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Estimation of genetic parameters for farrowing traits in purebred Landrace and Large White pigs

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Abstract

Genetic parameters were estimated for six reproductive traits related to farrowing events in Landrace and Large White pigs; total number born (TNB), number born alive (NBA), number stillborn (NSB), total litter weight at birth (LWB), mean litter weight at birth (MWB), and gestation length (GL). We analyzed 62,534 farrowing records for 10,637 Landrace dams and 49,817 farrowing records for 8,649 Large White dams. Estimated heritabilities of TNB, NBA, NSB, LWB, MWB, and GL by single-trait repeatability model analyses were 0.12, 0.12, 0.08, 0.18, 0.19, and 0.29, respectively, in Landrace, and 0.12, 0.10, 0.08, 0.18, 0.16, and 0.34, respectively, in Large White. Genetic correlation between NBA and NSB was unfavorable: 0.20 in Landrace and 0.33 in Large White. Genetic correlations of GL with the other five traits were weak: from −0.18 with NSB to −0.03 with NBA in Landrace, and from −0.22 with NSB to −0.07 with NBA in Large White. LWB had a highly favorable genetic correlation with NBA (0.74 in both breeds), indicating the possibility of using LWB for the genetic improvement of NBA.

KEYWORDS

farrowing traits, female pigs, genetic parameter, number born alive, repeatability model

1 | INTRODUCTION

One of the breeding goals for female pigs is the genetic improvement of the number of piglets weaned per sow. The primary requirement for achieving larger numbers of weaned piglets is an increase in the number born alive (NBA). Hence, selection in dam breeds or lines should consider the genetic correlations between the component traits of farrowing and mortality (Johnson, Nielsen, & Casey, 1999; Rydhmer, 2000).

Farrowing traits, including total number born (TNB), NBA, number stillborn (NSB), and gestation length (GL) defined as the interval between insemination and farrowing date, play an important role in pig breeding (Hanenberg, Knol, & Merks, 2001; Onteru et al., 2012). Various associations have been reported between those traits and other related traits. Selection on TNB leads to an increase in piglet mortality (Johnson et al., 1999; Su, Lund, & Sorensen, 2007) and a decrease in GL (Hanenberg et al., 2001). In addition, NSB increased with decreasing GL (Leenhouwers, van der Lende, & Knol, 1999). Negative associations have been reported between litter size and individual birth weight in some studies (Kerr & Cameron, 1995; Roehe, 1999; Sorensen, Vernersen, & Andersen, 2000). The heritability of NBA has been estimated to be low in the previous studies (e.g., Damgaard, Rydhmer, Løvendahl, & Grandinson, 2003; Farkas et al., 2007; Lopez, Kim, Makumbe, Song, & Seo, 2017). It is useful for genetic improvement of NBA to find a trait having heritability higher than, and showing an advantageous genetic correlation with NBA. However, there appear to be little published information on the heritabilities of and the genetic correlation among litter size and weight traits at birth and GL estimated simultaneously. It is, therefore, important to know the degree of genetic determination of farrowing traits and their relationships as accurately as possible to guide the effectiveness of selection on them.

In this study, aiming to obtain information necessary to improve NBA more efficiently, genetic parameters were estimated for the six farrowing traits of TNB, NBA, NSB, total litter weight at birth (LWB; kg), mean litter weight at birth (MWB; kg/NBA), and GL in purebred Landrace and Large White pigs, using large-scale datasets obtained from a single pig breeding company.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Approval of Animal Care and Use Committee was not required for this study because the data were acquired from an existing database.

2.2 | Phenotype and pedigree data

Farrowing records for 12,857 Landrace and 10,615 Large White dams born during 1999–2016 were provided by CIMCO Corporation (Tokyo, Japan), operating two GGP and GP farms by Specific Pathogen Free system located from northern to southern parts of Japan. Sows were serviced by artificial insemination. The number of insemination was three in principle, and the day of the first insemination was recorded as the mating date for the corresponding farrowing record. The number of farrowing records was 68,702 for Landrace and 55,755 for Large White pigs. Pedigree data for Landrace and Large White pigs included 79,224 and 68,615 animals, respectively. It must be noted that a relatively large proportion (estimated to be 70–80%) of records were obtained under using hormonal drugs (prostaglandin).

Traits analyzed were TNB, NBA, NSB, LWB, MWB, and GL. NBA was determined at the next day of the farrowing, and included the number of piglets dead when checking to determine NBA but seemed to be alive at farrowing. The number of mummified piglets was not included in NSB. TNB was calculated as the sum of NBA and NSB. LWB was recorded by measuring the weights of all piglets at birth regardless of whether each of them was dead or alive. MWB was obtained by dividing LWB by NBA. Records for GL were obtained by calculating the interval between mating and farrowing dates.

Any farrowing records exhibiting negative value for GL were first excluded because such records had incorrect mating and/or farrowing dates. Farrowing records exhibiting 0 for NBA were also excluded because MWB cannot be calculated for these records. Next, to remove obvious outliers, farrowing records with MWB not in the range of the average ± 3 *SD* were excluded. We assumed the average and standard deviation of MWB in both breeds were 1.48 and 0.23 as reported by Damgaard et al. (2003), but did not use the average and standard deviation calculated from our data, because these values were greatly affected by the existence of obvious outliers. Farrowing records with GL not in the range of their means ± 3 *SD*, which were calculated from GL records available, were also excluded. After that, only records for dams having two or more farrowing records were retained to relax confounding of the permanent environmental and temporary environmental effects. Finally, 62,534 and 49,817 farrowing records without missing phenotypic data from 10,637 Landrace and 8,649 Large White dams, respectively, were analyzed. The averages, standard deviations, minimum values, and maximum values of phenotypic records for TNB, NBA, NSB, LWB, MWB, and GL in Landrace and Large White pigs are listed in Table 1. Values of the average, standard deviation, minimum and maximum numbers of repeated records per dam were 5.88, 2.68, 2, and 16 for Landrace, and 5.76, 2.74, 2, and 16 for Large White.

2.3 | Statistical analyses

Heritabilities of and genetic correlations between the six farrowing traits were estimated for each breed. All traits were analyzed as dam traits. The statistical model used to describe the phenotypic data was as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{c} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of phenotypic records; $\mathbf{b}$ is the vector of fixed discrete effects of farrowing year, farrowing season, mating sire breed, farm, and parity; $\mathbf{a}$ is the vector of direct additive genotypic values of dams; $\mathbf{c}$ is the vector of permanent environmental effects of dams; $\mathbf{e}$ is the vector of residuals; and $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are the known design matrices relating $\mathbf{y}$ to

TABLE 1 The averages (Ave), standard deviations (SD), minimum values (Min), and maximum values (Max) of phenotypic records for total number born (TNB), number born alive (NBA), number stillborn (NSB), total litter weight at birth (LWB; kg), mean litter weight at birth (MWB; kg/NBA), and gestation length (GL; days) in Landrace and Large White dams

	Landrace				Large White			
Trait	Ave	*SD*	Min	Max	Ave	*SD*	Min	Max
TNB	10.9	3.0	1	27	11.0	2.8	1	23
NBA	10.1	2.7	1	23	10.1	2.5	1	21
NSB	0.8	1.1	0	12	0.9	1.2	0	10
LWB	15.3	3.8	1.0	31.0	15.8	3.6	1.0	29.0
MWB	1.6	0.2	0.8	2.2	1.6	0.2	0.8	2.2
GL	114.0	1.3	110	118	114.0	1.3	110	118

b, **a**, and **c**, respectively. Farrowing year was varied from 2000 to 2017 for both breeds. Farrowing season was determined as each of Spring (March to May), Summer (June to August), Autumn (September to November), and Winter (December to February) for both breeds. All Landrace and Large White dams were mated with Landrace, Large White, and Duroc sires. Records analyzed were obtained at seven farms including the two GGP farms for Landrace and eight farms including the two GGP farms for Large White. Range in parity order was from the first to seventeenth for Landrace and from the first to sixteenth for Large White.

A single-trait model was exploited to estimate the heritability, and the vectors **a**, **c**, and **e** were assumed to follow a multivariate normal distribution with mean and (co)variance structure of:

$$E\begin{bmatrix}\mathbf{a}\\\mathbf{c}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}0\\0\\0\end{bmatrix}\quad\text{and}\quad V\begin{bmatrix}\mathbf{a}\\\mathbf{c}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\sigma_a^2&0&0\\0&\mathbf{I}\sigma_c^2&0\\0&0&\mathbf{I}\sigma_e^2\end{bmatrix},$$

where σ_a^2 is the direct additive genetic variance; σ_c^2 is the permanent environmental variance; σ_e^2 is the residual variance; **A** is the additive genetic relationship matrix for all 79,224 pigs for Landrace and 68,615 pigs for Large White in pedigree data; and **I** is the identity matrix.

A two-trait model was exploited to estimate the genetic correlation, and **a**, **c**, and **e** were assumed to follow a multivariate normal distribution with mean and (co)variance structure of:

$$E\begin{bmatrix}\mathbf{a}\\\mathbf{c}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}0\\0\\0\end{bmatrix}\quad\text{and}\quad V\begin{bmatrix}\mathbf{a}\\\mathbf{c}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{G}\otimes\mathbf{A}&0&0\\0&\mathbf{C}\otimes\mathbf{I}&0\\0&0&\mathbf{R}\otimes\mathbf{I}\end{bmatrix},$$

where **G** is the direct additive genetic (co)variance matrix; **C** is the permanent environmental (co)variance matrix; and **R** is the residual (co)variance matrix.

Variance components were estimated by the average-information algorithm in ASREML software version 4.1 (Gilmour, Gogel, Cullis, Welham, & Thompson, 2015).

3 | RESULTS AND DISCUSSION

3.1 | Heritabilities and repeatabilities of the six farrowing traits

Estimated phenotypic variances (as the sum of additive genetic, permanent environmental, and residual variances), heritabilities, and repeatabilities of TNB, NBA, NSB, LWB, MWB, and GL, together with their standard errors, in Landrace and Large White pigs from the single-trait repeatability model analyses are shown in Table 2. Large differences were not observed between the breeds.

Heritability estimates for TNB, NBA, and NSB were around 0.1. Heritabilities of LWB and MWB were slightly lower than 0.2 and were both higher than those of TNB, NBA, and NSB. GL showed a heritability of approximately 0.3, which was the highest value obtained as the heritability in this study. These results were in agreeance with those previously estimated in the same breeds using a repeatability model (e.g., Damgaard et al., 2003; Farkas et al., 2007; Lopez et al., 2017).

Repeatability estimates for NSB were the smallest in this study, 0.13 for Landrace and 0.14 for Large White. Those were about 0.2 for TNB, NBA, and MWB, 0.3 for LWB, and 0.40 for GL. Tomiyama, Kubo, Takagi, and Suzuki (2011) reported the estimated heritability and the proportion of permanent environmental variance to the phenotypic variance of TNB using a repeatability model to be 0.10 and 0.09, respectively. Damgaard et al. (2003) estimated the variance components corresponding to the repeatability of 0.21 for NBA and that of 0.47 for MWB. Hanenberg et al. (2001), using the records from the second to sixth parities, reported the estimated heritabilities and the proportions of permanent environmental variance to

TABLE 2 Estimated phenotypic variances (σ_p^2), heritabilities (h^2), and repeatabilities (rep), together with their standard errors in parentheses, of total number born (TNB), number born alive (NBA), number stillborn (NSB), total litter weight at birth (LWB; kg), mean litter weight at birth (MWB; kg/NBA), and gestation length (GL; day) in Landrace and Large White dams[a]

	Landrace			Large White		
Trait	σ_p^2	h^2	rep	σ_p^2	h^2	rep
TNB	8.06	0.12	0.21	7.21	0.12	0.24
	(0.06)	(0.01)	(0.01)	(0.06)	(0.01)	(0.01)
NBA	6.68	0.12	0.19	5.91	0.10	0.22
	(0.05)	(0.01)	(0.01)	(0.05)	(0.01)	(0.01)
NSB	1.15	0.08	0.13	1.33	0.08	0.14
	(0.08)	(0.01)	(0.00)	(0.01)	(0.01)	(0.00)
LWB	12.97	0.18	0.26	12.05	0.18	0.30
	(0.11)	(0.01)	(0.01)	(0.12)	(0.01)	(0.01)
MWB	5.87×10^{-2}	0.19	0.24	6.03×10^{-2}	0.16	0.23
	(0.05×10^{-2})	(0.01)	(0.01)	(0.05×10^{-2})	(0.01)	(0.01)
GL	1.39	0.29	0.38	1.52	0.34	0.40
	(0.02)	(0.01)	(0.01)	(0.02)	(0.02)	(0.01)

[a]Values of 0.00 in parentheses mean that standard errors are lower than 0.01.

the phenotypic variance, corresponding to the repeatabilities of TNB, NBA, NSB, and GL to be 0.19, 0.17, 0.10, and 0.40, respectively. Lukovic, Uremovic, Konjacic, Uremovic, and Vincek (2007) estimated genetic parameters of NBA using a repeatability model and a random regression model, and the repeatability estimated using a repeatability model was 0.11 and that estimated using a random regression model was from 0.10 to 0.21.

A model including random maternal genetic and common litter effects was also used for variance component estimation. However, the estimated variance components for the two effects were too small (data not shown) to be considered in further analyses.

3.2 | Genetic correlations between the six farrowing traits

Estimated additive genetic and residual correlations, together with their standard errors, between TNB, NBA, NSB, LWB, MWB, and GL in Landrace and Large White pigs are shown in Table 3. As with the heritability, no remarkable differences were observed between the breeds.

Very high positive genetic correlations of 0.90 or higher were estimated between TNB and NBA. Roehe and Kennedy (1995) and Serenius, Sevón-Aimonen, Kause, Mäntysaari, and Mäki-Tanila (2004) also estimated genetic correlations of higher than 0.90 between TNB and NBA in both breeds. These suggest that TNB and NBA were genetically similar traits. Moderately high positive genetic correlations of 0.48 for Landrace and 0.62 for Large White were estimated between TNB and NSB, which were similar to those reported previously for both breeds (Hanenberg et al., 2001; Serenius et al., 2004; Thekkoot, Kemp, Rothschild, Plastow, & Dekkers, 2016). These imply that selection based on TNB may cause the increase in NSB (Satoh, 2006). Unfavorable genetic correlations of 0.20 for Landrace and 0.33 for Large White, were estimated between NBA and NSB. Serenius et al. (2004) estimated genetic correlations between NBA and NSB in Finnish Landrace and Large White populations to be −0.11 and 0.17, respectively. Thekkoot et al. (2016) showed the values of 0.15 and −0.08 as the genetic correlations in Canadian Landrace and Yorkshire populations, respectively. Holm, Bakken, Vangen, and Rekaya (2004) and Arango, Misztal, Tsuruta, Culbertson, and Herring (2005) reported negligible genetic correlations of −0.02 and −0.04, respectively. These indicate that there is a weak positive or negative genetic correlation between NBA and NSB, depending on the population analyzed.

Genetic correlations between LWB and MWB were positive, with the value of 0.44 and 0.54 for Landrace and Large White, respectively. Hermesch, Luxford, and Graser (2000) also reported positive values of 0.29–0.87 as the genetic correlations between LWB and MWB from the first to third parties. These imply that improvement of LWB can lead the increase in MWB.

Genetic correlations between LWB and NBA were estimated to be 0.74 in both breeds, and genetic correlations between LWB and NSB were 0.31 and 0.36 for Landrace and Large White, respectively. Negative values were obtained as the genetic correlations between MWB and NBA (−0.29 for Landrace and −0.17 for Large White). Damgaard et al. (2003) estimated the genetic correlation of −0.30 between MWB and NBA for Yorkshire pigs. David, Garreau, Balmisse, Bilon, and Canario (2017) showed low negative genetic correlations between MWB and NBA from the first to fifth parities for Large White pigs. Hermesch et al. (2000) estimated the genetic correlations between LWB and NBA from the first to third parties to be low positive or negative, and the genetic correlations between MWB and NBA at the corresponding parity combination were always nearer to −1. These imply that the selection for NBA may cause

TABLE 3 Estimated additive genetic and residual correlations (lower and upper triangular sections, respectively), together with their standard errors in parentheses, between total number born (TNB), number born alive (NBA), number stillborn (NSB), total litter weight at birth (LWB), mean litter weight at birth (MWB), and gestation length (GL) in Landrace and Large White dams[a]

	Landrace						Large White					
Trait	TNB	NBA	NSB	LWB	MWB	GL	TNB	NBA	NSB	LWB	MWB	GL
TNB		0.92	0.39	0.84	−0.35	−0.14		0.89	0.40	0.81	−0.33	−0.11
		(0.00)	(0.00)	(0.00)	(0.00)	(0.00)		(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
NBA	0.95		−0.01	0.81	−0.52	−0.11	0.95		−0.06	0.77	−0.54	−0.08
	(0.01)		(0.00)	(0.00)	(0.00)	(0.00)	(0.01)		(0.00)	(0.00)	(0.00)	(0.00)
NSB	0.48	0.20		0.23	0.33	−0.08	0.62	0.33		0.21	0.37	−0.08
	(0.05)	(0.06)		(0.00)	(0.00)	(0.00)	(0.05)	(0.06)		(0.00)	(0.00)	(0.00)
LWB	0.76	0.74	0.31		0.03	−0.05	0.73	0.74	0.36		0.08	−0.01
	(0.02)	(0.02)	(0.05)		(0.00)	(0.00)	(0.03)	(0.03)	(0.06)		(0.00)	(0.00)
MWB	−0.22	−0.29	0.19	0.44		0.12	−0.13	−0.17	0.08	0.54		0.11
	(0.05)	(0.05)	(0.05)	(0.04)		(0.00)	(0.06)	(0.06)	(0.06)	(0.04)		(0.00)
GL	−0.08	−0.03	−0.18	−0.13	−0.16		−0.13	−0.07	−0.22	−0.16	−0.13	
	(0.05)	(0.05)	(0.05)	(0.05)	(0.04)		(0.05)	(0.06)	(0.05)	(0.05)	(0.05)	

[a]Values of 0.00 in parentheses mean that standard errors are lower than 0.01.

the decrease in MWB. Low positive genetic correlations were estimated between MWB and NSB (0.19 for Landrace and 0.08 for Large White).

Genetic correlations of GL with TNB, NBA, NSB, LWB, and MWB were −0.08, −0.03, −0.18, −0.13, and −0.16, respectively, for Landrace, and −0.13, −0.07, −0.22, −0.16 and −0.13, respectively, for Large White. These were all weak, implying that GL would be genetically independent from the other five traits. For genetic correlations of GL with TNB, NBA, and NSB, low values have been reported from studies using datasets without hormonal treatments (Hanenberg et al., 2001; Rydhmer, Lundeheim, & Canario, 2008).

3.3 | Overall discussion

In this study, the genetic parameters were estimated for six farrowing traits in Landrace and Large White, the two major dam breeds in pig production. The traits studied can all be measured at the same time and there is a complex relationship between them. The genetic improvement of NBA is important to increase the number of piglets weaned, but the heritability of NBA is low, as also shown in this study (Table 2). Some trait may have a higher heritability than, and a high and favorable genetic correlation with NBA. Selection exploiting the information about such a trait could accelerate the improvement of NBA, even if the trait is recorded at the same time with NBA. On the other hand, several studies have reported the antagonistic relationship between litter size and individual birth weight (Kerr & Cameron, 1995; Roehe, 1999; Sorensen et al., 2000). Therefore, to simultaneously improve the number and weight of piglets, it is crucial to understand the genetic correlation between them.

TNB showed heritability similar to that of NBA, but had a higher positive genetic correlation with NSB than did NBA. This indicates that selection by NBA is more efficient than by TNB to genetically improve NBA while not increasing NSB (Satoh, 2006). However, the estimated genetic correlation between NBA and NSB was still not favorable. Moreover, the genetic correlation between NBA and MWB was negative. These results mean that a dam having a greater breeding value for NBA has the genetic tendency to produce more stillborn piglets and lighter piglets on average, which is inconvenient for improving both the number and the weight of piglets.

This study estimated a higher heritability of LWB than NBA, a considerably high positive genetic correlation between LWB and NBA, and a moderately high positive genetic correlation between LWB and MWB. Therefore, selection using LWB together with NBA could compensate for the antagonistic relationship between NBA and MWB, and the genetic improvement of NBA might be boosted. Further analysis is needed to investigate the efficacy of utilizing LWB for improving NBA. The estimated genetic correlation between LWB and NSB was also unfavorable, but this might be somewhat reduced using, if possible, litter weights measured for only piglets born alive.

Correlated response of GL to selection for NBA would be little although the highest heritability was estimated among the traits studied, according to its very weak genetic correlations with the other five traits. Estimated residual correlation between GL and MWB was very low but positive for both breeds, whereas genetic correlation between them was estimated to be negative (Table 3). Litter size is basically determined by ovulation and embryo mortality, which mainly take place in the early stages of gestation (Blasco, Bidanel, & Haley, 1995). On the other hand, the last days of gestation are crucial for the maturation of the piglet at birth because piglet weight at birth is mostly determined by growth in late gestation (Varona, Sorensen, & Thompson, 2007), and therefore, a gestation not shorter than the average (about 114 days) will result in better development of the piglet at birth and lower postnatal mortality (Rydhmer et al., 2008). The latter might be more related to the variation in phenotypic records of GL in this study.

Assistance at farrowing, farrowing length, and the time of farrowing can affect piglet survival. However, there was no information available about them. As already mentioned, a large proportion of farrowing records were obtained under using prostaglandin in this study. However, since the records did not include whether prostaglandin was used, consideration of the dosage as a fixed effect could not be implemented in this study. These might have had an impact on the genetic parameter estimation for several traits studied in this study, including NBA and GL. In this study, farrowing records from only dams having multiple records were analyzed, in terms of the estimation of permanent environmental variance. However, this editing might bring bias in variance component estimation because removed dams included ones culled after the first farrowing based on their farrowing performance.

Ohnishi and Satoh (2014) indicated the possibility of using teat number for improving NBA in Duroc pigs, which has a moderate heritability and can be measured in both male and female animals at a younger age. Likewise, continued efforts must be made to explore other promising new traits for accelerating the improvement of female fertility in dam breeds. Furthermore, genetic associations of the farrowing traits with traits measured at weaning should definitely be examined.

4 | CONCLUSION

In this study, the genetic parameters were estimated for TNB, NBA, NSB, LWB, MWB, and GL in Landrace and Large White pigs using a repeatability model. It was found that using LWB would be useful for the genetic improvement of NBA on the basis of the estimated heritabilities higher than NBA, and the high and favorable genetic correlation between LWB and NBA.

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