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Comparison of two models to estimate genetic parameters for number of born alive in pigs

Ayane Konta[1] | Shinichiro Ogawa[1] | Makoto Kimata[2] | Kazuo Ishii[3] | Yoshinobu Uemoto[1] | Masahiro Satoh[1]

[1]Graduate School of Agricultural Science, Tohoku University, Sendai, Japan

[2]CIMCO Corporation, Tokyo, Japan

[3]Division of Animal Breeding and Reproduction, Institute of Livestock and Grassland Science, NARO, Tsukuba, Japan

Correspondence
Ayane Konta, Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi 980-8572, Japan.
Email: ayane.konta.t6@gmail.com

Abstract

The performance of the two-trait animal model that regards the first parity and later parities as two different traits in estimating genetic parameters for number of born alive (NBA) was examined using real and simulated data. Genetic parameters for NBA were estimated in purebred Landrace and Large White pigs using a single-trait repeatability model (Model 1) that regards all parities as the same trait and a two-trait animal model (Model 2) that regards the first and the later parities as different traits. For Model 2, the permanent environmental effect was fitted to only the records of the later parities. Heritability for NBA estimated using Model 1 was 0.12 for Landrace and 0.11 for Large White. Estimated heritability for NBA of the first parity and the later parities was 0.21 and 0.16, respectively, for Landrace; 0.18 and 0.16, respectively, for Large White obtained using Model 2, and higher than those in both breeds obtained using Model 1. Further results based on data simulated using the Monte Carlo method suggest that estimated additive genetic variance could be more biased using Model 2 than Model 1.

KEYWORDS
genetic parameter estimation, Landrace, Large White, number of born alive, permanent environmental effect

1 | INTRODUCTION

Number of born alive (NBA) is a key trait in pig production, although the response to selection is generally small due to its low heritability (Satoh, 2006). Genetic parameters for NBA have conventionally been estimated using a single-trait repeatability animal model assuming that all records at different parities to be repeated measurements of the same trait. Multiple-trait animal model analyses have also been performed in which different parities were regarded as different traits (Fernández, Rodrigáñez, Zuzúarregui, Rodríguez, & Silió, 2008; Hanenberg, Knol, & Merks, 2001; Hermesch, Luxford, & Graser, 2000; Holm, Bakken, Vangen, & Rekaya, 2005; Ishii,

Kadowaki, Nishiura, Sasaki, & Satoh, 2010; Ogawa et al., 2019b; Serenius, Sevón-Aimonen, & Mäntysaari, 2003). The latter studies indicated the possibility of regarding NBA in the first parity as a trait of the gilt and NBA in the later parities as a trait of the sow, due to the minor genetic correlation between the first and later parities. The two-trait animal model has since been employed to estimate genetic parameters using real pig data in several studies (e.g., Fernández, Rodrigáñez, Rodríguez, & Silió, 2007; Oh, Lee, & See, 2005; Peškovičová, Wolf, Groeneveld, & Wolfová, 2002). Peškovičová et al. (2002) and Oh et al. (2005) concluded that the estimated heritability of the first parity could be higher than that of the later parities when a two-trait animal model was used

that assumed the first parity and the later parities to be different traits. However, there are no reports on the difference in heritability between the first parity and the later parities using computer simulation.

In this study, the genetic parameters for NBA were estimated using two animal models: one was a single-trait repeatability animal model that regarded all parities as the same trait, and the other was a two-trait animal model that regarded NBA in the first parity and the later parities as two different traits. We used two strategies: one was real data analysis from purebred Landrace and Large White pig populations, and the other was a Monte Carlo computer simulation.

The aim of this study was to investigate the bias of genetic parameter estimates when using the two-trait animal model. The accuracy of estimated breeding values (EBVs) was also employed to evaluate the two different models using computer simulation.

2 | MATERIALS AND METHODS
2.1 | Ethical statement

The approval of an Animal Care and Use Committee was not required for this study because the data were acquired from a Japanese private pig breeding company (CIMCO Corp.).

2.2 | Phenotype and pedigree data

Data for NBA from purebred Landrace and Large White dams that had been born between 1999 and 2016 were collected from CIMCO Corporation (Tokyo, Japan), operating two great grandparent (GGP) and grandparent (GP) farms using the Specific Pathogen Free system. The original data included 68,702 litter records for Landrace dams and 55,755 litter records for Large White dams. Details about data on NBA were in Ogawa et al. (2019a). NBA was determined the day after farrowing, and included the number of dead piglets that may have been alive when they were born. Litter records with no surviving piglets at birth were excluded. Farrowing records with mean litter weight at birth outside the range of the average ± 3 standard deviations (SD) were excluded to remove obvious outliers. We assumed the average and SD of mean litter weight at birth to be 1.48 and 0.23, respectively, in both breeds, as reported by Damgaard, Rydhmer, Løvendahl, and Grandinson (2003) instead of the average and SD calculated using our data because our average and SD were significantly affected by the presence of obvious outliers. We extracted farrowing records from the first to the eighth parities.

The final datasets included 58,739 records from 12,677 Landrace dams and 46,621 records from 10,405 Large White dams (Table 1). Pedigree datasets for Landrace and Large White included 79,224 and 68,615 pigs, respectively.

TABLE 1 Summary statistics for number of born alive in the first parity (NBA1) and the later parities (NBA2+) for Landrace and Large White pigs

Trait	Landrace		Large White	
	No. records	Mean ± SD	No. records	Mean ± SD
NBA1	11,675	9.2 ± 2.4	9,411	9.1 ± 2.4
NBA2+	47,064	10.4 ± 2.7	37,210	10.5 ± 2.5

2.3 | Statistical analyses

The single-trait repeatability animal model (denoted as Model 1) used to describe the phenotypic data was as follows:

$$y = Xb + Za + Wpe + e, \ E\begin{bmatrix} a \\ pe \\ e \end{bmatrix} = 0, \mathrm{var} \begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

Where y is the vector of phenotypic records of dams in each breed; b is the vector of fixed effects; a is the vector of breeding values of dams; pe is the vector of permanent environmental effects of dams; e is the vector of random error terms; X, Z, and W are the known incidence matrices relating y to b, a, and pe, respectively; $\sigma_a^2, \sigma_{pe}^2$, and σ_e^2 are the additive genetic variance, permanent environmental variance, and error variance; A is an additive genetic relationship matrix and I is an identity matrix. Fixed effects were farrowing year (18 levels), farrowing season (four levels), mating service boar breed (four levels), farm (seven levels for Landrace, eight levels for Large White), and parity (eight levels). The farrowing seasons were defined individually as spring (March to May), summer (June to August), autumn (September to November), or winter (December to February). All Landrace and Large White females were mated with Landrace, Large White, or Duroc males.

The two-trait animal model (denoted as Model 2) was as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} 0 \\ W_2 \end{bmatrix} pe_2 + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

$$E\begin{bmatrix} a_1 \\ a_2 \\ pe_2 \\ e_1 \\ e_2 \end{bmatrix} = 0, \mathrm{var} \begin{bmatrix} a_1 \\ a_2 \\ pe_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a1}^2 & A\sigma_{a12} & 0 & 0 & 0 \\ A\sigma_{a12} & A\sigma_{a2}^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{pe2}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_{e1}^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_{e2}^2 \end{bmatrix}$$

Where subscripts 1 and 2 correspond to NBA of the first parity and the later parities (second to eighth), respectively, and σ_{a12} is the additive genetic covariance. The fixed effects considered for the later parities were the same as in Model 1, whereas the effect of parity was not considered for the first parity.

Variance components were estimated using ASREML software version 4.1 (Gilmour, Gogel, Cullis, Welham, & Thompson, 2015).

2.4 | Computer simulation

To confirm the results of genetic parameter estimation using real data, the data created by Monte Carlo computer simulations were also analyzed. The pedigree information on Landrace and Large White pigs was used in this study. The infinitesimal additive genetic model (Bulmer, 1980) was used to generate the breeding values of individuals. To simplify the simulation, each female with at least one record in a real dataset had three observations (the first to third parities). Four scenarios were adopted for the true values of genetic parameters (Table 2). Model 1 and Model 2 in these Scenarios were used as described previously to estimate genetic parameters. Fixed effects were not considered in the data generation and analytical models. The results were the mean of 50 replicates of each Scenario. Correlation coefficients between true breeding values (TBVs) and EBVs of 12,677 dams with records for Landrace and 10,405 dams with records for Large White were calculated to assess the accuracy of EBVs. EBVs were calculated using the genetic parameters estimated for each iteration. Because genetic correlation between the first parity and the later parities was 0.9 in Scenarios 3 and 4, each animal has two TBV.

3 | RESULTS AND DISCUSSION

3.1 | Genetic parameter estimation using real phenotypic data

Estimated genetic parameters using real phenotypic data of Landrace and Large While dams are shown in Table 3. Heritability estimates using Model 1 were 0.12 for Landrace and 0.11 for Large White. Using Model 2, heritability estimates in the first parity and the later parities were 0.21 and 0.16, respectively, for Landrace; and 0.18 and 0.16, respectively, for Large White. Estimated genetic correlations using Model 2 were 0.89 for Landrace and 0.90 for Large White.

TABLE 2 True values of genetic parameters used for computer simulation[a]

Scenario	σ_p^2	σ_a^2	σ_{pe}^2	r_g
1	1.0	0.1	0.1	1.0
2	1.0	0.1	0.0	1.0
3	1.0	0.1	0.1	0.9
4	1.0	0.1	0.0	0.9

[a]σ_p^2 = phenotypic variance, σ_a^2 = additive genetic variance, σ_{pe}^2 = permanent environmental variance, r_g = genetic correlation between the first parity and the later (second and third) parities.

The estimated values of heritabilities using Model 2 were higher than those using Model 1. The heritabilities of the first parity were estimated as being higher than those of the later parities using Model 2 for both breeds. Similar findings have been reported by Peškovičová et al. (2002), Oh et al. (2005), and Fernández et al. (2007). Nakavisut, JN, NA, and Yuyeun (2009) reported that the heritability estimates of the first parity and the later parities using a two-trait animal model were about 0.10 and 0.08, respectively, for Landrace, and 0.06 and 0.07, respectively, for Large White. Wolf, Žáková, and Groeneveld (2005), Wolf (2010), and Wolf and Wolfova (2012) estimated genetic parameters using a multiple trait model including the other traits in addition to NBA in the first and the later parities as different traits for Czech Landrace and Large White populations. They reported that the heritabilities of the first parity and the later parities were similar in both breeds, and that the estimated genetic correlation between the first parity and the later parities was around 0.95 for Landrace and 0.80 for Large White.

In this study, heritability estimates were higher for Model 2 than Model 1. The reason for the higher value of estimated heritability of the first parity than that of the later parities might be partly due to incomplete segregation of additive genetic variance and permanent environmental variance, because although the phenotypic records for the first parity included permanent environmental effect, they were not taken into account in Model 2. The reason why the additive genetic variance in the later parities was also overestimated may be that the additive genetic variance in the first parity was overestimated and the genetic correlation between the two traits was high.

Genetic correlation estimates in this study were similar to those reported by Wolf et al. (2005) (0.996 and 0.96 for Czech Landrace breed, 0.80 and 0.88 for Czech Large White breed), Wolf (2010) (0.94 for Czech Landrace breed, 0.78 for Czech Large White breed), and Wolf and Wolfova (2012) (0.86–0.93 for Czech Landrace breed, 0.82–0.87 for Czech Large White breed).

3.2 | Genetic parameter estimation using simulated phenotypic data

Genetic parameter estimates using simulated data based on Landrace and Large White pedigree information are shown in Table 4, respectively. In all cases, the calculation by ASREML converged. Estimated values were similar between both breeds. For Model 1, all estimated values of genetic parameters were similar to their corresponding true values in Scenarios 1 and 2, but in Scenarios 3 and 4, estimated additive genetic variance and heritability were slightly lower than their true values. For Model 2, additive genetic variances and heritabilities of the first parity and the later parities were about double their true values, while permanent environmental variances were estimated at about half their true values in Scenarios 1 and 3. Also, genetic correlation between the first parity and the later parities was estimated to be higher than its true value in Scenario 3. On the other hand, the genetic

TABLE 3 Genetic parameter estimates and their standard errors (SE in parentheses) for number of born alive in Landrace and Large White pigs

Genetic Parameters[a]	Landrace						Large White					
	Model 1[b]		Model 2[c]				Model 1		Model 2			
			First parity		Later parities				First parity		Later parities	
σ_a^2	0.77	(0.06)	1.23	(0.10)	1.13	(0.07)	0.65	(0.06)	1.04	(0.10)	0.99	(0.07)
σ_{pe}^2	0.50	(0.04)	---	---	0.40	(0.04)	0.63	(0.04)	---	---	0.61	(0.05)
σ_p^2	6.62	(0.05)	5.89	(0.09)	6.96	(0.06)	6.01	(0.05)	5.81	(0.09)	6.21	(0.06)
h^2	0.12	(0.01)	0.21	(0.02)	0.16	(0.01)	0.11	(0.01)	0.18	(0.02)	0.16	(0.01)
pe^2	0.19	(0.01)	---	---	0.22	(0.01)	0.21	(0.01)	---	---	0.26	(0.01)
r_g	---	---	0.89		(0.02)		---	---	0.90		(0.03)	
r_p	---	---	0.16		(0.01)		---	---	0.15		(0.01)	

[a] σ_a^2 = additive genetic variance, σ_{pe}^2 = permanent environmental variance, σ_p^2 = phenotypic variance, h^2 = heritability, pe^2 = repeatability, r_g = genetic correlation between the first parity and the later (from second to eighth) parities, r_p = phenotypic correlation.

[b] A single-trait animal model.

[c] A two-trait animal model that regards the first parity and later parities as two different traits.

TABLE 4 Genetic parameter estimates using simulated data based on Landrace pedigree information

Scenario	Model 1[a]				Model 2[a]								
	σ_p^2	σ_a^2	σ_{pe}^2	h^2	σ_{p1}^2	σ_{p2}^2	σ_{a1}^2	σ_{a2}^2	σ_{a12}	σ_{pe2}^2	h_1^2	h_2^2	r_g
1	1.00	0.10	0.10	0.10	1.04	1.04	0.21	0.20	0.20	0.04	0.20	0.19	1.00
SD	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00
2	1.00	0.10	0.00	0.10	1.00	1.00	0.10	0.10	0.10	0.00	0.10	0.10	0.99
SD	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.01
3	1.00	0.10	0.10	0.10	1.04	1.03	0.22	0.19	0.20	0.05	0.21	0.18	0.97
SD	0.01	0.01	0.01	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01
4	1.00	0.09	0.00	0.09	1.00	1.00	0.10	0.10	0.09	0.01	0.10	0.10	0.90
SD	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.04

σ_p^2 = phenotypic variance, σ_a^2 = additive genetic variance, σ_{pe}^2 = permanent environmental variance, h^2 = heritability, σ_{p1}^2 = phenotypic variance for the first parity, σ_{p2}^2 = phenotypic variance for the second and third parities, σ_{a1}^2 = additive genetic variance for the first parity, σ_{a2}^2 = additive genetic variance for the second and third parities, σ_{a12} = genetic covariance between the first parity and the later (second and third) parities, σ_{pe2}^2 = permanent environmental variance for the second and third parities, h_1^2 = heritability for the first parity, h_2^2 = heritability for the second and third parities, r_g = genetic correlation between the first parity and the later (second and third) parities.

[a] See in footnote in Table 3.

parameters were estimated to be almost the same as their true values in Scenarios 2 and 4. These results suggest that the accuracies of genetic parameter estimation using Model 2 are high if the permanent environmental effect on the trait is negligible. Similar results were obtained when using the pedigree information on Large White (Table S1). The genetic parameter estimates were similarly biased when genetic correlations were 0.8 for Scenario 5 and 0.7 for Scenario 6 (Table S2). Genetic parameter estimates regardless of genetic correlation between the first parity and the later parities were similar to those in Scenarios 1 and 3.

When repeated phenotypic measurements including substantial permanent environmental effect, such as NBA, were applied to Model 2, the genetic parameters showed more biased estimations than when applied to Model 1. These results were similar to those from real data.

3.3 | Accuracy of EBVs

The accuracies of EBVs are shown in Table 5. In Scenario 1, the accuracies of EBVs were 0.68 for Landrace and 0.67 for Large White for Model 1. For Model 2, the accuracies of EBVs for the first parity and the later parities were both 0.65 for Landrace and both 0.64 for Large White, which were slightly lower than those obtained using Model 1. Similar results were observed in Scenario 3. On the other hand, Model 1 showed almost the same accuracies of EBVs as Model 2 in Scenarios 2 and 4.

3.4 | General discussion

NBA records can be collected multiple times throughout a dam's life, but the heritability is generally low. In this study, the heritability

Scenario	Correlation	Model 1[b]	SD	Model 2[b]	SD
1	TBV, EBV1	0.68	0.03	0.65	0.03
	TBV, EBV2			0.65	0.03
2	TBV, EBV1	0.69	0.02	0.69	0.02
	TBV, EBV2			0.69	0.02
3	TBV1, EBV1	0.64	0.03	0.62	0.03
	TBV2, EBV2	0.66	0.03	0.64	0.03
4	TBV1, EBV1	0.65	0.02	0.66	0.02
	TBV2, EBV2	0.68	0.02	0.68	0.02

[a]EBV1 = estimated breeding values obtained using Model 1 or estimated breeding values of first parity obtained using Model 2. EBV2 = estimated breeding values obtained using model 1 or estimated breeding values of second and third parities obtained using model 2. TBV = true breeding values. TBV1 = true breeding values of first parity. TBV2 = true breeding values of second and third parity.
[b]See in footnote in Table 3.

of NBA was also estimated to be low (Table 3). Ogawa et al. (2019b) estimated the genetic parameters of NBA in the same populations as in this study using a multiple-trait animal model assuming all parities to be mutually exclusive traits. They reported the estimated genetic correlations between the first and the second parities to be 0.85 for Landrace and 0.84 for Large White, and slightly lower than those between other neighboring parities. Other studies also state that the first and the later parities of NBA may be different (e.g., Fernández et al., 2008; Hermesch et al., 2000). Hence, the analysis using the two-trait model was considered to be useful.

Following their findings, we analyzed the data using the two-trait animal model, assuming that the first parity and the later parities were two different traits. When the two-trait animal model was fitted to real pig data, the estimated heritabilities were higher than those obtained using a single-trait repeatability animal model for both breeds.

Several studies regard NBA in the first and the later parities as two different traits. Some of these studies, and our results, also estimate the heritability of the first parity to be higher than that of the later parities (Oh et al., 2005; Peškovičová et al., 2002). Oh et al. (2005) proposed that the cause of the higher estimated heritability of the first parity than that of the later parities might be due to fitting the permanent environmental effect to the later parities. Peškovičová et al. (2002) also suggested that the heritability of the first parity was higher than that of the later parities because the first parity in the model did not include the permanent environmental effect.

From the above results, we hypothesized that the overestimation of genetic variance was caused by not including the permanent environmental effect of the first parity in Model 2. We therefore tested our hypothesis using a Monte Carlo computer simulation. The results revealed the heritability estimate using Model 2 was about twice as high as that using Model 1. Since this result in the simulation study was similar to that from real data in pigs, we conclude that the

repeatability model is better for estimating heritability than the two-trait model that regards NBA in the first parity and the later parities as two different traits.

There have been discussions, in previous studies, on the over-estimation of heritability of NBA using the two-trait model (Oh et al., 2005; Peškovičová et al., 2002). However, overestimation of the genetic correlation between the first parity and the later parities using the two-trait model has not been noted. In Scenario 3 (true genetic correlation = 0.9), the estimated genetic correlation was 0.97 for both breeds, which means that fitting Model 2 to repeated records could provide an upwardly biased estimation of genetic correlation. On the basis of our findings, any genetic correlations in previous studies using the two-trait animal model might be overestimated. From the real data, the genetic correlations between the first parity and the later parities were estimated to be 0.89 for Landrace and 0.90 for Large White (Table 3). Hence, in this study, true genetic correlation between the first parity and the later parities in the real population in this study would be lower than those estimated.

In Scenarios 1 and 3, the accuracies of EBVs using Model 1 were higher than those using Model 2, even if the genetic correlation was not unity. Hence, when using a two-trait animal model, it may be necessary to correct the phenotypic records of the first parity caused by the permanent environmental effect.

4 | CONCLUSIONS

The genetic parameters for NBA were estimated in Landrace and Large White pigs using the two-trait animal model, which regards the first and later parities as two different traits. Heritability was overestimated when using the two-trait animal model. When we estimated the genetic parameters for NBA using the two-trait animal model without correction of the first parity records based on the permanent environmental effect, the biases of estimated additive genetic and permanent environmental variances were more serious than when fitting the single-trait repeatability animal model. From the result of correlation between EBV and TBV, single-trait repeatability model was better than two-trait animal model.

ORCID

Ayane Konta https://orcid.org/0000-0002-4943-9909
Shinichiro Ogawa https://orcid.org/0000-0002-0537-3311
Yoshinobu Uemoto https://orcid.org/0000-0003-2569-9535
Masahiro Satoh https://orcid.org/0000-0002-9198-6666

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.