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Author(s): Erin L. Koen, , Eric Vander Wal, Ruth Kost, and Ryan K. Brook
Source: The American Midland Naturalist, 179(2):275-286.
Published By: University of Notre Dame
https://doi.org/10.1674/0003-0031-179.2.275
URL: http://www.bioone.org/doi/full/10.1674/0003-0031-179.2.275

Am. Midl. Nat. (2018) 179:275–286

Reproductive Ecology of Recently Established Wild Pigs in Canada

Erin L. Koen[1]
Department of Biology, Memorial University of Newfoundland, 230 Elizabeth Ave, St. John's, NL, Canada A1B 3X9

Department of Animal and Poultry Science, College of Agriculture and Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon, SK., Canada S7N 5A8

Eric Vander Wal
Department of Biology, Memorial University of Newfoundland, 230 Elizabeth Ave, St. John's, NI., Canada A1B 3X9

Ruth Kost
Department of Animal and Poultry Science, College of Agriculture and Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon, SK., Canada S7N 5A8

AND

Ryan K. Brook
Department of Animal and Poultry Science & Indigenous Land Management Institute, College of Agriculture and Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon, SK., Canada S7N 5A8

ABSTRACT.—An essential component of management efforts to control invasive species is the estimate of life history parameters, such as reproductive rate and litter size. Wild pigs (*Sus scrofa*), one of the most invasive terrestrial mammals worldwide, have recently become established on the Canadian prairies. We estimated life history traits in a population of wild pigs in Saskatchewan, Canada, at the current northern limit of their North American distribution. The average pregnant wild pig weighed 73.8 kg (46 – 130 kg; n = 7). Fifty-four percent of females ≥46 kg were pregnant in Feb., with an average of 5.6 fetuses per pregnant female (range 4 – 7; n = 7). Although small sample sizes precluded statistical significance, we found that larger females in better body condition tended to have more fetuses and that the sex ratio of fetuses tended to be female-biased. Based on the cohort that we sampled in Feb., we predicted parturition would occur between Feb. and May; this range of parturition dates may have been wider had we sampled wild pigs at other times of the year. We show that the number of fetuses of wild pigs in Saskatchewan is similar to other areas, suggesting that population growth and spread could be just as rapid. Our estimates represent the first empirical life history measures of wild pigs in Canada and are an essential step in developing science-based eradication plans for this highly invasive species.

Introduction

Invasive species are one of the main drivers of species endangerment and extinction worldwide (Clavero and Garcia-Berthou, 2005; Bellard *et al.*, 2016), impacting native ecosystems and agriculture (Pimentel *et al.*, 2005). Therefore, a major challenge in management and conservation is control and eradication of invasive species (Mack *et al.*, 2000). Models of population growth and spread can help to predict current and future

[1] Corresponding author: telephone: 709-770-8291; E-mail: erinkoen@hotmail.com

invasions (*e.g.*, Muirhead *et al.*, 2006) and assess the efficacy of potential management strategies (*e.g.*, Bieber and Ruf, 2005; Goldstein *et al.*, 2016). Life history is one important predictor of the invasion success of mammals (Forsyth *et al.*, 2004; Jeschke and Strayer, 2006). As such, modelling population growth and spread depends on empirical estimates of life history traits, such as reproduction and survival.

Wild pigs (*Sus scrofa*), one of the most invasive and destructive terrestrial mammals in North America and worldwide (Lowe *et al.*, 2000), were introduced to the United States in the 16th century (Mayer and Brisbin, 1991) and have since expanded to over 6 million animals in at least 37 states (Mayer, 2014). Wild pigs represent a large and widespread threat to native plant and animal communities through predation, competition, disease transmission, and habitat destruction (Barrios-Garcia and Ballari, 2012; Bevins *et al.*, 2014) and have contributed to the decline of numerous species at risk (USDA, 2002; Parkes *et al.*, 2010). Populations of introduced wild pigs have recently become established in large parts of Saskatchewan, Alberta, and Manitoba, Canada (Brook and van Beest, 2014), and there have been occasional sightings of wild pigs in most other Canadian provinces. Originally, domesticated European wild boar were imported into western Canada from different parts of Europe in the 1980s and 1990s to diversify agriculture (Brook and van Beest, 2014). Indeed, domesticated wild boar farming remains common: in 2011 there were over 9000 domesticated wild boar on 150 farms across Canada (Michel *et al.*, 2017). Farming for meat production and penned sport shooting operations are the original sources of free-living wild pig populations in Canada (Michel *et al.*, 2017). Wild pigs are extremely fecund in other parts of their native and introduced range (Comer and Mayer, 2009), making established populations notoriously difficult to control and almost impossible to eradicate (Cruz *et al.*, 2005; Barrios-Garcia and Ballari, 2012). For consistency we refer to the population in Canada as "wild pigs" (Keiter *et al.*, 2016), as we do not know whether these nonnative, free-living animals are pure feral European wild boar, feral domestic pigs, or hybrids of wild boar and domestic pigs.

Although there are estimates of reproductive rates and litter sizes for wild pig populations across much of their worldwide distribution, these rates vary (reviewed by Comer and Mayer, 2009). As such, local estimates of these parameters are essential for effective management. It is predicted that range-edge populations have reduced reproductive output (Gaston, 2009), whereas life history theory predicts that expanding populations will have higher reproductive rates (Philips *et al.*, 2010). Interestingly, litter size of European wild boar in Europe tends to increase with latitude (Bywater *et al.*, 2010). Little is known about the reproductive ecology of wild pig populations in Canada, currently at the northern limit of their distribution in North America. Here, we report number of fetuses, fetal sex ratio, parturition dates, and the relationship between reproduction and maternal condition of wild pigs in Saskatchewan, Canada, representing the first reported life history estimates of wild pigs in their Canadian distribution following their initial introductions.

METHODS

Our study area (51.110"N, 103.231"W) was based in the Prairie Ecozone, an agriculture-dominated landscape in southeastern Saskatchewan, Canada. The average (SD) temperature over 10 y (2007–2016) in our study area was -13.9 C (2.4) in Jan. and 18.5 C (1.6) in Jul. (Environment and Climate Change Canada, 2017). The average (SD) daily temperature during Feb. 2017, the time of our study, was -10 C (8.4), with an average (SD) snow depth of 8.6 cm (4.9; Environment and Climate Change Canada, 2017). Large monocultures of annual and perennial crops were interspersed with fragments of deciduous forest cover and

Prairie Pothole wetlands. Potential predators of wild pigs, including wolves (*Canis lupus*) and black bears (*Ursus americanus*), were generally rare in our study area. Wild pigs are harvested for sport throughout Saskatchewan, where there is no bag limit and hunting is allowed continuously throughout the year. Within the overall study area we identified wild pigs in two areas that included central and southern study sites.

In Feb. 2016 we captured wild pigs using a net-gun fired from a helicopter or corral-style traps in our central and southern study sites in Saskatchewan. We fitted each animal with a Global Positioning System (GPS) tracking collar (Telonics, Mesa, Arizona, U.S.A.). We did not anesthetize animals during this process. In Feb. 2017 we relocated and recaptured the surviving collared wild pigs with a net gun fired from a helicopter and attempted to also capture all members of their group. Our capture team physically restrained the pigs and euthanized them using a penetrating bolt gun to the head and confirmed immediately that they were dead. We transported carcasses to a nearby mobile lab for processing. The University of Saskatchewan Animal Research Ethics Board approved all aspects of animal capture, handling, and euthanasia (Animal Use Protocol no. 20150024).

We measured head-body length (tip of nose to base of tail), shoulder height (front hoof to spine), chest girth, body weight (using a digital scale), and back fat thickness. We measured back fat thickness by making a cut directly through the back fat layer on the rump at the base of the tail, parallel to the spine, and measured fat thickness at the deepest point along the cut, from the connective tissue above the muscle to the top of the fat against the skin. We estimated body condition by palpitation of hip and backbone and visually using a standardized set of five diagrams on a scale from one to five according to Muirhead and Alexander (1997): (1) emaciated, backbone very prominent; (2) thin, backbone prominent; (3) moderate, backbone just palpable; (4) slightly overweight, backbone not detectable; and (5) obese, body rotund, backbone not detectable. Female wild pigs are capable of giving birth to their first litter at < 1 y old (*e.g.*, Taylor *et al.*, 1998; Moretti, 2014), and, rarely, as young as 3–4 mo old (Dzięciołowski *et al.*, 1992; Comer and Mayer, 2009); therefore, we pooled all age classes in our analyses. For pregnant females, we counted fetuses, determined fetus sex, and measured fetus length (crown to rump). We estimated fetus age based on crown-to-rump length according to Henry (1968a). Assuming a 115 d gestation (Henry, 1968b), we estimated the date of conception and predicted the date of parturition using the average fetus length in each litter.

Most of our body size measurements were correlated among pregnant wild pigs (Table A1, available in the Appendix). Therefore, we conducted a principal component (PC) analysis with the psych package (Revelle, 2017) in R (R Core Team, 2017) on body weight, back fat, head-body length, shoulder height, and chest girth for pregnant wild pigs. We used the scores from the first PC axis (Table A2) as an index of body size and condition. We used linear models, pooled over study area, to compare the number of fetuses to both maternal body size (indexed by the first PC axis) and our field assessment of maternal body condition (on a scale of 1–5). We conducted power analyses with the pwr package (Champely, 2017) in R to estimate the sample size required to detect a statistically significant relationship between number of fetuses and both maternal body size and condition and field-estimated maternal body condition given the effect sizes that we observed in our data. We used a binomial test in R to assess whether the sex ratio of fetuses, pooled over study area and mother, differed from 1:1. We conducted a power analysis with the pwr package to estimate the number of fetuses we would need to sample to detect a fetal sex ratio that differed significantly from 1:1 given our data. These power analyses give us an indication of biological

TABLE 1.—Wild pig (*Sus scrofa*) group size in two study areas in Saskatchewan, Canada, necropsied Feb. 19–24, 2017

Study area	Group size	F	M	Pregnant
Central	8[a]	1		1
	11[b]	5	5	1
	12	6	6	2
	unknown	1		1
	1	0	1	0
	1	0	1	0
	1	0	1	0
	1	0	1	0
South	3[c]	3	0	0
	6[d]	3	2	2
	5[e]	2	3	0
	1[f]			0

[a] 7 members of unknown age or sex not in the sample
[b] 1 member of unknown sex not in the sample; 1 F (unknown pregnancy status) recorded here was not in the necropsied sample
[c] 1 female (unknown pregnancy status) recorded here was not in the necropsied sample
[d] 1 individual of unknown sex in the necropsied sample
[e] At least 5 animals in the group
[f] Unknown sex, solitary

significance (*i.e.*, whether the lack of statistical significance we observed was due to small sample size or small effect size).

We sought to provide managers of wild pigs in SK with a guide as to whether relatively easy to obtain field-based estimates of body condition (on a scale of 1–5) can be used as an index of more difficult to obtain measures of body size and condition (*i.e.*, back fat). We pooled our data over study area, sex, and age, and assessed the relationship between field-based measures of body condition and: (1) the first axis of a PCA based on the highly correlated variables body weight, head-body length, shoulder height, and chest girth (Tables A3 and A4); and (2) back fat, with linear models in R.

RESULTS

In 2016 we captured 12 female and 10 male wild pigs using a net-gun fired from a helicopter (n = 17) or corral-style traps (n = 5). In Feb. 2017, we necropsied 23 wild pigs from four groups and an additional four solitary males in the central study area (Table 1). In the southern study area, we necropsied 13 wild pigs from three groups and one individual that was solitary (Table 1). Average (SD) observed group size was 10.3 (2.1) in the central study area (n = 3) and 4.7 (1.5) in the southern study area (n = 3); these could be underestimates as we cannot be certain that we detected all members of each group.

For our sample of wild pigs collected in Feb. 2017, we estimated that conception occurred between Nov. and Feb. and that parturition would occur between Feb. and May (Table 2). Mean weight of nonpregnant females was 45.0 kg (SD = 20.6 kg, range = 25–97 kg, n = 12). Mean weight of pregnant females was 73.8 kg (SD = 29.1 kg, range = 46–130 kg, n = 7). Seven of the 13 females that weighed $\geq$46 kg were pregnant in Feb.; five of six in the central study area and two of seven in the southern study area. The average number of fetuses per

TABLE 2.—Number of wild pig (*Sus scrofa*) fetuses and dates of conception and birth in two study areas in Saskatchewan, Canada, necropsied Feb. 19–24, 2017

Study area	Weight of pregnant F (kg)	No. of fetuses	Sex ratio of fetuses		Date of conception[a]	Date of birth[a]
			M	F		
Central	130	6	3	3	2 Nov 2016	25 Feb 2017
	74	5	2	3	13 Nov 2016	8 Mar 2017
	55[b]	5	1	4	30 Nov 2016	25 Mar 2017
	81	7	2	5	8 Dec 2016	2 Apr 2017
	46[b]	5	-[c]	-	2 Feb 2017[d]	28 May 2017[d]
South	48[e]	4	1	3	23 Dec 2016	17 Apr 2017
	83[e]	7	3	4	29 Dec 2016	23 Apr 2017

[a] Estimated based on crown-to-rump measurement of fetuses (Henry 1986a) and assuming a 115 day gestation period (Henry 1986b)

[b] Two pregnant females in the same group

[c] Embryo-stage when necropsied on 19 Feb 2017, therefore we could not determine sex ratio

[d] Embryo-stage when necropsied on 19 Feb 2017. These estimates are the latest conception and birth dates assuming that implantation occurred 17 days after conception (Henry, 1986a)

[e] Two pregnant females in the same group

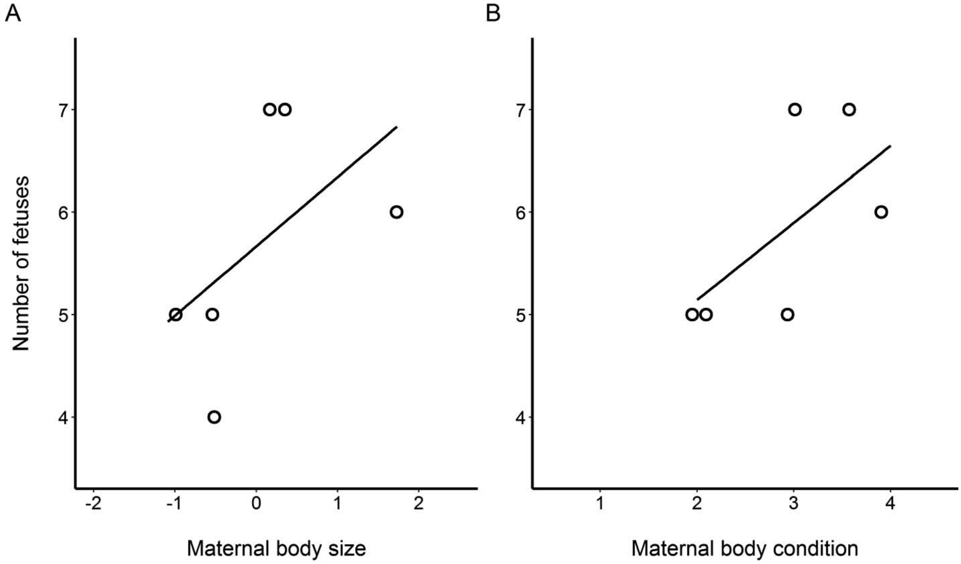

FIG. 1.—The number of fetuses in six pregnant female wild pigs (*Sus scrofa*) from two study areas in Saskatchewan, Canada versus (**A**) maternal body size and condition as indexed by the first principal component axis describing body weight, head-body length, shoulder height, chest girth, and back fat, and (**B**) maternal body condition as estimated in the field on a scale of 1–5

pregnant female, pooled over study area, was 5.6 (SD = 1.1, range = 4–7, n = 7; Table 2). Larger females, as indexed by the first PC axis, tended to have more fetuses ($R^2 = 0.31$; n = 6), although this relationship was not statistically significant (P = 0.25, Fig. 1a). We would need a sample size of ≥21 animals to have a 90% probability of detecting a significant effect of maternal body size on fetus count given our data (effect size = 0.56, $\alpha = 0.05$). Females in better body condition, as estimated in the field based on visual examination and palpitation of hip and backbone, also tended to have more, but not significantly more, fetuses ($R^2 = 0.38$, P = 0.19, n = 6, Fig. 1b). We would need a sample of ≥20 animals to have a 90% probability of detecting a significant effect of maternal body condition on fetus count given our data (effect size = 0.60, $\alpha = 0.05$). In five of six pregnant females (note that one litter was at the embryo stage and we were unable to estimate sex ratio), the sex ratio of the fetuses was female-biased (proportion of females = 0.65, 95% CI = 0.46 – 0.80, n = 34), but not significantly (P = 0.12; Table 2). We would need a sample of 117 fetuses to detect a sex ratio that differed significantly from 1:1 given our data. Although not statistically significant at $\alpha = 0.05$, our effect sizes (effect size of 0.5 is a medium effect [Cohen, 1988]) and power analyses (only a 2.5-fold increase in the sample size of pregnant females and a 2.4-fold increase in the sample size of fetuses required to reach statistical significance) suggest that the slight female bias in the fetal sex ratio is biologically relevant.

After pooling samples over study area and sex, we found that body condition (on a scale of 1–5) was positively related to both body size, as indexed by the first PC axis based on weight, length, height, and girth ($R^2 = 0.23$, $P < 0.01$, n = 29), and back fat ($R^2 = 0.25$, $P < 0.01$, n = 29).

DISCUSSION

The invasion of wild pigs, especially at their northern range edge on the Canadian prairies, has presented novel challenges for management agencies because predictions of reproductive output at the expansion front are unclear. Although it is hypothesized that populations at their range limits have reduced reproductive output (Gaston, 2009; Sexton *et al.*, 2009), theory predicts that expanding populations have relatively high reproductive rates (Philips *et al.*, 2010) and empirical evidence suggests that litter size of European wild boar increases with latitude (Bywater *et al.*, 2010). Conversely, current models in the continental United States (US) have suggested that environmental and climatic conditions in the northern states adjacent to Canada should be limiting to wild pig invasion (McClure *et al.*, 2015; Snow *et al.*, 2017). Our findings show that wild pigs are, indeed, breeding in the wild on the Canadian prairies and that these animals are at least as fecund as other wild pig populations across their native and introduced distributions (Comer and Mayer, 2009). We found an average of 5.6 fetuses per pregnant female wild pig in Saskatchewan, comparable to wild pig (5–6 fetuses per female) and Eurasian wild boar (4–5 fetuses per female) litters across their distributions (Taylor *et al.*, 1998; Comer and Mayer, 2009). As a result, we might expect population growth and spread of wild pigs at the northern edge of their distribution in North America to be comparable to the rapid range expansion of wild pigs observed elsewhere, although regional variation in the number of litters/female/year and survival of neonates, juveniles, and adults, also affects population growth. The relationship between latitude and litter size of European wild boar in Europe (Bywater *et al.*, 2010) would predict, based on latitude, that the average litter size of wild pigs in our study would be 5.5–5.6 (*see* Fig. 1c in Bywater *et al.*, 2010), which is consistent with our findings.

We found a tendency toward a female bias in the fetal sex ratio of wild pigs in Saskatchewan, although our sample size was small. This finding is in contrast to the tendency toward a male bias in wild pigs across the rest of the distribution (reviewed by Comer and Mayer, 2009). Other studies have found that the sex ratio of wild pig litters tends to be independent of both resource availability (Fernández-Llario and Mateos-Quesada, 2005; Servanty *et al.*, 2007) and maternal condition (Fernández-Llario *et al.*, 1999).

Our study is admittedly based on a small sample of pregnant wild pigs. As such, we were unable to include covariates for age and study area; if there was an effect of either of these variables, pooling our data added noise. Litter size in wild pigs and Eurasian wild boar tend to vary with age of the mother (Gethöffer *et al.*, 2007, Comer and Mayer, 2009). We were unable to estimate age-specific litter sizes, but our estimates likely reflect averages across the population given the range of body weights that we observed for pregnant females. Our data suggest that wild pigs give birth between Feb. and May, but this timeframe is limited because our sample was collected in Feb. only; had we sampled wild pigs during other months, we may have found a wider range of parturition dates. Eurasian wild boar typically have one defined breeding season per year, whereas in most wild pig populations, females give birth in every month of the year, usually with one or two peaks (reviewed by Comer and Mayer, 2009). Although wild pigs are physiologically capable of producing >1 litter per year, this appears rare (Comer and Mayer, 2009), and our data do not allow us to assess the frequency of multiple litters in our study area. We also note the possibility that we were unable to detect pregnancy in females that were <30 d pregnant (Henry 1968a). Finally, in other parts of their distribution, female wild pigs breed at >24 kg (Dzięciołowski *et al.*, 1992; Servanty *et al.*, 2009). We found that breeding females weighed at least 46 kg, and it is possible that, with a larger sample, we could find that females that weigh <46 kg are also capable of breeding. Despite these limitations, our findings are a significant first step toward understanding the life history of a species that appears to be thriving much farther north in North America than models otherwise predict (McClure *et al.*, 2015; Snow *et al.*, 2017).

Future research on wild pigs in Canada should focus on refining local estimates of life history characteristics that can be used to model the efficacy of different management plans and help predict population growth and spread. Understanding the relative contribution of age-specific mortality and recruitment to population growth will help to identify the life history stages where management will be most effective (*e.g.*, Beiber and Ruf, 2005; Mellish *et al.*, 2014). A better understanding of the local timing of conception and birth peaks could ensure that culls occur before females give birth, as removal efforts are complicated by the presence of large numbers of young. As reproductive output in wild pigs tends to vary in response to resource availability (Servanty *et al.*, 2009; Gamelon *et al.*, 2017), a local understanding of how spatial and temporal resource pulses in a seasonal environment influence reproductive rate will inform local management plans: managers could increase control efforts prior to resource and resultant birth pulses (Keiter and Beasley, 2017). Knowledge of how population density influences local reproductive rate will also help to refine management plans; reduced density might be compensated for with increased recruitment and immigration in some wild pig populations (Hanson *et al.*, 2009). Management plans for wild pigs in Canada will also benefit from local estimates of survival rates for wild pigs in all age classes. Finally, hybridization of wild boar with domestic pigs leads to larger litter sizes (Fulgione *et al.*, 2016), and an understanding of the relative contribution of hybridization to population growth of wild pigs in Canada will be an important avenue of future research.

Effective eradication programs must remove individuals at a faster rate than they reproduce (Bomford and O'Brien, 1995). Accordingly, management plans for invasive species will benefit from local estimates of these life history traits. Our estimates of the number of fetuses, fetal sex ratio, and parturition dates of wild pigs in Saskatchewan are a first step toward modeling spatial and temporal population growth and the efficacy of potential management solutions. At present, we know little about wild pig populations in Canada. Their establishment on the Canadian prairies is relatively recent (Brook and van Beest, 2014), and thus we may have an opportunity to effectively manage the problem with science-based management initiatives. If the ultimate goal is the complete eradication of wild pigs on the Canadian landscape, then management efforts coordinated across provinces and aimed at removal of the entire social group is necessary. In the US, the wild pig population has increased dramatically in both abundance and distribution (Bevins *et al.*, 2014; Snow *et al.*, 2017), and is one of the most damaging introduced species in the country (Vitousek *et al.*, 1996; Pimentel *et al.*, 2005). Rapid response to new invasions is necessary for successful eradication (Robertson *et al.*, 2016; Keiter and Beasley, 2017), and our study is one of the first contributions toward a science-based management plan for wild pigs in Canada.

Acknowledgments.—Funding for this study was provided by the United States Animal and Plant Health Inspection Service National Feral Swine Damage Management Program (RKB), the University of Saskatchewan (RKB), the Saskatchewan Fish and Wildlife Development Fund (RKB), the Cyril Capling Trust Fund at the University of Saskatchewan (RKB), Memorial University (EVW), and the Natural Sciences and Engineering Research Council of Canada (ELK). This study would not have been possible without logistic support from R. Powers, B. Brickley, T. Caswell, T. Caswell, S. Adams, T. Bollinger, M. Zimmer, C. Letain, J. Fouhse, D. Aiken, and R. Gooding. Wild pig capture was conducted by our helicopter pilot and capture crew from Wildlife Capture Management including M. Reed, B. Matheson, S. Oakley, and fixed-wing pilot G. David from Mitchinson Flying Services. We thank E. H. Ellington for helpful discussions.

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SUBMITTED 10 AUGUST 2017 ACCEPTED 14 DECEMBER 2017

TABLE A1.—Pearson correlation coefficients of body size and body condition measurements from six pregnant wild pigs (*Sus scrofa*) sampled from two study areas in Saskatchewan, Canada

	Weight	Back fat[1]	Length[2]	Height[3]	Girth[4]
Weight					
Back fat	0.89				
Length	0.97	0.79			
Height	0.82	0.56	0.85		
Girth	0.96	0.78	0.98	0.87	

[1] We measured back fat thickness by making a 45° cut directly through the back fat layer on the rump at the base of the tail and measuring fat thickness at the deepest point along the cut, from the connective tissue above the muscle to the top of the fat against the skin

[2] Tip of nose to base of tail

[3] Front hoof to spine

[4] Chest girth

TABLE A2.—Axis loadings from a principal component (PC) analysis[1] of five variables describing body size of six pregnant wild pigs (*Sus scrofa*) from two study areas in Saskatchewan, Canada. We used the first PC axis as the dependent variable indexing body size and condition

Body size measurements[2]	PC 1	PC 2
Weight	0.99	0.10
Back fat	0.86	0.50
Length	0.98	-0.05
Height	0.88	-0.44
Chest girth	0.98	-0.07

[1] Eigenvalues for the first two PC axes were 4.41 and 0.46. PC1 explained 88% of the variation and PC2 explained 9% of the variation

[2] We measured back fat thickness by making a 45° cut directly through the back fat layer on the rump at the base of the tail and measuring fat thickness at the deepest point along the cut, from the connective tissue above the muscle to the top of the fat against the skin. We measured head-body length from the tip of the nose to the base of the tail. We measured shoulder height from the front hoof to the spine

TABLE A3.—Pearson correlation coefficients of body size and body condition measurements from 41 wild pigs (*Sus scrofa*)[1] sampled from two study areas in Saskatchewan, Canada

	Weight	Back fat[2]	Length[3]	Height[4]	Girth[5]
Weight					
Back fat	0.24				
Length	0.91	0.03			
Height	0.87	-0.04	0.83		
Girth	0.94	0.16	0.91	0.85	

[1] Pooled over sex and study area
[2] We measured back fat thickness by making a cut directly through the back fat layer on the rump at the base of the tail, parallel to the spine, and measured fat thickness at the deepest point along the cut, from the connective tissue above the muscle to the top of the fat against the skin
[3] Tip of nose to base of tail
[4] Front hoof to spine
[5] Chest girth

TABLE A4.—Axis loadings from a principal component (PC) analysis[1] of four variables describing body size of 29 wild pigs (*Sus scrofa*)[2] from two study areas in Saskatchewan, Canada. We used the first PC axis as the dependent variable indexing body size

Body size measurements[3]	PC 1	PC 2
Weight	0.97	-0.09
Length	0.95	-0.20
Height	0.93	0.36
Chest girth	0.98	-0.06

[1] Eigenvalues for the first two PC axes were 3.67 and 0.18
[2] Pooled over sex and study area
[3] We measured head-body length from the tip of the nose to the base of the tail and shoulder height from the front hoof to the spine