildlife management area land (i.e., Crackerneck Wildlife Management Area and Ecological Reserve or CWMA&ER) located directly across South Carolina Highway 125 from the Three Rivers Solid Waste Authority landfill (M. B. Caudell, South Carolina Department of Natural Resources, personal communication). Mayer et al. (2021) found that wild pigs found around and foraging in that landfill were significantly larger than the pigs found on the rest of the SRS. That fact likely accounted for the 204-kg male. Overall, only 3 animals (i.e., 0.002 percent) in the present study were over 175 kg in total body mass. All of those animals were adult males. Only 20 SRS wild pigs (i.e., 0.016 percent of the total) were over 150 kg. All of these animals were adults, with 14 being males and 6 being females. For an SRS wild pig to reach 225 kg as an adult, it would have to have been 169 kg as a subadult (i.e., based on an estimate of subadults being 75 percent of the adult body mass). The closest subadult to that body mass was a male that weighed 150 kg. Maximum estimations can thus be estimated by calculating from younger age classes. Based on the weight of the maximum observations for the juvenile, yearling and subadult samples, and assuming the respective mean percentages of the adult body mass (i.e., juvenile – 31%; yearling – 55%; and subadult – 75%), the maximum body mass of an SRS wild pig would be projected to be in the range of approximately 190-200 kg. In addition, in spite our large samples, no animals were seen on the site near these maximum body mass ranges in the younger age classes since the early 1990s. Assuming that the reported weight was accurate, the male harvested on CWMA&ER in 2017 would likely represent the maximum total body mass.

It should also be noted that in October of 2016, local hunters, using trained hunting dogs, caught and killed a large boar on a farm immediately north of the SRS (Fig. 5-2). Using a set of truck scales, that feral boar weighed in a total of 327 kg. This animal was known to have been an escaped domestic boar that had gone wild/feral and was causing damage to local farms (R. E. Hamilton, Wild Hog Control, personal communication). Given the close proximity to the site boundary where this boar was harvested, there was the potential for this animal to have wandered onto the SRS and been harvested there. In the future, should a wild pig be harvested on the SRS that weighs in excess of 300 kg, such a scenario of a recently escaped animal of domestic origin should be suspected and investigated.

Fig. 5-2. Photo of the 327-kg boar that was killed immediately north of the SRS in 2016.

The average and observed ranges of body weights also varies with the type of wild pig. In general, feral hogs were the most variable, having the lowest minimum and also the largest maximum documented adult weights. Eurasian wild boar typically had the highest body mass means reported. Hybrids appeared to weigh slightly more than the range reported for feral hogs. Based on the previously mentioned 55 data sets, Eurasian wild boar, feral hogs and hybrids had average adult body mass (i.e., mean of means) of 95, 66 and

71 kg, respectively. In addition, breaking down the feral hog references into short term and long-term subsets, the adult body mass means were 49 and 80 kg for long- and short-term ferals, respectively.

Mean adult SRS wild pig body mass was between the comparable averages for wild boar and hybrids. The ancestry of the SRS population is varied and has gone through significant shifts during the past five decades. Given this shift from short-term feral to the present short term feral/long term feral/hybrid mixture, any decrease in the total body mass was to be expected. However, although such a decrease was expected, the magnitude of the drop was not as large as projected. The increase in body mass data in the UP subpopulation would further corroborate this taxonomic-based shift.

In addition to the impacts of a varying ancestry driving a change in body mass, the availability of forage resources could have also played a role in this drop in body mass. Although specific levels of these resources (e.g., mast crop) were not available over the period of this study, it was possible to estimate the population of these animals at SRS over the 50+ years. In comparing the overall body mass data of the SRS wild pigs with the population size, when the population increased, the body mass decreased. This could be an indication of the reduced availability of forage resources due to competition. Massei et al (1996) speculated that density might play an important role in increasing intraspecific competition, finding that when the density was higher, body weights of wild boar decreased. The same could have been true for the SRS wild pigs.

6.0 Conclusions

Total body mass variation exhibited by the SRS wild pigs was similar to that previously reported for other populations of this species. General consistencies with previous studies included the observed range of body mass data (by sex and age class), the overall male-dominated sexual dimorphism, and the higher absolute weight gain in males. However, the SRS population differed in the percent difference of sexual dimorphism, the age at which sexual dimorphism became significant, and age-related seasonal variation in body mass.

Temporal differences in body mass in the SRS wild pigs were consistent with the documented changes in the ancestral taxonomic makeup of this population over time. However, these differences were likely also affected by environmental factors (e.g., quality of forage resources, regional climate), that were not quantified in the present study. Although the effects of such extrinsic variables on wild pig body mass have been studied, the consequences of ancestral taxonomic makeup (especially changes over time) has not been generally considered, and the present study confirms the importance of evaluating this factor as a source of body mass variation and in drawing management conclusions from such data.

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