Genetic parameters for reproductive traits at different parities in Large White pigs

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ABSTRACT: Univariate or bivariate animal models were used to estimate the variance components and co-variance components for eight reproductive traits: total number born (TNB), number born alive (NBA), total litter weight of piglets born alive (BALWT), number of healthy births (NHB), number of weak births (NWB), number of deformed fetuses (NDF), number of stillborn (NSB), and number of mummified pigs (MUMM). In addition, the phenotypic and genetic correlations between traits at different parities were also estimated. The results showed that the heritabilities of the eight reproductive traits were lower than 0.10. Genetic correlations between NHB and TNB, NBA, or BALWT were 0.68, 0.84 and 0.89 respectively; whereas genetic correlations between NHB and NWB, NDF, NSB or MUMM were negative or close to 0, ranging from -0.28 to 0.13. NHB was relatively identified as an ideal informative trait for selection for improved reproduction. Furthermore, genetic correlations between different parities for all traits, except for NDF were strongly positive, showing that it was reasonable to consider different parities as the same trait. For NDF, genetic correlations between the first and the other parities were low, indicating that it was probably unreasonable to cull pigs according to the NDF at first parity. Optimum reproductive traits were observed at the third parity, and reinforcing the management of sows in the first and > 4 parities can be a practical method for improving reproductive traits.

Key words: genetic correlation, heritability, Large White pig, parity, reproductive trait

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INTRODUCTION

The reproductive traits of pigs have low heritability of approximately 0.10 (Holm et al., 2004; Crovetti et al., 2010; Lee et al., 2015), which is influenced by various factors, including breed, parity, and environment (Leite et al., 2011; Knecht et al., 2015). In China, a majority of Great-grand parents (**GGP**) groups of pure breed pigs (Duroc, Large White, and Landrace) originated from abroad, including Canada, America, and Denmark. Both joint breeding programs and major companies play an important role in pig

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breeding in China. For Large White pigs, selection is based mainly on reproductive traits. Breeders want to obtain higher total number born (**TNB**) and number born alive (**NBA**), while striving to reduce the number of stillborn (**NSB**) and number of mummified pigs (**MUMM**). Meanwhile, genetic parameters are specific for different populations (**Darfour-Oduro et al.**, 2009). In this regard, estimates of heritability and genetic correlations are essential for breeders to analyze the variability of these traits in China.

In this study, heritability was estimated for TNB, NBA, litter weight of piglets born alive (**BALWT**), number of healthy births (**NHB**), number of weak births (**NWB**), number of deformed fetuses (**NDF**), NSB, and MUMM in a specific Large White population using a univariate Ye et al.

repeatability model. Genetic correlations between different traits were estimated using a bivariate repeatability model. In addition, phenotypic and genetic differences between different parities were also estimated.

MATERIALS AND METHODS

The population used for the present study is from a Large White GGP pig farm managed by Guangdong Wens Foodstuffs Group Co., Ltd. The base population for this farm comprised approximately 600 Large White pigs which were imported from France in 2010. Currently, the core group of this farm is approximately 620 sows, with an additional 800 or more sows in a propagation population. The traits incorporated in the selection index were TNB, NHB, AGE (age at 100 kg live weight) and BF (backfat at 100 kg live weight). The sows are selected in three stages: within 24 h of birth, and at weight 25 kg and 100 kg. Individuals showing genetic defects were immediately eliminated. The selection intensity of breeding sows is 10% and the replacement rate is about 60%. Furthermore, the pigs were also selected using a combination of body condition score and single maker-assisted selection (MAS).

Data Description

Phenotypic records on a total of 14,097 sows and 40,262 litters. Data was recorded at a central test station for a period of 6 yr (2011 to 2017). The traits used for analysis in the present study were TNB, NBA, BALWT, NHB, NWB, NDF, NSB, and MUMM. Notably, TNB includes all piglets both alive and dead. NHB indicates the number of piglets for which birth weight is over 1 kg, whereas NWB indicates those with birth weight below 1 kg. Number born alive is the sum of NHB and NWB. The summary statistics for these traits are shown in Table 1.

Table 1. Summary statistics for the studies reproductive traits (n = 40,262)

Trait	Mean	SD	Min	Max	Skew	Kurtosis
TNB	13.84	3.56	1	29	-0.37	0.52
NBA	12.22	3.63	0	27	-0.66	0.99
BALWT	14.95	4.79	0	37.2	-0.26	0.51
NHB	10.35	3.15	0	23	-0.80	1.24
NWB	1.64	1.74	0	18	1.54	3.75
NDF	0.23	0.61	0	13	4.27	34.96
NSB	1.19	1.79	0	21	3.15	16.39
MUMM	0.43	1.00	0	23	5.71	62.11

Variance Component Estimation

A univariate animal model was fitted to each trait using the BLUPF90 (AI-REML) software package to estimate the variance components. A bivariate animal model was used to estimate covariance components for calculating genetic correlations. The models used were as follows:

$$Y = Xb + Za + Wpe + e,$$

where, Y is the vector of observations, b is the vector of fixed effects (included the effects of parity and herd-year-month), a and pe are vectors of unknown additive genetic and permanent environment effects, e is a vector of residuals, and X, Z, and W are incidence matrices for the fixed, additive genetic, and permanent environmental effects, respectively.

RESULTS AND DISCUSSION

Basic Statistics

The descriptive statistics of the study population are shown in Table 1. The mean of TNB was 13.84 (±3.56 SD), which represents the sum of NHB, NWB, NDF, NSB, and MUMM. The proportions of NDF, NSB, and MUMM contributing to TNB were 1.67%, 8.60%, and 3.11%, respectively. The effects of parity and herd-year-month (h-y-m) are all highly significant (P < 0.01).

The Effect of Parity

The mean and significance of the examined reproductive traits at different parities are shown in Table 2. The results show that the best performance in terms of TNB, NBA, BALWT, and NHB is 14.19, 12.82, 16.21, and 10.87 at third parity and that these values are significantly different (P < 0.05) from those at other parities. The values for other traits (NWB, NDF, NSB, and MUMM) were lower at third parity, and highest at either the first or fifth parity.

The effect of parity on reproductive traits is not clear. Takai and Koketsu (2008) considered that the performance of sows was best at the first or second parity; however, some researchers have confirmed that the sows will be more productive at or beyond third parity (Hoving et al., 2011; Knecht et al., 2015). From a comparing the TNB and NSB for different parities of Duroc, Large White, Landrace, and Meishan pigs, Meishans were found to have lower NSB scores and showed little fluctuation,

Parity	n	TNB	NBA	BALWT	NHB	NWB	NDF	NSB	MUMM
1	13,341	13.81 ^{c,*}	12.10 ^c	14.23 ^d	10.25°	1.60 ^b	0.25ª	1.25ª	0.47ª
2	8,840	13.70°	12.29ь	15.41 ^b	10.57 ^b	1.50°	0.22 ^b	1.05°	0.37 ^b
3	6,312	14.19 ^a	12.82 ^a	16.21 ^a	10.87^{a}	1.70^{a}	0.24ª	0.99°	0.38 ^b
4	4,657	14.06 ^b	12.45 ^b	15.53 ^b	10.42 ^b	1.79ª	0.23ª	1.17 ^b	0.44 ^a
5	3,337	13.85 ^b	12.10 ^c	14.98°	10.09°	1.79 ^a	0.21 ^b	1.29 ^a	0.46 ^a

Table 2. The effect of parity on reproductive performance traits

*The superscript letters a, b, c, d in the same row signify statistical differences between parities, at P < 0.05.

whereas in western breeds, NSB initially decreases and subsequently increases across parities (Canario et al., 2006). In the present study, we found that performance is best at third parity, and accordingly suggest that the management and feed design should be different for other parities. Shannon (2011) found that sows at first parity ration with more than 10%–15% protein to satisfy their own growth and development requirements, and that sows of higher parity also need more energy for maintenance. In order to obtain more weaning piglets, we accordingly need more refinement of the management of piglets born at first and > 4 parities.

Phenotypic and Genetic Correlations at Different Parities

Tables 3 and 4 show the phenotypic and genetic correlations between parities for TNB and NDF, respectively. TNB has a strong positive genetic correlation ($0.50\sim0.99$) between different parities. With the exception of NDF, the correlations for other traits showed a similar pattern (Supplementary Appendices 1 to 6). For NDF, the genetic correlations between first parity and the other parities were between -0.07 and 0.17, whereas if the first parity was excluded, the genetic correlations were between 0.19 and 0.71.

Roehe and Kennedy (1995) estimated the phenotypic and genetic correlation between parities 1 to 4 for the TNB and NBA of Large White and Landrace breeds, and showed that for Large White pigs, the genetic correlation was between 0.589 and 1.000, whereas for Landrace the value was between 0.782 and 0.998, which are similar to the values obtained in the present study. Similarly, the genetic correlations for TNB, NBA, and NSB at different parities in a Dutch Large White population were also comparable to those obtained in the present study (Ehat et al., 2001); however, there have been limited reports of correlations for other reproductive traits. Analyses performed in the present study indicate that although there is only a moderate correlation between the first and other parities in NDF, there are strong correlations between parities 2 to 5, inadvisable to select sows according to after only one parity.

Variance Components and Genetic Parameters

The phenotypic, additive genetic, permanent environmental, and residual variances for eight selected reproductive traits are shown in Table 5. The heritabilities for the traits TNB, NBA, BALWT, NHB, NWB, NDF, NSB, MUMM were 0.07, 0.06, 0.06, 0.05, 0.07, 0.01, 0.05, 0.01 respectively, the repeatabilities were 0.17, 0.14, 0.16, 0.14, 0.12, 0.03, 0.09, 0.03 respectively, indicating that they are all low-heritability traits and repeatability is variable from different traits.

Numerous studies have provided estimates for the heritability of TNB, with values ranging between 0.02 and 0.11 (Imboonta et al., 2007; Lundgren et al., 2010). Strange et al. (2013) estimated the heritabilities of NWB and NSB to be 0.09 and 0.08 respectively, whereas Shen (2012) estimated the heritabilities of NDF and MUMM for different breeds, which were found to be in the range 0.01~0.02. Thus, the range of heritabilities of all reproductive traits determined in the present

Table 3. Correlations^a between the total number of piglets born at different parities

Parity	1	2	3	4	5
1		0.09 ± 0.02	0.12 ± 0.02	0.08 ± 0.02	0.08 ± 0.02
2	0.63 ± 0.23		0.12 ± 0.02	0.13 ± 0.02	0.11 ± 0.02
3	0.50 ± 0.21	0.99 ± 0.16		0.15 ± 0.02	0.15 ± 0.02
4	0.74 ± 0.20	0.81 ± 0.22	0.88 ± 0.18		0.15 ± 0.02
5	0.66 ± 0.26	0.72 ± 0.23	0.62 ± 0.20	0.95 ± 0.20	

^aEstimation of genetic correlation below the diagonal and phenotypic correlation above the diagonal.

study (0.01~0.07) is reasonably consistent with the values presented in previous studies.

The phenotypic and genetic correlations for the eight reproductive traits are shown in Table 6. For TNB, NBA, BALWT, and NHB, for which we want to select high phenotypic values, the ranges of phenotypic and genetic correlations were 0.68~0.89 and 0.50~0.89. In the case of NWB, NDF, NSB, and MUMM, for which lower performance value are preferable, the phenotypic correlations were close to 0. Although the genetic correlation between NDF and MUMM was 0.50, the correlations between other traits were also close to 0. In this study, strong positive correlations we found between both TNB and NBA and NWB, whereas the correlations between both BALWT and NHB with NWB were weak. However, there was a moderately positive correlation between BALWT and NDF. Notably, we detected strong positive genetic correlations between NHB and "positive traits," whereas the correlations between NHB and "negative traits" were weak. Accordingly, NHB can be considered an ideal trait for reproductive trait selection.

Numerous studies have provided estimates for the genetic correlation between TNB and NBA, with values ranging between 0.88 and 0.98 (Oh et al., 2006; Lee et al., 2015; Zhang et al., 2000), whereas Ehat et al. (2001) estimated that the correlation between TNB and NSB was between 0.29 and 0.50. These findings are consistent with the results obtained in the present study. Strange et al. (2013) showed that the genetic correlation between NWB and NSB was 0.35 and 0.16 when using a sire model and dam model, respectively. These values are slightly higher than those obtained in the present

Table 4. Correlations^a between the number of deformed fetuses at different parities

Parity	1	2	3	4	5
1		0.03 ± 0.02	0.04 ± 0.02	0.01 ± 0.02	0.03 ± 0.02
2	0.06 ± 0.14		-0.01 ± 0.02	0.04 ± 0.02	0.02 ± 0.02
3	-0.07 ± 0.12	0.38 ± 0.10		0.05 ± 0.02	0.04 ± 0.02
4	0.17 ± 0.13	0.61 ± 0.09	0.19 ± 1.49		0.05 ± 0.02
5	0.02 ± 0.13	0.60 ± 0.09	0.71 ± 0.08	0.51 ± 1.39	

^aEstimation of genetic correlation below the diagonal and phenotypic correlation above the diagonal.

m 1.	σ_a^2	σ_{pe}^2	σ_e^2	σ_p^2		
Trait	u	PC	e	P	h^2	r
TNB	0.786	0.937	10.039	11.761	0.07 ± 0.007	0.17 ± 0.006
NBA	0.749	0.977	10.739	12.465	0.06 ± 0.007	0.14 ± 0.006
BALWT	1.233	1.871	16.048	19.153	0.06 ± 0.008	0.16 ± 0.006
NHB	0.445	0.847	8.120	9.412	0.05 ± 0.007	0.14 ± 0.006
NWB	0.203	0.135	2.487	2.826	0.07 ± 0.007	0.12 ± 0.006
NDF	0.003	0.008	0.350	0.361	0.01 ± 0.003	0.03 ± 0.005
NSB	0.133	0.112	2.604	2.849	0.05 ± 0.006	0.09 ± 0.006
MUMM	0.011	0.015	0.936	0.961	0.01 ± 0.003	0.03 ± 0.004

Table 5. Estimates of variance components^{*a*} and heritabilities for the reproductive traits

 ${}^{a}\sigma_{a}^{2}$ = genetic variance, σ_{pe}^{2} = permanent environmental variance, σ_{e}^{2} = residual variance, σ_{p}^{2} = phenotypic variance, h^{2} = heritabilities, r = repeatability.

Table 6. Correlations ^a between	the selected re	productive traits
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	TNB	NBA	BALWT	NHB	NWB	NDF	NSB	MUMM
TNB		0.83 (0.002)	0.68 (0.003)	0.68 (0.003)	0.47 (0.004)	0.11 (0.005)	0.21 (0.005)	0.13 (0.005)
NBA	0.87 (0.023)		0.84 (0.002)	0.86 (0.001)	0.48 (0.004)	0.12 (0.005)	-0.29 (0.005)	-0.18 (0.005)
BALWT	0.50 (0.058)	0.64 (0.047)		0.89 (0.001)	0.10 (0.006)	0.07 (0.005)	-0.30 (0.005)	-0.18 (0.005)
NHB	0.68 (0.049)	0.84 (0.026)	0.89 (0.019)		0.01 (0.005)	-0.05 (0.005)	-0.32 (0.005)	-0.18 (0.005)
NWB	0.57 (0.056)	0.60 (0.057)	-0.23 (0.077)	0.09 (0.087)		-0.02 (0.005)	-0.03 (0.005)	-0.04 (0.005)
NDF	0.22 (0.156)	0.18 (0.16)	0.31 (0.148)	0.13 (0.168)	0.02 (0.143)		-0.02 (0.005)	-0.02 (0.005)
NSB	0.30 (0.085)	-0.21 (0.089)	-0.29 (0.085)	-0.28 (0.093)	0.03 (0.086)	0.06 (0.161)		0.06 (0.005)
MUMM	0.43 (0.128)	0.02 (0.145)	0.10 (0.146)	0.01 (0.154)	-0.03 (0.126)	0.50 (0.196)	0.10 (0.001)	

^aEstimation of genetic correlation below the diagonal and phenotypic correlation above the diagonal, the SE is in the bracket.

study; however, it might indicate that NSB is connected with inheritance from the sire. Moreover, the correlation between NHB and NWB shown by other research, which ranged from 0.172 to 0.348 (Shen, 2012), are also higher than the values obtained in the present study, which can probably be explained by differences in the population structure. Correlations between NHB and other traits do not appear to have been reported previously.

In conclusion, in order to improve reproductive performance, it is important to acquire phenotypic records at different parities. Parity not only influences estimates of genetic parameters, but also has an influence on Estimated Breeding Value (EBV) ranking. Furthermore, most sows show different physiological status at different parities, which also influences the performance of offspring (Belstra, 2003). Some researchers have analyzed genetic parameters by considering the first parity as an isolated trait (Roehe and Kennedy, 1995; Ehat et al., 2001; Oh et al., 2006), they considered that variance must be biased at high parities because of previous selection (Rothschild et al., 1979). However, in China, culling is usually passive, mainly caused by foot and leg disease. Furthermore, genetic correlations between different parities are strong and positive (Roehe and Kennedy, 1995), therefore it is also reasonable to consider different parities as the same trait. For parity management, sows at first parity have a narrow birth canal (Pejsak, 1984), whereas sows of higher parities have a longer parturition interval (Farmer and Robert, 2003), and thus both tend to be associated with higher numbers of dead births (Vanderhaeghe et al., 2013). Optimum reproductive performance is generally attained at parities 2 and 3. Accordingly, it is important to implement different measures for specific parities.

IMPLICATIONS

Parity is associated with the performance of reproductive traits, with TNB being an optimum performance and NSB at a minimum at third parity. Management measures should accordingly be specific for particular sows at different parities. The genetic correlations for NDF at different parities differ from those of other traits, indicating that it is unreasonable to weed out sows based on the NDF of first parity. Apart from NDF, the genetic correlations were strong and positive between different parities. Thus, for other traits, sows can be selected at the start of their reproductive life based on the information for these traits. Nevertheless, we found that the heritabilities of the eight reproductive traits analyzed in the present study were slightly lower than 0.10, and thus the accuracies of selection might not be high. NHB is an interesting trait, because by selecting for this trait, we can not only increase the number of births, but also decrease the number of deaths at birth. Accordingly, NHB is potentially the most informative reproductive trait in the studied population.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

LITERATURE CITED

- Belstra, B. A. 2003. Parity associated changes in reproductive performance: physiological basis or record keeping artifact? (Online). https://projects.ncsu.edu/project/swine_ extension/swinereports/2003/belstra.htm (Accessed 5 March 2018).
- Canario, L., E. Cantoni, E. Le Bihan, J. C. Caritez, Y. Billon, J. P. Bidanel, and J. L. Foulley. 2006. Between-breed variability of stillbirth and its relationship with sow and piglet characteristics. J. Anim. Sci. 84:3185–3196. doi:10.2527/jas.2005-775.
- Crovetti, A., R. Bozzi, C. Pugliese, and A. Acciaioli. 2010. Genetic parameters of productive and reproductive traits in Cinta Senese pig. Ital. J. Anim. Sci. 4:82–84. doi:10.4081/ijas.2005.2s.82.
- Darfour-Oduro, K. A., A. Naazie, B. K. Ahunu, and G. S. Aboagye. 2009. Genetic parameter estimates of growth traits of indigenous pigs in Northern Ghana. Livestock Sci. 125:187–191. doi:10.1016/j.livsci.2009.04.007.
- Ehat, H., E. F. Knol, and M. Jwm. 2001. Estimates of genetic parameters for reproduction traits at different parities in Dutch Landrace pigs. Livestock Prod. Sci. 69:179–186. doi:10.1016/S0301-6226(00)00258-X.
- Farmer, C., and S. Robert. 2003. Hormonal, behavioural and performance characteristics of Meishan sows during pregnancy and lactation. Can J. Anim. Sci. 83:1–12. doi:10.4141/A02-034.
- Holm, B., M. Bakken, G. Klemetsdal, and O. Vangen. 2004. Genetic correlations between reproduction and production traits in swine. J. Anim. Sci. 82:3458–3464. doi:10.2 527/2004.82123458x.
- Hoving, L. L., N. M. Soede, E. A. M. Graat, H. Feitsma, and B. Kemp. 2011. Reproductive performance of second parity sows. Relations with subsequent reproduction. Livestock Sci. 140:124–130. doi:10.1016/j.livsci.2011.02.019.
- Imboonta, N., L. Rydhmer, and S. Tumwasorn. 2007. Genetic parameters and trends for production and reproduction traits in Thai Landrace sows. Livestock Sci. 111:70–79. doi:10.1016/j.livsci.2006.12.001.
- Knecht, D., S. Środoń, and K. Duziński. 2015. The impact of season, parity and breed on selected reproductive performance parameters of sows. Arch. Anim. Breed. 58:49–56. doi:10.5194/aab-58-49-2015.
- Lee, J. H., K. D. Song, H. K. Lee, K. H. Cho, H. C. Park, and K. D. Park. 2015. Genetic parameters of reproductive and meat quality traits in Korean Berkshire pigs. Asian-Australas. J. Anim. Sci. 28:1388–1393. doi:10.5713/ ajas.15.0097.

- Leite, C. D., J. F. Lui, L. G. Albuquerque, and D. N. Alves. 2011. Environmental and genetic factors affecting the weaning-estrus interval in sows. Genet. Mol. Res. 10:2692– 2701. doi:10.4238/2011.November.4.2.
- Lundgren, H., L. Canario, K. Grandinson, N. Lundeheim, B. Zumbach, O. Vangen, and L. Rydhmer. 2010. Genetic analysis of reproductive performance in Landrace sows and its correlation to piglet growth. Livestock Sci. 128:173–178. doi:10.1016/j.livsci.2009.12.002.
- Oh, S. H., D. H. Lee, and M. T. See. 2006. Estimation of genetic parameters for reproductive traits between first and later parities in pig. Asian-Austral. J. Anim. Sci. 19:7– 12. doi:10.5713/ajas.2006.7.
- Pejsak, Z. 1984. Some pharmacological methods to reduce intrapartum death of piglets. Pig News & Information.
- Roehe, R., and B. W. Kennedy. 1995. Estimation of genetic parameters for litter size in Canadian Yorkshire and Landrace swine with each parity of farrowing treated as a different trait. J. Anim. Sci. 73:2959–2970. doi:10.2527/1995.73102959x.
- Rothschild, M. F., C. R. Henderson, and R. L. Quaas. 1979. Effects of selection on variances and covariances of simulated first and second lactations. J. Dairy Sci. 62:996–1002.

- Shannon, M. 2011. Nutrition and feeding for optimum reproductive performance (Online) https://pdfs.semanticscholar. org/a9d9/1f3889ee8b8cbcbff1c5be1927f7e8674afa.pdf (Accessed 5 March 2018).
- Shen, J. Y., Y. Yu, X. Wang, P. P. Ma, S. E. Zhu, W. Q. Shi, Y. C. Wang, and Q. Zhang. 2012. Factors analysis and genetic parameter estimation of female reproductive traits in pigs. Hereditas. 5:591–596. doi:10.3724/SP.J.1005.2012.00591.
- Strange, T., B. Ask, and B. Nielsen. 2013. Genetic parameters of the piglet mortality traits stillborn, weak at birth, starvation, crushing, and miscellaneous in crossbred pigs. J. Anim. Sci. 91:1562–1569. doi:10.2527/jas.2012-5584.
- Takai, Y., and Y. Koketsu. 2008. Number of services and the reservice intervals in relation to suboptimal reproductive performance in female pigs on commercial farms. Livestock Sci. 114:42–47. doi:10.1016/j.livsci.2007.04.007.
- Vanderhaeghe, C., J. Dewulf, A. de Kruif, and D. Maes. 2013. Non-infectious factors associated with stillbirth in pigs: a review. Anim. Reprod. Sci. 139:76–88. doi:10.1016/j. anireprosci.2013.03.007.
- Zhang, S., B. Jean-Pierre, B. Thierry, L. Christian, and N. Jean. 2000. Genetic parameters and genetic trends in the Chinese × European Tiameslan composite pig line. II. Genetic trends. Gen. Select. Evol. 32:1–16. doi:10.1186/1297-9686-32-1-57.