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Management and Conservation

Reproduction in a Population of Wild Pigs (*Sus scrofa*) Subjected to Lethal Control

STEPHEN S. DITCHKOFF,[1] *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*
D. BUCK JOLLEY, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*
BILL D. SPARKLIN, *U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA*
LAURA B. HANSON, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*
MICHAEL S. MITCHELL, *U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA*
JAMES B. GRAND, *U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, AL 36849, USA*

ABSTRACT The continued range expansion of wild pigs (*Sus scrofa*) in North America is an increasing cause for concern because of the numerous negative impacts that wild pigs have on ecosystem structure and function. Once populations are established, wild pigs have proven to be extremely difficult to control, and close to impossible to eradicate. If effective control and removal techniques are to be developed, we must determine if wild pig populations respond to reductions in density by increasing reproductive output. This study was designed to examine if reproductive parameters of female wild pigs display a density-dependent response following a concentrated removal effort. We compared reproductive parameters and condition of adult sows that were collected between a control area and a treatment area where lethal removal occurred. From August 2004 to May 2006, we focused a concentrated removal effort within the treatment area. Although the population density was more than 65% greater in the control area than the treatment area during the study, we did not detect differences between areas for condition, litter size, ovarian mass, corpus luteum mass, or corpora lutea number. Several years of heavy mast production during the study may have negated any effect on condition and subsequent reproduction between the 2 study areas. These data suggest that reproductive parameters of wild pigs do not exhibit density-dependence during periods when pig populations are in good condition.

KEY WORDS condition, corpora lutea, density dependence, lethal control, reproduction, *Sus scrofa*, wild pig.

The wild pig (*Sus scrofa*) is an introduced species in North America that is a source of ecological concern because of the variety of negative impacts that pig populations have on the ecosystem. Wild pigs are known to alter soil chemistry (Singer et al. 1984), decrease plant diversity (Singer et al. 1984), and directly and indirectly compete with native wildlife for resources (Coblentz and Baber 1987, Mayer and Brisbin 1991). These impacts occur across the current range of wild pigs and, to compound the problem, the range of the wild pig has expanded rapidly in recent years, with populations now present in the majority of the United States (Gipson et al. 1998). After wild pigs become established, they are difficult to control and nearly impossible to eradicate partially because of their high rate of reproduction (Dzieciolowski et al. 1992). Humans have increased the reproductive capacity of domestic, and subsequent wild pigs in North America, from the less-fecund wild swine that were originally domesticated in Europe (Hagen and Kephart 1980, Mauget 1991, Mayer and Brisbin 1991).

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[1]*E-mail: ditchss@auburn.edu*

Female wild pigs are non-seasonal, polytocous species that have recurring estrous cycles approximately every 21 days and are capable of reaching sexual maturity at 5 months (Dzieciolowski et al. 1992), a relatively young age compared with other large mammals (Read and Harvey 1989). Mean litter size ranges from 4.8 to 7.5 piglets, but can be as great as 12 (Henry 1968, Barrett 1978, Sweeney et al. 1979, Baber and Coblentz 1987, Taylor et al. 1998, Geisert 1999). Adult females are prolific breeders that typically produce 2 litters a year but are capable of producing 3 litters within 14 months (Baber and Coblentz 1987, Dzieciolowski et al. 1992).

With wild pigs increasing in range and distribution, the development of population control programs has become more critical to protect native ecosystems. Population control efforts directed at wild pigs can be effective for short time periods (Hone and Pedersen 1980); however, early puberty combined with large and frequent litters enables populations to rebound quickly (Dzieciolowski et al. 1992). As is common in most wildlife species, body condition is positively associated with wild pig reproduction (Warren and Ford 1997). On Santa Catalina Island, California, Baber and Coblentz (1987) found that body condition positively influenced reproduction in wild pigs. They suggested that conception in sows was dependent on attaining a certain threshold of body condition. They also reported that pregnant sows had markedly greater levels of body fat than non-pregnant individuals, suggesting that availability of food resources was a strong influence on reproduction. This association between body condition and reproduction has been found in other mammalian species, including the collared peccary (*Tayassu tajacu*; Lochmiller et al. 1986), North American elk (*Cervus elaphus*; Stewart et al. 2005), black bear (*Ursus americanus*; Rogers 1976), house mouse (*Mus musculus*; Meikle and Westberg 2001), and feral donkey (*Equus asinus*; Choquenot 1991). Body condition can be strongly influenced by population density (Choquenot 1991, Mattioli and Pedone 1995, Stewart et al. 2005), and thus changes in population density can ultimately influence reproductive rates in free-ranging animals. Choquenot (1991) found that feral donkeys living at high density exhibited poorer physical condition and lower fecundity than donkeys living at low density. Similarly, Singleton et al. (2001) found that the feral house mouse exhibited an inverse relationship between litter size and population density in Australia.

The positive association that has been reported between body condition and reproduction in wild pigs (Matschke 1964, Baber and Coblentz 1987) suggests that wild pigs could respond to control efforts and subsequent reductions in population density by increasing their rate of reproduction. However, no study to date has attempted to assess how reproduction in wild pigs responds to changes in density. An understanding of this aspect of wild pig ecology would help predict success and increase effectiveness of population control programs. Our objective was to determine if reproduction was associated with population density in wild pigs. We predicted that pigs in an experimentally reduced population would have greater fat reserves and increased rates of fecundity than pigs from a control population.

STUDY AREA

Fort Benning Military Installation was 73,655 ha in size and located in west-central Georgia and east-central Alabama (32°21′N, 84°58′W). The installation was split by 2 physiographic regions, the Peidmont and Upper Coastal Plain, and was characterized by level sandy ridge tops and gentle slopes with an average annual rainfall of 124 cm (Dilustro et al. 2002). Forests at Fort Benning were managed primarily for the longleaf pine (*Pinus palustrus*) ecosystem driven by the conservation mandate to protect the federally endangered red-cockaded woodpecker (*Picoides borealis*). Therefore, a frequent fire regime was used as a management tool to regenerate longleaf pine and reduce understory plants. Sandy ridges were dominated by pine (*Pinus* spp.) forests, and were separated by hardwood bottoms. Pine forests at Fort Benning were composed of loblolly pine (*P. taeda*), longleaf pine, shortleaf pine (*P. echinata*), and mixed pine-hardwoods. Oak-hickory (*Quercus* spp.-*Carya* spp.) forests dominated the low hardwood areas of the installation (Doresky et al. 2001).

METHODS

We separated Fort Benning into 2 areas for the purposes of this study. One area of approximately 50 km^2 was used as the treatment area (e.g., lethal removal), and the remaining area on the installation, not including a 1-km buffer surrounding the treatment area, served as the control. In the treatment area, we collected wild pigs by a combination of trapping and shooting from August 2004 to May 2006. Traps were spring-loaded box traps ($1.2 \times 2.4 \times 1$ m^3) baited with corn. Throughout the study, we used 15–20 traps per night on average for a total of 2,600 trap nights, with traps being set on average between 4 and 5 nights each week. In conjunction with trapping, we also located and collected pigs using a 75 mm Raytheon Palm IR 250 digital thermal camera (Raytheon Commercial Infrared, Dallas, TX) attached to a vehicle window mount with the visual signal routed to a 19-cm television affixed on the dash of the vehicle (Ditchkoff et al. 2005). We drove along roads throughout the installation until we spotted pigs and collected them using firearms aided by spotlight. Collection of pigs in the control area was limited to this technique, as all trapping effort was focused on the treatment area. Fort Benning was managed primarily for military training; however, recreational hunting was allowed when it did not interfere with military training. Therefore, pig hunting occurred on the majority of the installation throughout the study. Hunting pressure was considered to be comparable between the treatment and control areas.

After collection, we removed all reproductive tracts from sows and froze them until later analysis. We only included sows estimated to be 5 months or older in this study because that is the minimum reported pubertal age for wild pigs (Dzieciolowski et al. 1992). We assigned age categories (<5 months old, 5 months–1 yr old, and >1 yr old) according to Matschke (1967). In the laboratory, we thawed reproductive tracts to room temperature and removed the ovaries. We then examined reproductive tracts for fetuses, and recorded fetus count and sex. We measured the length of each fetus from the crown of the skull to the base of the tail (crown-rump length) to the nearest 1 mm and used it to estimate time of conception and projected parturition (Henry 1968). We weighed ovaries to the nearest 0.001 g and examined them for corpora lutea. After we removed individual corpora lutea from the ovaries, we weighed them to the nearest 0.001 g. To assess physical condition, we removed kidneys and attached perirenal fat and froze them in sealed plastic bags for later analysis. In the laboratory, we thawed kidneys and trimmed the surrounding fat perpendicular to the long axis at both ends of the kidney. We weighed the kidney with remaining attached fat to the nearest 0.01 g, and then completely removed the attached fat from the kidney and weighed the kidney. We calculated a kidney fat index (Riney 1955) as the ratio of the weight of the remaining fat to the kidney $\times 100$.

We assessed pig density via capture-mark-recapture techniques during the summers of 2004, 2005, and 2006, which consisted of trapping pigs using whole corn and box traps with spring-activated doors during 18-day trapping sessions

(Hanson et al. 2009). We spaced traps at 1–2-km intervals across the study areas, prebaited traps for 2 weeks prior to the beginning of each trapping session, and checked traps each morning of each trapping session. We analyzed these data using Chao's (1988) moment estimator in Program CAPTURE (Rexstad and Burnham 1991) to estimate density. A more thorough description of the field and analytical methodology used to estimate density was previously provided by Hanson et al. (2009). Research was approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2003-0531). We obtained a State of Georgia collection permit (29-WSF-05-20) for specimen collection.

We used a repeated measure analysis of variance (ANOVA; PROC GLM; SAS Institute, Inc. 1990) to compare ovary and corpus luteum mass between treatment areas where ovary and corpus luteum mass were nested within individual pigs. Litter size, corpora lutea number, and kidney fat index were compared between treatment areas with ANOVA. We evaluated all models for normality and homogeneity of variance and made appropriate transformations when we found deviations.

RESULTS

From August 2004 to May 2006, we removed 298 pigs from the installation for research purposes. We removed 162 (3.24 pigs/km^2) pigs from the treatment area and 136 (0.21 pigs/km^2) from the control area. Of the 63 sexually mature sows collected, 55% ($n = 38$) were pregnant; we collected 35 of these in the treatment area and 28 in the control area. Mean litter size (in utero) for this population was 5.9, and litter size ranged from 3 to 11 (Table 1). Mean ovarian mass, corpora lutea number, and corpus luteum mass of reproductively active pigs were 2.57 g, 7.19 g, and 0.32 g, respectively. Mean litter size ($F_{1,36} = 7.40$; $P = 0.010$), ovarian mass ($F_{1,27} = 9.90$; $P = 0.004$), and corpora lutea number ($F_{1,35} = 4.20$; $P = 0.048$) were greater in sows older than 1 year than in sows 5 months to 1 year of age (Table 1). We found no differences in corpus luteum mass ($F_{1,35} = 2.40$; $P = 0.130$) or kidney fat index ($F_{1,33} = 2.37$; $P = 0.133$) between age classes of sows. Sexually mature sows reproduced throughout the year, with 2 general periods of conception and parturition (Fig. 1). The first and most prominent period of conception occurred between September and January. The second period was more defined and centered on the month of April. Parturition followed the same trend, but approximately 114 days later because of gestation length.

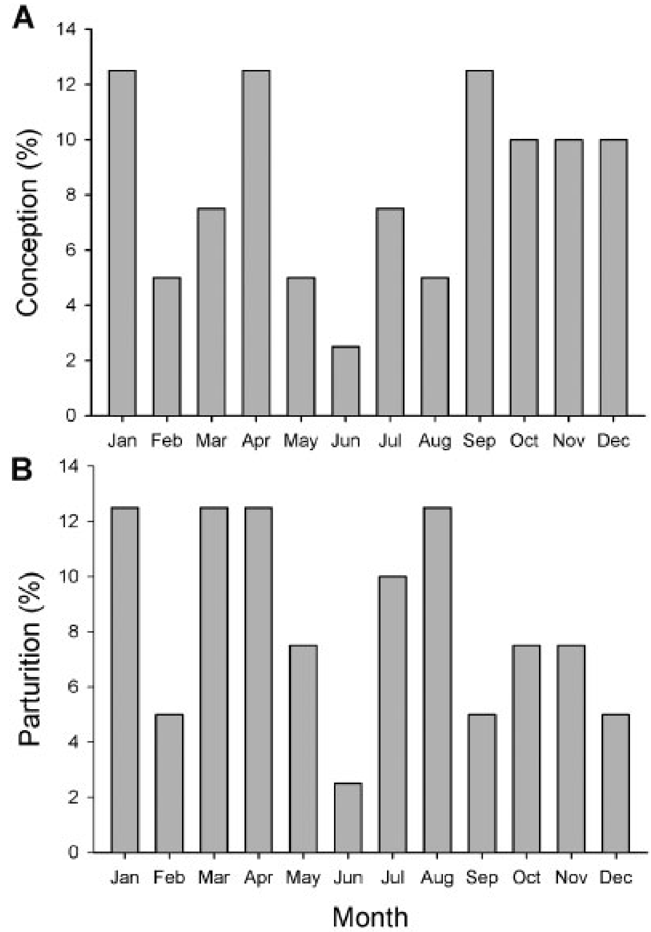

Figure 1. Annual conception (A) and parturition (B) of female wild pigs collected on Fort Benning, Georgia during August 2004 to May 2006.

Density of wild pigs was greater in the control than the treatment area for the duration of the study (Table 2; Hanson et al. 2009). However, we found no differences in litter size ($F_{1,35} = 0.07$; $P = 0.729$), ovarian mass ($F_{1,14} = 0.42$; $P = 0.528$), kidney fat index ($F_{1,33} = 1.19$; $P = 0.283$), corpus luteum mass ($F_{1,35} = 0.73$; $P = 0.400$), or corpora lutea number ($F_{1,35} = 2.80$; $P = 0.103$) between the treat-

Table 1. Reproductive parameters and condition measurements in 2 age classes of female wild pigs that were collected from Fort Benning, Georgia during August 2004 to May 2006.

	Sows 5 months to 1 yr old			Sows >1 yr old			All sows					
Parameter	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	F^a	Df	*P*
CL mass (g)[b]	77	0.285	0.009	200	0.338	0.009	277	0.323	0.009	2.40	1,35	0.130
CL number[c]	12	6.1	0.2	25	7.7	0.4	37	7.2	0.3	4.20	1,35	0.048
Ovarian mass (g)	26	1.825	0.186	32	3.097	0.378	58	2.527	0.238	9.90	1,27	0.004
Litter size	12	4.8	0.3	26	6.4	0.4	38	5.9	0.3	7.40	1,36	0.010
KFI[d]	15	42.42	5.78	20	32.74	3.31	35	36.89	3.18	2.37	1,33	0.133

[a] Statistical tests compared reproductive parameters between age classes.
[b] Corpus luteum mass.
[c] Number of corpora lutea per female.
[d] Kidney fat index calculated according to Riney (1955).

Table 2. Density estimates (pigs/km^2) of wild pigs in both a treatment (lethal control) and control area on Fort Benning, Georgia from 2004–2006.

	Lethal removal			Control		
Year	Density	Lower 95% CI	Upper 95% CI	Density	Lower 95% CI	Upper 95% CI
2004	1.07	0.80	2.34	1.79	1.27	3.46
2005	1.26	0.87	2.69	2.45	1.52	5.68
2006	1.61	1.16	2.81	2.74	1.85	4.52

ment and control areas (Table 3). Kidney fat index showed a tri-modal trend with the mode peaks occurring during December 2004, May 2005, and December 2005 (Fig. 2). The lowest point in the index was during the first 3 months of the study when the kidney fat index dipped to 14% during September and October 2004. Beginning in November 2004, the kidney fat index increased to 26% and never decreased below 20% for the remainder of the study period.

DISCUSSION

The data did not support our original hypothesis that reproductive output would be greater in wild pigs subjected to intense lethal removal than pigs that were not subjected to a removal program. One possible explanation for this finding is that our sample sizes may have been inadequate to detect statistical difference between the 2 areas. If reproduction had been greater in the treatment area because of our removal efforts and we were unable to detect the differences because of low statistical power, we would have expected most or all of the parameters to show a trend to be greater in the treatment area. However, this was not the case. Mean values of some parameters (corpus luteum mass and corpora lutea number) were greater in the treatment area, whereas mean values of the remaining variables were greater in the control area. This lack of a defined trend suggests that our removal efforts had little if any effect on reproduction. However, our sample sizes were low because of the difficulty of collecting reproductively active pigs on the installation. As a result, we may have been unable to detect any statistical differences because of low power, and the lack of differences in reproductive parameters in our data set may not necessarily be reflective of actual differences between treatments.

The lack of difference in reproductive parameters between the 2 areas suggests that body condition of pigs in the treatment and control areas were not different. This was confirmed by the kidney fat index data. As demonstrated previously (Warren and Ford 1997), wild pigs increase reproductive output during times of elevated food availability or when body condition is high. In addition, Baber and Coblentz (1987) found that pig reproduction was strongly associated with body fat as measured by kidney fat index. When their population of wild pigs had a mean kidney fat index of 10%, reproduction was relatively low compared to times when the kidney fat index was >10%. The Fort Benning kidney fat index increased to >20% after November 2004, was as high as 42%, and never decreased below 20% throughout the study. If a threshold exists where condition negatively influences reproduction in wild pigs, as suggested by Baber and Coblentz (1987), then we believe that the Fort Benning population was not nutritionally restricted for most of the study.

A density-dependent response in reproduction assumes that the greater density population is limited by resources. During the time of this study, the Fort Benning population of wild pigs was in very good condition, as indicated by the high kidney fat index measurements. The large mast crops that occurred during the time of this study may have confounded our ability to reduce population density to the point that condition changes would influence reproduction. When examining 4 years of mast (e.g., hard and soft) data from the installation (Jolley 2008), the 2004–2005 and 2005–2006 year crops were 64% and 13% greater than the 4-year average, respectively. Considering the nutritional influence that mast crops can have on condition of wildlife populations (Rogers 1976, Wolff 1996) and the influence that condition has on reproduction in wild pigs (Matschke 1964, Baber and Coblentz 1987), we suspect that the high mast production during our study masked any density-dependent differences that may have been incurred by our removal efforts. If the high-density population (control area) had been limited by

Table 3. Reproductive parameters and condition measurements in female wild pigs from a population subjected to a lethal removal program and a control population from Fort Benning, Georgia during August 2004 to May 2006.

	Control			Treatment					
Parameter	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	F^a	Df	*P*
CL mass (g)[b]	77	0.323	0.031	124	0.338	0.262	0.73	1,35	0.400
CL number[c]	18	6.6	0.5	19	7.7	0.4	2.80	1,35	0.103
Ovarian mass (g)	18	3.606	0.664	14	3.173	0.307	0.42	1,14	0.528
Litter size	17	5.9	0.4	20	5.8	0.4	0.07	1,35	0.789
KFI[d]	19	40.06	4.88	16	33.12	3.79	1.19	1,33	0.283

[a] Statistical tests compared reproductive parameters between treatments.
[b] Corpus luteum mass.
[c] Number of corpora lutea per female.
[d] Kidney fat index calculated according to Riney (1955).

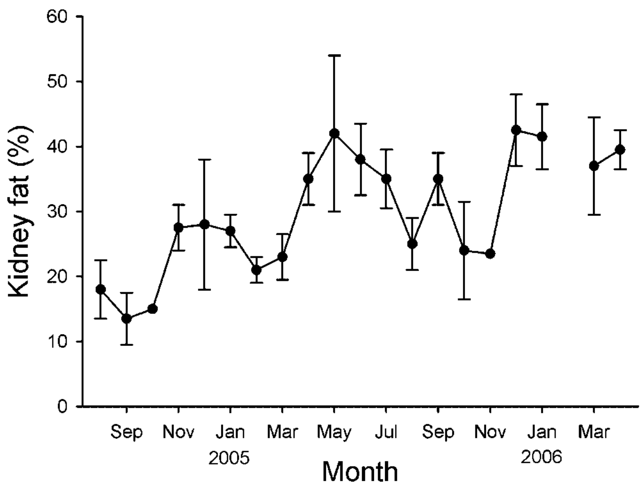

Figure 2. Mean kidney fat index of adult wild pigs collected from Fort Benning, Georgia during August 2004 to May 2006.

food resources during the time of the study, the pigs should have exhibited conditional and reproductive differences between the 2 areas. In a demographic analysis conducted concurrently with this study (Hanson et al. 2008, 2009), population density was estimated to be more than 65% greater in the control area than the treatment area. However, density increased by approximately 50% in both areas from 2004 to 2006, regardless of our removal efforts. If the populations were increasing in both areas, then either the pigs were not saturated in the control area, or some other factor (e.g., nutrition) was playing a role in increasing the pig population over the entire installation, and our removal efforts had little impact.

Reproductive parameters (e.g., litter size, ovary mass, corpus luteum mass, and corpora lutea number) of female wild pigs at Fort Benning were similar to data reported for other populations (Henry 1968, Barrett 1978, Sweeney et al. 1979, Baber and Coblentz 1987, Taylor et al. 1998). Patterns in conception and parturition also mirrored reports for other wild pig populations, where reproduction occurred during all months of the year, but primarily during 2 periods. We were not surprised that wild pigs in the southeastern United States would breed year-round because of the moderate seasonal variation in the region and high availability of food throughout the entire year. Conception occurred throughout the year but showed a bi-modal pattern with conception decreasing between May and August. Although nutrients are often considered to be abundant during the warm summer months because of lush vegetation, fewer pigs were conceived during this period. This may stem from the warm temperatures (27–32° C) typically associated with summers at Fort Benning. Heat stress is known to decrease reproductive output of domestic sows (Omtvedt et al. 1971) and has been attributed to decreased pig reproduction in South Texas (Taylor et al. 1998).

MANAGEMENT IMPLICATIONS

Our efforts at lethal removal were not substantial enough to cause a measurable change in reproduction. This suggests that moderate efforts toward reduction of wild pig populations that would be found in most management scenarios (public and private) will not cause substantial enough changes in pig densities to result in concomitant increases in reproduction. Because most public and private agencies cannot mobilize the resources (logistic or economic) required to sustain a large removal effort, their results will most likely be similar to ours. In addition, confounding effects of fluctuating food availability (e.g., mast production) and resulting body condition changes, as well as the opportunistic manner in which wild pigs are able to use a wide range of available food sources (Ditchkoff and Mayer 2009), may serve to ensure that densities of wild pig populations are only rarely reduced to the point that density-dependent effects in condition and reproduction can be found. As a result, we expect that most land managers will not witness measurable changes in reproduction of pigs as a result of removal efforts.

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