https://doi.org/10.17221/23/2017-CJAS

Placental Characteristics of German Landrace Sows and Their Relationships to Different Fertility Parameters

Andreas Vernunft[1]*, Melanie Maass[2], Klaus-Peter Brüssow[3]

[1]Institute for Reproductive Biology, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany

[2]Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

[3]Centre for Veterinary Sciences, Nicolaus Copernicus University in Torun, Torun, Poland

*Corresponding author: vernunft@fbn-dummerstorf.de

ABSTRACT

Vernunft A., Maass M., Brüssow K.-P. (2018): **Placental characteristics of German Landrace sows and their relationships to different fertility parameters**. Czech J. Anim. Sci., 63, 339–346.

The placenta is the central foetal organ that ensures a sufficient exchange of nutrients and metabolites for adequate foetal growth. Specific data profiles for placental characteristics from modern pig lines with high fertility and today's genetics are not currently available. This study focuses on describing the placental weight and size of German Landrace pigs and any subsequent relationship to litter number and important fertility parameters for these sows. As a basis for data collection, 55 litters from primi- and multiparous German Landrace sows with a total of 832 piglets were used. From these births, 766 placentas were recovered and weighed, with their lengths measured and the placental efficiency per litter also calculated. Mean placental weights ranged from 179 ± 60 to 422 ± 96 g between litters, and the mean length was between 61 ± 12 and 145 ± 19 cm. The placental efficiency was at a level of 5.1 ± 0.7. The investigated parameters were only slightly affected by the litter number ($r = 0.3$), and the means did not significantly differ between different litter numbers. With increasing litter size, the piglet weights and placental lengths were significantly decreased ($r = –0.4$ and $r = –0.3$), possibly due to limited uterine space. However, litter size had a strong positive correlation with the total litter placental weight ($r = 0.7$); therefore, in this study, the placental efficiency was not affected by a higher number of piglets per sow. Higher means for placental weights ($r = 0.7$) and lengths ($r = 0.7$) in a particular litter significantly improved the piglet birth weights. The reported variability in placental characteristics between litters suggests that there is an opportunity to selectively breed for improved piglet weight and homogeneity and thus improved piglet health and survival.

Keywords: pig; placenta; fecundity; placental efficiency; litter number; litter size

The reproductive performance of sows has continuously improved over the past few years due to specific breeding efforts (Waehner and Huehn 2016). By high fertility performance of the sows, the production costs for the piglets can be decreased in a sustainable manner. Therefore, breeders prioritize large litter sizes. In combination with retaining animal vitality, piglet production aims to yield high, homogeneous numbers of live born piglets and weaners with high vitalities that have homogeneous weights and performances after birth, weaning or rearing (Bruessow and Waehner 2008). However, there has been a negative correlation between high numbers of piglets per litter and mean piglet weights recognized in the field (Beaulieu et al. 2010), indicating that large

https://doi.org/10.17221/23/2017-CJAS

litter sizes lead to retarded and inhomogeneous offspring (Zhang et al. 2016). The accompanying reduction in vitality of the smaller piglets leads to a significant increase in piglet losses during the suckling and weaning periods (Rootvelt 2014; Zhang et al. 2016). Apart from the ethical problem of high piglet mortality, the positive economic effect of having large litters is lost.

With an increase in the number of offspring, the size of the sow's uterus is almost always unproportionally increased. Therefore, the available uterine space and surface provided to each foetus, as well as the uterine capacity, become limited with large litters (Wu et al. 1989; Bruessow and Waehner 2008). The central foetal organ which is necessary to ensure sufficient exchange of nutrients and metabolites from the mother to the offspring is the placenta. With optimal utilization of uterine capacity, well-developed placentas with high efficiencies can contribute to a sow's fecundity (Ford and Vonnahme 2002; Freking et al. 2007). An underdeveloped placenta during early pregnancy provokes reduced survivability and retarded growth of the foetuses (Knight et al. 1977; Johnson et al. 1999; Bruessow and Waehner 2008). Selective breeding for high placental efficiency has been reported to be possible in pigs and to support and enhance the vitality of the piglets (Wilson et al. 1999). However, placental characteristics, such as placental weight and area or placental efficiency, have only been described a few times for pigs in previous literature. Only older data are available, which were partially obtained using exotic pig breeds such as Meishan, or in Yorkshire pigs and other cross breeds with low fertility when compared to modern pig breeds (Biensen et al. 1998; Mesa et al. 2006, 2012). Specific data regarding placental weight or length in relation to the economically important Landrace breed, especially in lines with high fertility and today's genetics, are not currently available. Therefore, this study focuses on a novel and current description of the placental characteristics of German Landrace sows and any correlation with important sow fertility parameters and litter numbers.

MATERIAL AND METHODS

Animals. Measurements and data collection were taken in the Experimental Pig Unit of the Leibniz Institute for Farm Animal Biology (FBN) in Dummerstorf, Germany. As a basis for data collection, 55 litters from German Landrace sows (purebred) with a total of 832 piglets were used, with 766 placentas being recovered, measured, and analysed. The litters used for this study originated from 12 primiparous sows and 43 multiparous sows (2nd litter n = 12, 3rd litter n = 10, 4th litter n = 9, ≥ 5th litter n = 12). The sows were bred in groups after oestrus synchronization and fixed-time artificial insemination. Gilts were bred after reaching 220 days of life. They were synchronized by a daily oral administration of 16 mg of altrenogest (Regumate®; Boehringer Ingelheim International GmbH, Germany) for 15 days. Gilts received 850 IE of eCG (Pregmagon®; IDT Biologika, Germany) 24 h after the final altrenogest administration to stimulate the ovaries, and 80 h later, they were given 50 µg of gonadorelin (Gonavet®; Veyx-Pharma, Germany) to induce ovulation. Artificial insemination was performed 24 h and 38 h after ovulation induction. Multiparous sows were fixed-time inseminated after a 28-day suckling period with a synchronization protocol similar to the gilts, with the day of weaning being equivalent to the last day of altrenogest administration in the gilts. Insemination was carried out with sperm from different German Landrace boars at two boar stations. The average herd performance for the experimental pig facility between 2013 and 2016 reached 14.5 total piglets born, 13.5 live born and 0.9 stillborn piglets per litter under the described conditions.

During the study, the number of total born (TB), live born (LB), and stillborn (SB) piglets per litter, litter weights, and weights of the sows at 105 days of pregnancy were recorded. The numbers of live born and stillborn piglets as well as their birth weights were estimated directly after the sows completed farrowing. Only the piglets that died directly during farrowing were considered to be stillborn. The weights of the stillborn piglets were estimated and included in the analysis because their placentas were also included in the analysis, and the placentas belonged to the vital and alimented foetal tissue of the sow. Mummified foetuses were not considered in this study because they did not belong to the vital and alimented foetal tissue. Litter sizes and weights were calculated by summing live and stillborn piglets in a litter.

Estimation of placental characteristics. The collection of placentas occurred during and after

https://doi.org/10.17221/23/2017-CJAS

farrowing (day 115 of pregnancy) for each sow, regardless of the chronological order, until all of the farrowing was completed. The collected placentas from one litter were weighed, and their lengths were also measured. Preterm or late farrowing sows and sows with dystocia were excluded from the placenta collection, and in some cases, the placentas of a litter could not be completely collected due to being lost in the manure. If less than 70% of the placentas from a litter (number of total born piglets = 100%) could have been evaluated, the sow and litter were excluded from the study. Therefore, 43 sows out of the 98 farrowing sows had to be excluded from the analysis. Of the remaining 55 litters analysed, in 10 sows 10% of their placentas were not available for calculating the means of the litter, while 13 sows had up to 20% and 4 sows had up to 30% of their placentas not available.

Placental weight and placental efficiency. To measure placental weights and lengths, the placentas were spread out on a desk in a way that made the inner surface and umbilical cords visible for separating and proving their completeness. The estimations of placental weights were done using a commercial, calibrated, electronic scale approximated to the gram. The mean placental weight per litter was calculated from all of the available placentas of a litter. The calculation of the total litter placental weight (in kg) was done by summing all placental weights, and in the case of litters with missing placentas, the mean placental weight of that litter was added according to the number of missing placentas. Placental efficiency per litter was calculated by the ratio of the mean weight of the total born piglets and the mean placental weight of the litter (Wilson et al. 1999). Therefore, this parameter indicates how many grams of foetal tissue were supported by 1 g of placental tissue.

Placental length. The outer placental length was estimated in centimetres using a measuring tape. The separated placentas were spread out carefully on a metal desk to avoid erroneous data caused by tissue fissures and missing tissue parts, then visually examined for completeness. All placentas were arranged with the inner (foetal) surface on the outside and the umbilical cord in the middle to standardize the measurements. The estimation of the length of the demilune organ was performed along the major curve, which is opposite to the base of the umbilical cord (Figure 1). Only the length of the chorion bearing tissue was measured, with dead or non-functional tissue parts at the ends of the placenta being excluded. Mean placental lengths were calculated per litter using the measured data of all available placentas from a litter.

Statistical analysis. For data analysis, a descriptive statistic was made with IBM SPSS Statistics (Version 22) by International Business Machines Corporation (IBM) for all numbers, means, standard deviations, variances, minima, and maxima. Normality of the data was tested using the nonparametric Kolmogorov-Smirnov test. For dependent parameters, a one-way analysis of variance (ANOVA) was performed, and significant differences between groups were tested with a Tukey test or Tukey-Kramer test depending on the litter number. Correlation coefficients between studied parameters were calculated with a Spearman correlation analysis using SPSS Statistics (Version 22). Additionally, a linear regression was computed between the parameters piglet weight, number of total born piglets and placental weight, length and efficiency. Graphs were created using SigmaPlot 11.0 (Systat Software GmbH). If not otherwise stated, results are presented as means with their standard deviation. Differences between means and correlation coefficients were considered as significant if the *P*-value was below 0.05.

RESULTS AND DISCUSSION

The observed general fertility performance during the study was 15.1 total born, 14.0 live born, and 1.2 stillborn piglets per litter (Table 1). This

Figure 1. Representative picture of different sized porcine placentas of one litter; the line demonstrates the measurement of placental length (from **A** to **B**)

https://doi.org/10.17221/23/2017-CJAS

Table 1. Overview of recorded placental and fertility parameters (sample size, means, standard deviations (SD), minima, and maxima). Placental weights, lengths, and efficiencies minima and maxima are shown as means per sow

	n	Mean	SD	Minimum	Maximum
Litter weight (kg)	55	20.8	0.6	12.34	30.26
Piglet weight (kg)	832	1.40	0.23	0.87	2.07
Total number born	832	15.1	3.5	7	21
Live born	780	14.0	3.3	7	21
Stillborn	52	1.2	1.4	0	5
Placental characteristics					
Litter placental weight (kg)	55	4.13	1.11	1.95	6.84
Placental weight (g)	776	276.8	54.1	179	422
Placental length (cm)	776	88.4	15.1	61	145
Placental efficiency	55	5.14	0.78	3.82	7.51

was slightly higher but comparable to the average performance observed in the herd for three previous years (14.5 TB; 13.5 LB; 0.9 SB). These results are also similar to other reports for German Landrace purebred herds (de Jong et al. 2013). Therefore Landrace sows can be considered to be fertility oriented lines of pigs. The sows from this study showed their highest fertility potential in their third litter with 17.5 TB (Table 2). The mean placental weight was 276.8 ± 54 g, and the mean placental length was 88.4 ± 15.1 cm, which was close to results reported for Yorkshire sows (Biensen et al. 1998; Wilson et al. 1999; Mesa et al. 2006). The average litter placental weight was 4.13 ± 1.1 kg (total placental mass of a litter), which was comparable to other studies that reported litter placental weights between 3.2 and 4.3 kg (Nobelet et al. 1985; Dourmad et al. 1999; Borges et al. 2005). However, in the mentioned studies (published more than ten years ago) litter sizes were much lower, with only approximately 11 born piglets. It is interesting to note that these placental characteristics remained comparable to those of the modern, highly fertile Landrace sows with much more piglets. In Table 1, the minimum and maximum means of the investigated litters are presented. Notably, the mean placental weights between litters of different sows can range from 179 to 422 g and mean lengths from 61 to 145 cm. These extremes must be interpreted along with the number of piglets in the litters (correlations shown in Table 3), but the data seem to indicate that sows can be distinguished by and selected for based on placental characteristics, as has occurred

Table 2. Number (*n*) of analysed sows, placentas, piglets, and the corresponding fertility and placental parameters dependent on litter number

Number of litter	1	2	3	4	≥ 5
Sows (*n*)	12	12	10	9	12
Placentas (*n*)	147	183	145	125	148
piglets (*n*)	166	191	175	134	166
Total born (*n*)	13.8 ± 2.8	15.9 ± 2.9	17.5 ± 2.0	14.9 ± 4.1	13.8 ± 4.2
Stillborn (*n*)	1.1 ± 1.6	0.8 ± 1.2	1.3 ± 1.3	1.8 ± 1.8	1.0 ± 1.1
Piglet weight (kg)	1.26 ± 0.23	1.41 ± 0.23	1.40 ± 0.14	1.44 ± 0.19	1.51 ± 0.23
Litter weight (kg)	17.01 ± 3.0^{a}	22.09 ± 3.6^{b}	24.42 ± 3.3^{b}	21.03 ± 4.9	20.23 ± 5.3
Placental weight (g)	242 ± 42	279 ± 64	282 ± 33	279 ± 47	304 ± 62
Placental length (cm)	82.4 ± 13.7	85.3 ± 9.2	85.5 ± 9.6	94.4 ± 15.0	95.3 ± 21.8
Litter placental weight (kg)	3.3 ± 0.7^{a}	4.3 ± 1.1	4.9 ± 0.8^{b}	4.2 ± 1.5	4.00 ± 0.9
Placental efficiency	5.26 ± 0.8	5.19 ± 0.9	4.99 ± 0.5	5.27 ± 0.9	5.01 ± 0.7

a : b = $P < 0.05$

https://doi.org/10.17221/23/2017-CJAS

in other studies (Wilson et al. 1999; Freking et al. 2007). The ratio of piglet weight to placental weight is defined as placental efficiency (Wilson et al. 1999). The mean placental efficiency was 5.1 ± 0.7, which is considered to be a median level of placental efficiency. The range of placental efficiency of the investigated litters was from 3.8 to 7.5 in the current study and was comparable to other reports (Wilson et al. 1999; Vallet et al. 2002; Mesa et al. 2006, 2012). Placental efficiency, however, summarizes the impact of many factors that can influence the weights of piglets and placentas. Nonetheless, the selection for placental efficiency can be successful for increasing sow fertility and piglet vitality (Wilson et al. 1999; Fort et al. 2002; Freking et al. 2007). Similar to what was reported by Vallet et al. (2002), in the current study significant negative correlations for placental efficiency were seen with the placental weight (r = –58) and litter placental weight (r = –0.53) (Table 3). This correlation gives the growth of the placental tissue more importance than other factors for realizing good fertility performance due to appropriate placental functions. Despite no differences observed between placental efficiency and the litter number, fertility performance and other placental characteristics differed between the different investigated litter numbers (Tables 2, 3). Litter number was slightly positively correlated with piglet weight (r = 0.32), placental weight (r = 0.31), and placental length (r = 0.27). Sows had the most piglets in their third litter, which resulted in the highest litter weights (significantly higher compared to the first litters). This is contrary to a previous belief that assumes that fertility performance increases up until the fifth litter. It is notable that the sows from the third litter also had the highest litter placental weights. This indicates that sows with most piglets in the current study have not reached the point when the total placental weight becomes reduced due to limited space in the uterus. For large litters, the uterus has to grow proportionally to provide at least 36 cm of uterus per foetus (Wu et al. 1989). If there are more than 14 piglets, the growth of the uterus is no longer proportional, and the uterine space can become critically limited (Fischer et al. 2011). The current study suggests that this limit may be more important for placental length than

Table 3. Correlation coefficients and P-values between studied parameters

	PW	Pl W	Pl L	PE	LPl W	LW	TB	LB	SB	SW
NL	**0.32** 0.018	**0.31** 0.021	**0.27** 0.049	–0.13 0.360	0.22 0.109	0.20 0.146	0.04 0.772	–0.02 0.873	0.08 0.558	**0.86** ≤ 0.001
PW	1	**0.66** ≤ 0.001	**0.67** ≤ 0.001	0.19 0.169	0.06 0.693	**0.28** 0.041	**–0.37** 0.006	**–0.32** 0.017	–0.16 0.245	0.21 0.129
Pl W		1	**0.70** ≤ 0.001	**–0.58** ≤ 0.001	**0.47** ≤ 0.001	**0.28** 0.038	–0.14 0.298	–0.19 0.171	0.04 0.756	**0.29** 0.032
Pl L			1	–0.19 0.176	0.12 0.383	0.10 0.451	**–0.30** 0.024	**–0.28** 0.038	–0.13 0.358	**0.21** 0.032
PE				1	**–0.53** ≤ 0.001	–0.06 0.684	–0.22 0.11	–0.13 0.331	–0.16 0.248	–0.20 0.128
LPl W					1	**0.83** ≤ 0.001	**0.73** ≤ 0.001	**0.69** ≤ 0.001	0.08 0.542	**0.34** 0.012
LW						1	**0.74** ≤ 0.001	**0.66** ≤ 0.001	0.20 0.149	**0.28** 0.036
TB							1	**0.89** ≤ 0.001	0.18 0.184	0.15 0.281
LB								1	–0.21 0.124	0.05 0.707
SB									1	0.25 0.072

NL = number of litter, PW = piglet weight, Pl W = placental weight, Pl L = placental length, PE = placental efficiency, LPl W = litter placental weight, LW = litter weight, TB = total number born, LB = live born, SB = stillborn, SW = sow weight on pregnancy day 105
significant correlation coefficients are shown in bold

https://doi.org/10.17221/23/2017-CJAS

for placental weight. The correlations shown in Table 3 support the theory that while the number of total or live born piglets (TB, LB) is significantly negatively correlated to the piglet weight (PW) and placental length (PL), the placental weight is not affected. Moreover, litter placental weight and litter weight increase simultaneously with TB (r = 0.73 and r = 0.7) and LB (r = 0.69 and r = 0.66). Therefore, the placental efficiency remains at the same level, independent of litter size or litter number (Tables 2 and 3). However, having a higher placental efficiency in large litters would be desirable for decreasing the negative effects that high piglet numbers may have on piglet weight (Knight et al. 1977; Johnson et al. 1999; Bruessow and Waehner 2008). This study demonstrates that sows with many piglets and reduced placental lengths can rescue placental function and efficiency, partly due to adequate placental weight, as demonstrated in Figure 2. High piglet weights are accompanied by high placental weight (Figure 2A), and high numbers of piglets coincide with shorter placentas (Figure 2B). However, since placental weight did not decrease with higher piglet numbers to the same degree as with placental length, the functions of small placentas can be improved due to higher efficiency (Figure 2C). This indicates that a high placental weight is mostly accompanied by but not always necessary for an adequate piglet weight, as is seen in the case of high placental efficiency. This was also observed in Yorkshire sows (Biensen et al. 1998; Vallet and Freking 2006, 2007). Biensen et al. (1998) reported that Yorkshire sows with relatively low litter sizes had heavy piglets with large placentas, whereas Meishan sows had higher litter sizes with lighter piglets and smaller placentas. Meishan sows have a more intensive vascularization in their smaller placentas, and therefore, they can realize the nutrition of the foetuses with a higher placental efficiency (Biensen et al. 1999; Vonnahme and Ford 2003). This was also observed when Meishan and Yorkshire embryos were implanted together into a Yorkshire sow (Wilson et al. 1998).

Reduction of placental size with a simultaneous increase in piglet number shows a high variability (Figure 2B). In this study, there was a high level of variability in placental sizes between litters and also within litters, as demonstrated in Figure 1. The standard deviations of the placental weights were significantly positively correlated to the litter number (r = 0.32), placental weight (r = 0.5), pla-

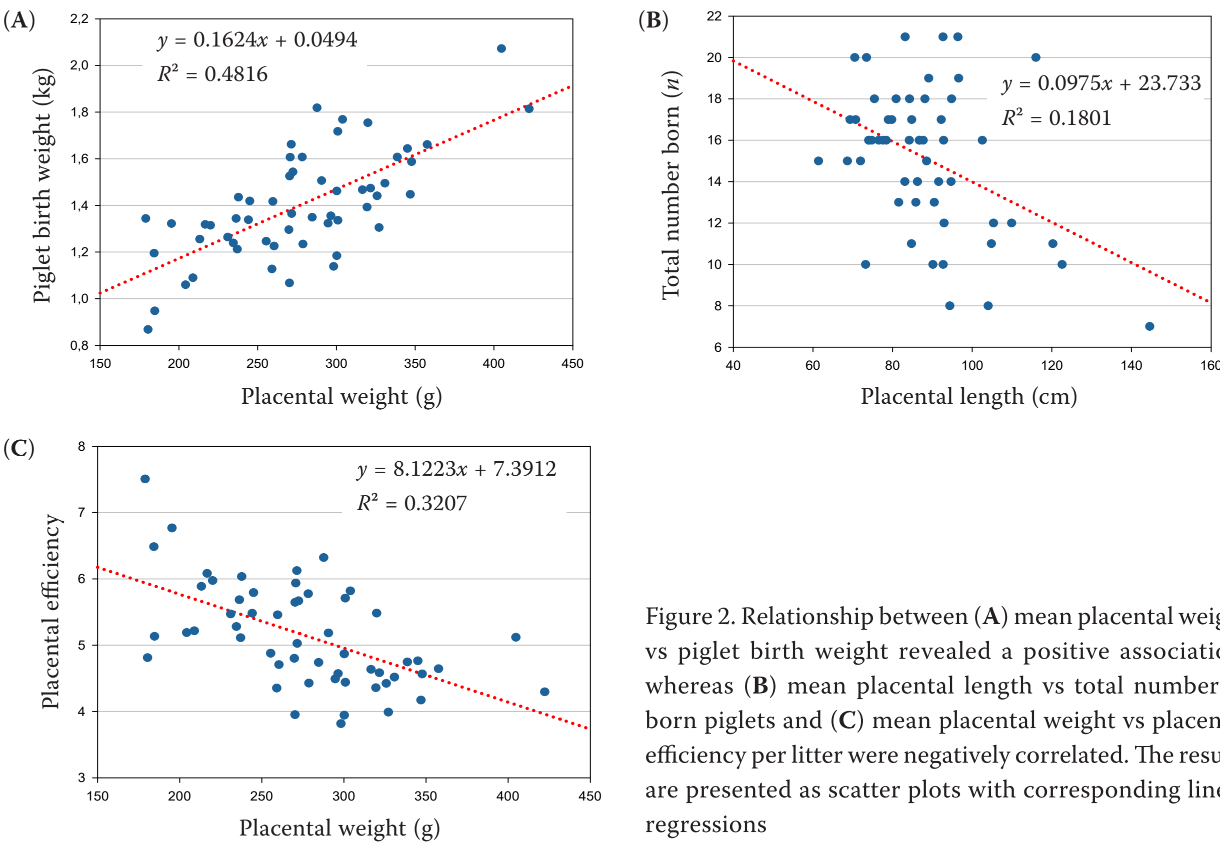

Figure 2. Relationship between (**A**) mean placental weight vs piglet birth weight revealed a positive association, whereas (**B**) mean placental length vs total number of born piglets and (**C**) mean placental weight vs placental efficiency per litter were negatively correlated. The results are presented as scatter plots with corresponding linear regressions

https://doi.org/10.17221/23/2017-CJAS

cental length (r = 0.34), and litter placental weight (r = 0.27), but negatively correlated with placental efficiency (r = –0.4). Moreover, the standard deviation for the piglet weight was significantly positively correlated with the standard deviation for the placental weight (r = 0.57) and placental length (r = 0.37; data not presented). Therefore, inhomogeneity of piglets, known to increase with larger litter sizes and older sows (Zhang et al. 2016), is reflected by the inhomogeneity (higher standard deviations) of the placentas in this study. This is in accordance with reports made by Vallet et al. (2002) and Mesa et al. (2006) who demonstrated a strong relationship between individual piglet size and its placental size. Contrary to the above situation, the opposite effect of having a non-limited uterine space was observed in the sows with five or more litters from this study (Table 2). With increasing litter numbers, the body weight of the sows increased significantly (r = 0.86) (Table 3), and with increasing body weight, the length of the uterus increased as well (Tummaruk and Kesdangsakonwut 2014). Sows with five or more litters had on average the highest placental weight and length, and when they had unaffected placental efficiency, they also had the heaviest piglets; however, they had also a lower number of total piglets born (Table 2). Although differences were not significant between the means of these characteristics in older sows and the means of lower litter numbers (Table 2), piglet weight, placental weight, and placental length were significantly positively correlated with the number of litters (Table 3). Additionally, placental weight and length is significantly positively correlated with sow weight (correlation coefficients approximately 0.3; Table 3), but not with placental efficiency. This indicates that the space that is provided in the larger uterus of the older sows can support the growth of the foetus with a better blood and nutrient supply (Pere and Etienne 2000), and the foetus can fully realize its placental growth potential (Mesa et al. 2012).

Improving piglet birth weight for a better level of offspring health and vitality (and sow fertility performance) may be possible with two different breeding strategies. Greater placental length can improve piglet birth weight (r = 0.67), or on the other hand a higher placental weight (r = 0.66) (Table 3). For the first breeding strategy, sows will be selected for high growth levels of uterine length during pregnancy to increase the uterine space and capacity for placental growth (Fischer et al. 2011; Freking et al. 2016). For the second strategy, sows with short, heavy placentas will be selected (Mesa et al. 2012) to ensure foetal nutrition. Although placental efficiency was not directly dependent on the current fertility parameters of one investgated litter of a sow in this study, placental efficiency could be genetically determined, as suggested by Biensen et al. (1999). Therefore, the additional selection for placental efficiency could improve both of the described breeding strategies (Wilson et al. 1999), but this seems to be difficult in Western pig breeds (Mesa et al. 2012). To better utilize placental improvement in breeding strategies, the genetic backgrounds and genetic correlations of these traits require further investigation.

CONCLUSION

This study provides current and novel data regarding the placental characteristics of modern, fertility-oriented Landrace sows. Means of placental weights, lengths, and the placental efficiency of a litter were not significantly different between litter numbers and were still comparable to published data from other pig breeds. This study shows that with an increased litter size, piglet weight and placental length decrease, possibly due to limited uterine space. However, litter size was strongly positively correlated with the total litter placental weight, and therefore, placental efficiency was not affected by the high fertility of the sows in this study. High means for placental weights and lengths in a litter improved the piglet birth weight. The variability in placental characteristics between litters may offer an opportunity to develop a breeding selection strategy.

REFERENCES

Beaulieu A.D., Aalhus J.L., Williams N.H., Patience J.F. (2010): Impact of piglet birth weight, birth order, and litter size on subsequent growth performance, carcass quality, muscle composition, and eating quality of pork. Journal of Animal Science, 88, 2767–2778.

Biensen N.J., Wilson M.E., Ford S.P. (1998): The impact of either a Meishan or Yorkshire uterus on Meishan or Yorkshire fetal and placental development to days 70, 90, and 110 of gestation. Journal of Animal Science, 76, 2169–2176.

https://doi.org/10.17221/23/2017-CJAS

Biensen N.J., Wilson M.E., Ford S.P. (1999): The impacts of uterine environment and fetal genotype on conceptus size and placental vascularity during late gestation in pigs. Journal of Animal Science, 77, 954–959.

Borges V.F., Bernardi M.L., Bortolozzo F.P., Wentz I. (2005): Risk factors for stillbirth and foetal mummification in four Brazilian swine herds. Preventive Veterinary Medicine, 70, 165–176.

Bruessow K.-P., Waehner M. (2008): Biological potentials of fecundity of sows. Zuchtungskunde, 80, 370–377. (in German)

de Jong E., Kauffold J., Engl S., Jourquin J., Maes D. (2013): Effect of a GnRH analogue (Maprelin) on the reproductive performance of gilts and sows. Theriogenology, 80, 870–877.

Dourmad J.-Y., Noblet J., Pere M.C., Etienne M. (1999): Mating, pregnancy and prenatal growth. In: Kyriazakis I. (ed.): A Quantitative Biology of the Pig. CABI Publishing, Wallingford, UK, 129–151.

Fischer K., Brussow K.P., Schlegel H., Wahner M. (2011): Cluster analysis as a tool to assess litter size in conjunction with the amount of embryonic and fetal losses in pigs. Biotechnology in Animal Husbandry, 27, 785–790.

Ford S.P., Vonnahme K.A., Wilson M.E. (2002): Uterine capacity in the pig reflects a combination of uterine environment and conceptus genotype effects. Journal of Animal Science, 80, E66–E73.

Freking B.A., Leymaster J.L., Vallet J.L., Christenson R.K. (2007): Number of fetuses and conceptus growth throughout gestation in lines of pigs selected for ovulation rate or uterine capacity. Journal of Animal Science, 85, 2093–2103.

Freking B.A., Lents C.A., Vallet J.L. (2016): Selection for uterine capacity improves lifetime productivity of sows. Animal Reproduction Science, 167, 16–21.

Johnson R.K., Nielsen M.K., Casey D.S. (1999): Responses in ovulation rate, embryo survival and litter traits in swine to 14 generations of selection to increase litter size. Journal of Animal Science, 77, 541–557.

Knight J.W., Bazer F.W., Thatcher W.W., Franke D.E., Wallace H.D. (1977): Conceptus development in intact and unilaterally hysterectomized-ovariectomized gilts: interrelations among hormonal status, placental development, fetal fluids and fetal growth. Journal of Animal Science, 44, 620–637.

Mesa H., Safranski T.J., Cammack K.M., Weaber R.L., Lamberson W.R. (2006): Genetic and phenotypic relationships of farrowing and weaning survival to birth and placental weights in pigs. Journal of Animal Science, 84, 32–40.

Mesa H., Cammack K.M., Safranski T.J., Green J.A., Lamberson W.R. (2012): Selection for placental efficiency in swine: conceptus development. Journal of Animal Science, 90, 4217–4222.

Noblet J., Closet W.H., Heavens R.P. (1985): Studies on the energy metabolism of the pregnant sow. 1. Uterus and mammary tissue development. British Journal of Nutrition, 53, 251–265.

Pere M.C., Etienne M. (2000): Uterine blood flow in sows: effects of pregnancy stage and litter size. Reproduction Nutrition Development, 40, 369–382.

Rootwelt V., Reksen O., Farstad W., Framstad T. (2014): Postpartum deaths: piglet, placental, and umbilical characteristics. Journal of Animal Science, 91, 2647–2656.

Tummaruk P., Kesdangsakonwut S. (2014): Uterine size in replacement gilts associated with age, body weight, growth rate, and reproductive status. Czech Journal of Animal Science, 59, 511–518.

Vallet J.L., Freking B.A. (2006): Changes in fetal organ weights during gestation after selection for ovulation rate and uterine capacity in swine. Journal of Animal Science, 84, 2338–2345.

Vallet J.L., Klemcke H.G., Christenson R.K. (2002): Interrelationships among conceptus size, uterine protein secretion, fetal erythropoiesis, and uterine capacity. Journal of Animal Science, 80, 729–737.

Vonnahme K.A., Ford S.P. (2003): Selection for above-average placental efficiency increased placental expression of the vascular endothelial growth factor (VEGF) receptor system in pigs. Biology of Reproduction, 68 (Suppl. 1), 205.

Waehner M., Huehn U. (2016): 80 years periodic farrowing systems in piglet production in Germany – A review: 1. Production systems for group farrowing from 1990 to present time. Zuchtungskunde, 88, 353–370.

Wilson M.E., Biensen N.J., Youngs C.R., Ford S.P. (1998): Development of Meishan and Yorkshire littermate conceptuses in either a Meishan or Yorkshire uterine environment to day 90 of gestation and to term. Biology of Reproduction, 58, 905–910.

Wilson M.E., Biensen N., Ford S.P. (1999): Novel insight into the control of litter size in pigs using placental efficiency as a selection tool. Journal of Animal Science, 77, 1654–1658.

Wu M.C., Chen Z.Y., Jarrell V.L., Dziuk P.J. (1989): Effect of initial length of uterus per embryo on fetal survival and development in the pig. Journal of Animal Science, 67, 1767–1772.

Zhang T., Wang L.-G., Shi H.-B., Yan H., Zhang L.-C., Liu X., Pu L., Liang J., Zhang Y.-B., Zhao K.-B., Wang L.-X. (2016): Heritabilities and genetic and phenotypic correlations of litter uniformity and litter size in Large White sows. Journal of Integrative Agriculture, 15, 848–854.

Received: 2017–03–10
Accepted after corrections: 2018–06–29