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Genetic analysis for sow stayability at different parities in purebred Landrace and Large White pigs

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
Shinichiro Ogawa, Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi 980-8572, Japan.
Email: shinichiro.ogawa.d5@tohoku.ac.jp

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Abstract

Genetic parameters for sow stayability were estimated from farrowing records of 10,295 Landrace sows and 8192 Large White sows. The record for sow stayability from parity k to parity $k + 1$ ($k = 1, ..., 6$) was 0 when a sow had a farrowing record at parity k but not at parity $k + 1$, and 1 when a sow had both records. Heritability was estimated by using single-trait linear and threshold animal models. Genetic correlations among parities were estimated by using two-trait linear–linear and single-trait random regression linear animal models. Genetic correlations with litter traits at birth were estimated by using a two-trait linear–linear animal model. Heritability estimates by linear model analysis were low (0.065–0.119 in Landrace & 0.061–0.157 in Large White); those by threshold model analysis were higher (0.136–0.200 & 0.110–0.283). Genetic correlations among parities differed between breeds and models. Genetic correlation between sow stayability and number born alive was positive in many cases, implying that selection for number born alive does not reduce sow stayability. The results seem to be affected by decisions on culling made by farmers.

KEYWORDS
binary trait, genetic parameter estimation, Landrace, Large White, sow stayability

1 | INTRODUCTION

Sow lifetime productivity is an economically important complex trait for efficient pork production (e.g., Rohrer et al., 2017; Serenius & Stalder, 2006; Stalder et al., 2003). As it is determined by the number of piglets weaned, or an indicator trait such as number born alive (NBA), and the overall parity number (e.g., Kang et al., 2018; Sasaki & Koketsu, 2008; Serenius & Stalder, 2004), it is crucial to elucidate

their associations. The number of piglets weaned and NBA have low estimated heritabilities (e.g., Ogawa et al., 2019a, 2019c; Putz et al., 2015). Overall parity can be measured first after culling. The distribution of the measurements is often obscure: factors influencing the reason for culling can change with time, and it is difficult to distinguish between voluntary and involuntary culling (e.g., Serenius & Stalder, 2006; Sölkner & Ducrocq, 1999; Visscher et al., 1999). Furthermore, heritability has been estimated to be low in many cases (e.g., Le et al., 2016; Paixão et al., 2019; Sobczyńska et al., 2013), and therefore, it is thought to be difficult to efficiently improve sow lifetime productivity by direct selection for overall parity number

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(Le et al., 2016; Serenius & Stalder, 2006). These facts are the same for total lifetime litter size and the length of sow productive life (e.g., Le et al., 2016; Paixão et al., 2019; Sobczyńska et al., 2013).

Genetic parameter estimation for stayability, which is defined as a binary trait relating to survivability in a given environment and is treated as an indicator trait for longevity, has been widely conducted in pigs (Aasmundstad et al., 2014; Abell et al., 2016; Hong et al., 2019; Le et al., 2016; López-Serrano et al., 2000; Poulsen et al., 2020; Serenius et al., 2006; Tholen et al., 1996), dairy cattle (e.g., Abe et al., 2020; Bijma & Jensen, 1996; VanRaden et al., 2016), beef cattle (e.g., Fennewald et al., 2018; Martinez et al., 2005; Silva et al., 2003), horses (e.g., Albertsdóttir et al., 2012; Bugislaus et al., 2005; Langlois & Vrijenhoek, 2004), sheep (Lee et al., 2015; McIntyre et al., 2012), and goats (Scholtens et al., 2018). In pigs, genetic parameters for sow stayability from first parity to a particular time, especially second parity, have been estimated, and threshold model analyses have been performed (Abell et al., 2016; Hong et al., 2019; Le et al., 2016). Genetic correlations of sow stayability with production traits, exterior and leg conformations, lameness, farrowing interval, days open, and NBA at first parity have been also studied (Hong et al., 2019; Le et al., 2016; López-Serrano et al., 2000; Tholen et al., 1996). On the other hand, no study has estimated genetic correlations with number stillborn (NSB), survival rate of piglets at birth (SVB), total litter weight at birth (LWB), and mean litter weight at birth (MWB). Several studies have performed random regression analysis of stayabilities in cattle (e.g., Jamrozik et al., 2008; Jamrozik et al., 2013; Veerkamp et al., 2001) and in Thai Landrace and Large White commercial populations (Plaengkaeo et al., 2020). Factors affecting sow stayability and their effect size could change over time, but there appears to be little published information on the genetic associations of sow stayabilities among different parities.

Here, to obtain information necessary to efficiently improve sow lifetime productivity, we estimated the heritabilities of sow stayabilities at different parities, defined as binary traits, and the genetic correlations of sow stayabilities among parities and with NBA, NSB, SVB, LWB, and MWB in purebred Landrace and Large White pigs using large-scale datasets obtained from a single Japanese pig breeding company.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

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

2.2 | Phenotypic information and pedigree data

CIMCO Corporation (Tokyo, Japan) provided 72,606 farrowing records for 13,747 Landrace sows and 59,116 records for 11,345 Large White sows, obtained during 2000–2018, and pedigree data covering 83,333 Landrace pigs and 72,168 Large White pigs. CIMCO operates two great-grandparent and several grandparent farms on a Specific-Pathogen-Free system across Japan (Ogawa et al., 2019c).

We excluded farrowing records with a negative gestation length, NBA = 0, or MWB outside the mean ± 3 standard deviation (SD); we assumed a mean MWB of 1.48 and SD = 0.23 in both breeds (Damgaard et al., 2003), because the values calculated from our data were greatly affected by obvious outliers (Konta et al., 2019, 2020; Ogawa et al., 2019a, 2019b, 2019c). Next, we extracted sows having all farrowing records from first through final or seventh parities. This gave 43,215 records for 10,295 Landrace sows and 33,513 records for 8192 Large White sows.

Six binary traits for sow stayability—from first to second (STAY12), second to third (STAY23), third to fourth (STAY34), fourth to fifth (STAY45), fifth to sixth (STAY56), and sixth to seventh parities (STAY67)—were defined. The sow stayability from parity k to parity $k + 1$ ($k = 1, ..., 6$) was recorded as 0 when a sow had a calving record at parity k but not at parity $k + 1$, 1 when a sow had both records, and missing when a sow did not have a record at parity k (Figure 1). Table 1 summarizes phenotypic measurements of the traits studied.

2.3 | Numerical analyses

Two kinds of single-trait animal models—linear and threshold—were used to estimate the heritability of sow stayability. The following single-trait linear animal model (denoted as Model 1) was used:

$$y = Xb + Za + e,$$

where y is the vector of phenotypic records; b is the vector of macro-environment effects (farrowing year, 2000–2018; farrowing season, spring [March to May], summer [June to August], autumn [September to November], winter [December to February]; farm, seven levels for Landrace, eight levels for Large White; mating sire breed, Landrace, Large White, Duroc); a is the vector of breeding values; e is the vector

Sow	Has a farrowing record at each parity?						
	1st	**2nd**	**3rd**	**4th**	**5th**	**6th**	**7th**
1	Yes	Yes	Yes	Yes	Yes	Yes	Yes
2	Yes	Yes	Yes	Yes	No	No	No
3	Yes	No	No	No	No	No	No

Sow	STAY12	STAY23	STAY34	STAY45	STAY56	STAY67
1	1	1	1	1	1	1
2	1	1	1	0	Missing	Missing
3	0	Missing	Missing	Missing	Missing	Missing

FIGURE 1 Phenotypic recording of sow stayability traits

TABLE 1 Descriptive statistics of phenotypic measurements of the traits studied

Trait	Abbreviation	Landrace					Large White				
		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
Number born alive	NBA	43,215	10.23	2.72	1	22	33,513	10.21	2.57	1	22
Number stillborn	NSB	43,215	0.66	1.02	0	10	33,513	0.74	1.08	0	10
Survival rate of piglets at birth	SVB	43,215	0.94	0.08	0.33	1.00	33,513	0.94	0.09	0.36	1.00
Total litter weight at birth (kg)	LWB	43,215	15.34	3.77	1.0	31.0	33,513	15.65	3.61	1.1	28.0
Mean litter weight at birth (kg)	MWB	43,215	1.53	0.24	0.79	2.17	33,513	1.56	0.24	0.80	2.17
Stayability from first to second parity	STAY12	10,295	0.80	0.40	0	1	8192	0.80	0.40	0	1
Stayability from second to third parity	STAY23	8276	0.85	0.36	0	1	6563	0.84	0.37	0	1
Stayability from third to fourth parity	STAY34	7008	0.85	0.36	0	1	5507	0.84	0.37	0	1
Stayability from fourth to fifth parity	STAY45	5956	0.83	0.37	0	1	4606	0.81	0.39	0	1
Stayability from fifth to sixth parity	STAY56	4956	0.79	0.41	0	1	3716	0.77	0.42	0	1
Stayability from sixth to seventh parity	STAY67	3903	0.72	0.45	0	1	2860	0.72	0.45	0	1

Abbreviations: Max, maximum value; Min, minimum value; *N*, number of phenotypic records; SD, standard deviation.

of random errors; and **X** and **Z** are the design matrices relating **y** to **b** and **a**, respectively. The mean and variance–covariance of the vectors **a** and **e** were as follows:

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

where σ_a^2 is the additive genetic variance, σ_e^2 is the error variance, **A** is the additive relationship matrix, and **I** is the identity matrix. Variance components were estimated in GIBBS3F90 software (Misztal et al., 2002). A total chain length of 110,000 rounds was run in a single long chain. After the first 10,000 samples were discarded as the burn-in, 1 in every 10 samples was stored. Parameter estimates and their standard errors (SEs) were obtained by calculating the averages and SDs of the 10,000 samples stored, and the 95% confidence intervals (CIs) of were also obtained by using the 10,000 samples.

Estimated heritability, $\widehat{h}^2$, was converted to a liability scale (e.g., Dempster & Lerner, 1950; Gianola, 1982; Robertson & Lerner, 1949), to compare with the results from threshold model analysis, as follows:

$$\frac{\widehat{h}^2 p(1-p)}{z^2},$$

where *p* is the overall incidence of a score of 1 in a population; *z* is an ordinate of a standard normal density function corresponding to a threshold that divides the probability mass into proportions *p* and $1 - p$; and $\frac{p(1-p)}{z^2}$ takes a minimum value of 1.57 when $p = 0.5$.

The following single-trait threshold animal model (Model 2) was used:

$$\boldsymbol{\eta} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where η is the vector of liabilities. The mean and variance–covariance of the vectors **a** and **e** were as follows:

$$E\begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and } \text{var}\begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}.$$

Variance components were estimated in THRGIBBS1F90 software (Tsuruta & Misztal, 2006).

Two kinds of animal models were used to estimate the genetic correlation of sow stayability between parities. First, the following two-trait linear–linear animal model (Model 3) was used:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}.$$

The mean and variance–covariance of the vectors $\mathbf{a}_1$, $\mathbf{a}_2$, $\mathbf{e}_1$, and $\mathbf{e}_2$ were as follows:

$$E\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and } \text{var}\begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a1}^2 & \mathbf{A}\sigma_{a12} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma_{a2}^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{e1}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{e2}^2 \end{bmatrix},$$

where $\sigma_a 12$ is the additive genetic covariance; and the error covariance was fixed at 0 (e.g., Árnason, 1999; Árnason et al., 2012; Meyer & Thompson, 1984). Variance components were estimated in GIBBS3F90 software.

Second, the following single-trait linear random regression animal model (Model 4) was used (Plaengkaeo et al., 2020):

$$y_{ik} = F_{ik} + \sum_{j=0}^{2} \varphi_j(k)b_j + \sum_{j=0}^{2} \varphi_j(k)a_{ij} + \sum_{j=0}^{2} \varphi_j(k)pe_{ij} + e_{ik},$$

where y_{ik} is the record of sow i; F_{ik} is the sum of the macro-environment effects (farrowing year by parity, 103 levels for Landrace, 102 levels for Large White; farrowing season by parity, 24 levels for both breeds; mating sire breed by parity, 18 levels for both breeds; farm by parity, 42 levels for Landrace, 48 levels for Large White); b_j is the regression coefficient of the jth-order Legendre polynomial at parity k, $\varphi_j(k)$ ($j = 0$, 1, or 2); a_{ij} is the regression coefficient of $\varphi_j(k)$ for breeding value of sow i; pe_{ij} is the regression coefficient of $\varphi_j(k)$ for permanent environmental effect of sow i; and e_{ik} is the error. This model can be described in matrix notation as

$$\mathbf{y} = \mathbf{Xb} + \sum_{j=0}^{2} \mathbf{Z}_j \mathbf{a}_j + \sum_{j=0}^{2} \mathbf{W}_j \mathbf{pe}_j + \mathbf{e},$$

The mean and variance–covariance of the vectors $\mathbf{a}_j$, $\mathbf{pe}_j$, and $\mathbf{e}$ were as follows:

$$E \begin{bmatrix} \mathbf{a}_0 \\ \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{pe}_0 \\ \mathbf{pe}_1 \\ \mathbf{pe}_2 \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and}$$

$$\text{var} \begin{bmatrix} \mathbf{a}_0 \\ \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{pe}_0 \\ \mathbf{pe}_1 \\ \mathbf{pe}_2 \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a0}^2 & \mathbf{A}\sigma_{a01} & \mathbf{A}\sigma_{a02} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a01} & \mathbf{A}\sigma_{a1}^2 & \mathbf{A}\sigma_{a12} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a02} & \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma_{a2}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{pe0}^2 & \mathbf{I}\sigma_{pe01} & \mathbf{I}\sigma_{pe02} & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{pe01} & \mathbf{I}\sigma_{pe1}^2 & \mathbf{I}\sigma_{pe12} & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{pe02} & \mathbf{I}\sigma_{pe12} & \mathbf{I}\sigma_{pe2}^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}.$$

Variance components were estimated in GIBBS3F90 software.

The following two-trait linear–linear animal model (Model 5) was used to estimate the genetic correlation of sow stayability at each parity with NBA, NSB, SVB, LWB, and MWB:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{0} \\ \mathbf{W}_2 \end{bmatrix} \mathbf{pe}_2 + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix},$$

where $\mathbf{pe}$ is the vector of permanent environmental effect; $\mathbf{W}$ is the design matrix relating $\mathbf{y}$ to $\mathbf{pe}$; subscripts 1 corresponds to any sow stayability trait, and subscript 2 corresponds to any of NBA, NSB, SVB, LWB, and MWB. Macro-environmental effects for NBA, NSB, SVB, LWB, and MWB were parity, farrowing year, farrowing season, farm, and mating sire breed (Konta et al., 2019, 2020; Ogawa et al., 2019a, 2019b, 2019c). The mean and variance–covariance of vector $\mathbf{a}_1$, $\mathbf{a}_2$, $\mathbf{pe}_2$, $\mathbf{e}_1$, and $\mathbf{e}_2$ were as follows:

$$E \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{pe}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and var} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{pe}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a1}^2 & \mathbf{A}\sigma_{a12} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{a12} & \mathbf{A}\sigma_{a2}^2 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{pe2}^2 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{e1}^2 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_{e2}^2 \end{bmatrix},$$

where the error covariance was fixed at 0 (e.g., Konta et al., 2019; Ogawa et al., 2020; Wolf et al., 2005). Variance components were estimated in GIBBS3F90 software.

3 | RESULTS AND DISCUSSION

3.1 | Descriptive statistics of sow stayability

Mean phenotypic records for sow stayability were similar between breeds (Table 1). STAY12 averaged 0.80, lower than STAY23, STAY34, and STAY45 and higher than STAY56 and STAY67 in both breeds. Means differed among other studies; for example, STAY12 was 0.82 in Landrace and 0.79 in Large White (López-Serrano et al., 2000), 0.85 in Yorkshire (Hong et al., 2019), 0.41 in Landrace (Aasmundstad et al., 2014), 0.63 in Landrace (Abell et al., 2016), and 0.68 in Yorkshire (Le et al., 2016). These differences might be caused in part by the timing of data collection and population management, which both depend on decision making by farmers for culling. In this regard, Tholen et al. (1996) noted different average values of STAY12 among herds.

3.2 | Heritability of sow stayability

Heritabilities of sow stayability estimated using Model 1 were low regardless of breed and parity, ranging from 0.065 to 0.119 in Landrace and from 0.061 to 0.157 in Large White, and additive genetic and error variances varied among parity within breed (Table 2). Heritabilities estimated using Model 2 were also low but were higher than those estimated using Model 1, ranging from 0.136 to 0.200 in Landrace and from 0.110 to 0.283 in Large White. SEs of heritability estimates using Model 2 were larger than those obtained using Model 1, and their 95% CIs largely overlapped with each other. Heritabilities estimated using Model 1 converted to a liability scale ranged from 0.118 to 0.275 in Landrace and from 0.122 to 0.355 in Large White, within the range of 95% CIs of the estimates obtained using Model 2 in most cases.

Previous studies have consistently estimated the heritability of purebred sow stayability to be low by using linear model (Aasmundstad et al., 2014; Le et al., 2016; López-Serrano et al., 2000; Poulsen et al., 2020; Serenius et al., 2006; Tholen et al., 1996) and threshold model (Hong et al., 2019; Le et al., 2016). Aasmundstad et al. (2014), López-Serrano et al. (2000), Poulsen et al. (2020), and Tholen et al. (1996) considered information on reproductive performance of sows, such as age at first farrowing and litter size, into model as macro-environment effects. Some studies considered the common litter environmental effects (Aasmundstad et al., 2014; Hong et al., 2019; López-Serrano et al., 2000; Serenius et al., 2006), and Serenius et al. (2006) reported that the heritability was estimated to be slightly lower when using model considering the common litter environmental effects than when using model ignoring it, which were also observed for several body measurement and meat production traits (Ogawa et al., 2021; Ohnishi & Satoh, 2018). Le et al. (2016) estimated the heritability of STAY12 to be higher when using

TABLE 2 Genetic parameters for sow stayability traits estimated by using single-trait linear and threshold animal models (Models 1 and 2)

Trait	Linear model							Threshold model		
	Phenotypic variance			Heritability				Heritability		
	Estimate	SE	95%CI	Estimate	SE	95%CI	Converted[a]	Estimate	SE	95%CI
Landrace										
STAY12	0.139	0.002	0.135 to 0.143	0.105	0.024	0.066 to 0.168	0.217	0.200	0.039	0.117 to 0.274
STAY23	0.107	0.002	0.103 to 0.110	0.119	0.025	0.077 to 0.170	0.275	0.189	0.034	0.121 to 0.264
STAY34	0.107	0.002	0.104 to 0.111	0.087	0.021	0.049 to 0.126	0.204	0.141	0.042	0.067 to 0.220
STAY45	0.124	0.002	0.120 to 0.129	0.107	0.023	0.060 to 0.151	0.237	0.174	0.042	0.105 to 0.272
STAY56	0.142	0.003	0.136 to 0.148	0.065	0.016	0.041 to 0.104	0.130	0.136	0.040	0.056 to 0.210
STAY67	0.173	0.004	0.165 to 0.181	0.066	0.025	0.017 to 0.118	0.118	0.154	0.041	0.096 to 0.252
Large White										
STAY12	0.138	0.002	0.134 to 0.142	0.061	0.015	0.034 to 0.090	0.125	0.200	0.039	0.117 to 0.274
STAY23	0.112	0.002	0.107 to 0.116	0.157	0.027	0.107 to 0.210	0.355	0.189	0.034	0.121 to 0.264
STAY34	0.116	0.002	0.112 to 0.121	0.084	0.029	0.043 to 0.145	0.189	0.141	0.042	0.067 to 0.220
STAY45	0.134	0.003	0.129 to 0.140	0.116	0.028	0.058 to 0.174	0.241	0.174	0.042	0.105 to 0.272
STAY56	0.144	0.003	0.137 to 0.151	0.092	0.023	0.059 to 0.139	0.176	0.136	0.040	0.056 to 0.210
STAY67	0.173	0.005	0.164 to 0.182	0.068	0.028	0.027 to 0.128	0.122	0.154	0.041	0.096 to 0.252

Note: See Table 1 for abbreviations of trait names.
Abbreviations: 95% CI, 95% confidence interval; SE, standard error.
[a]Heritability estimates by linear model analyses were converted to a liability scale according to Robertson and Lerner (1949).

threshold model (0.18) than when using linear model (0.08), which was also observed in this study (Table 2). On the other hand, only Abell et al. (2016) estimated the heritability of STAY12 in purebred Landrace sows to be 0.81 using threshold model and denoted that this was not unexpected because selection decisions are made based on the genetic potential of a sow; however they did not estimate the heritability by using linear model. Poulsen et al. (2020) proposed that the difference in estimated heritability among studies could be due to the difference not only in statistical modeling but also in the type and number of farms analyzed (e.g., nucleus vs. commercial). None of the previous studies compared the value of heritability estimated using linear model and converted to a liability scale with that estimated using threshold model.

3.3 | Genetic correlation of sow stayability among parities

By Model 3, estimated genetic correlations of sow stayability among parities ranged from −0.138 to 0.685 in Landrace and from −0.490 to 0.779 in Large White (Table 3), with similar additive genetic and error variances to those estimated by single-trait linear animal model analysis. Patterns of estimated genetic correlations seem to differ between breeds and to be less associated with parity than those in the previous study of NBA (Ogawa et al., 2019b). Here, the error covariance was fixed at 0 (e.g., Árnason, 1999; Árnason et al., 2012; Meyer & Thompson, 1984), which might bias estimates of genetic parameters (Árnason et al., 2012). Gates et al. (1999) assessed the

performance of multiple- (including binary) trait analysis, estimated the error covariances by computer simulation and "quasi-REML" approach, and discussed the effect of the overall incidence, selection, confounding, and sign of the value of the true error correlation on estimating genetic and error correlations. However, in our study, the record at a lower parity of a sow, which also has a record at a higher parity, is always 1 (e.g., Árnason, 1999; Árnason et al., 2012; Meyer & Thompson, 1984), unlike in Gates et al. (1999). Here, we attempted to estimate the error covariance, but the results were hard to interpret because the estimated additive genetic and error variances were different from those estimated by single-trait analysis, and genetic and error correlations were sometimes both negative.

By Model 4, the estimated genetic correlations ranged from −0.022 to 0.952 in Landrace and tended to decrease as the parities were more distance (Table S1). Those between adjacent parities ranged from 0.733 to 0.952, sometimes lower than the threshold of 0.8 suggested by Robertson (1959). However, the values were inconsistent with those estimated by two-trait model analysis. In Large White, on the other hand, the estimated error variance was very small, and the phenotypic variance was overestimated (Table S1), causing the "blowing up" phenomenon (Hoeschele & Tier, 1995). The possibility of the "extreme category problem" increases in categorical trait analysis when the modeling becomes more complicated (e.g., Hoeschele & Tier, 1995; Luo et al., 2001; Misztal et al., 1989). In this study, the number of records was lower for Large White (Table 1), which might also be a reason why the blowing up phenomenon was observed only for Large White. Macro-environment effects included in the random regression model were set to be similar to those in

TABLE 3 Genetic correlations ± standard errors (SEs) and 95% confidence intervals in parentheses of sow stayability traits among parities estimated by using a two-trait linear–linear animal model (Model 3)

Trait	STAY12	STAY23	STAY34	STAY45	STAY56	STAY67
STAY12		0.756** ± 0.117 (0.489 to 0.923)	0.779** ± 0.144 (0.470 to 0.943)	0.353* ± 0.209 (−0.009 to 0.707)	0.494** ± 0.171 (0.088 to 0.736)	−0.357* ± 0.232 (−0.745 to 0.054)
STAY23	0.225* ± 0.162 (−0.084 to 0.533)		−0.139 ± 0.225 (−0.492 to 0.353)	0.320* ± 0.183 (−0.070 to 0.649)	−0.073 ± 0.170 (−0.359 to 0.252)	0.201 ± 0.238 (−0.340 to 0.539)
STAY34	0.105 ± 0.218 (−0.343 to 0.473)	0.625** ± 0.114 (0.391 to 0.796)		0.258* ± 0.169 (−0.124 to 0.561)	0.336* ± 0.171 (−0.057 to 0.615)	0.129 ± 0.328 (−0.454 to 0.657)
STAY45	0.278** ± 0.128 (0.033 to 0.528)	0.615** ± 0.169 (0.286 to 0.926)	0.107 ± 0.175 (−0.288 to 0.473)		−0.063 ± 0.225 (−0.474 to −0.364)	−0.490** ± 0.190 (−0.746 to 0.017)
STAY56	−0.138 ± 0.254 (−0.566 to 0.454)	0.394* ± 0.198 (−0.061 to 0.699)	0.112 ± 0.310 (−0.408 to −0.673)	0.654** ± 0.191 (0.287 to 0.905)		0.021 ± 0.238 (−0.509 to 0.415)
STAY67	0.447* ± 0.279 (−0.026 to 0.875)	0.211 ± 0.332 (−0.551 to 0.648)	0.685** ± 0.126 (0.444 to 0.888)	0.414** ± 0.126 (0.171 to 0.642)	0.351* ± 0.249 (−0.074 to 0.830)	

Note: See Table 1 for abbreviations of trait names. Bottom left, Landrace; top right Large White.

*The absolute value of the estimate was greater than SE.

**The absolute value of the estimate was greater than 2 SE.

the two-trait animal model, which might make the modeling too complicated. Plaengkaeo et al. (2020) used a simpler model including only the discrete effect of herd–year–season and the linear covariate of age at first farrowing as macro-environment effects. Here, the macro-environment effects in the single-trait model were determined according to previous studies of this population (Konta et al., 2019, 2020; Ogawa et al., 2019a, 2019b, 2019c), which could complicate the analytical model. Using a simpler model might reduce the possibility of blowing up (Hoeschele & Tier, 1995), but the estimated value could be biased owing to confounding (Gates et al., 1999).

3.4 | Genetic correlations of sow stayability with litter traits at farrowing

Estimated genetic correlations with NBA using Model 5 ranged from 0.159 to 0.595 in Landrace and from −0.014 to 0.556 in Large White, being positive except for the almost negligible correlation of −0.014 with STAY12 in Large White (Table 4). The results imply that selection for NBA would not immediately harm sow stayability. Estimated values tended to be higher when the parity was higher, which seems to be dependent on the sow culling scheme. On the GGP farms, male and female animals with estimated breeding values for NBA and total litter weight at weaning greater than their sires and dams, respectively, are selected as candidates at 20 weeks of age based on their phenotypic performance for 18 body and leg conformation traits only from litters without piglet having hernia or prolapse (Ogawa et al., 2019c). Estimated breeding values of replacement gilts with higher reliabilities can be obtained after recording one or more farrowing performances of their own, and sows in production herd with worse estimated breeding values have more risk of being culled. These facts might affect our results. Hong et al. (2019) estimated the genetic correlation between STAY12 and NBA at first parity to be 0.31 in Yorkshire pigs of a Korean company.

The estimated genetic correlation of sow stayability was negative with NSB and positive with SVB in both breeds, but the absolute values were larger for SVB than for NSB. A possible reason is that SVB includes information not only on NSB but also on NBA. The estimated genetic correlation with MWB was negative. MWB might be higher when NBA is lower or oversized piglets are born. Some of the sows with a higher MWB might be culled because such a farrowing could be related to reproductive disorders including dystocia especially at first parity, although one of the major culling reasons could be lower NBA. The estimated genetic correlation with LWB was negative for STAY12 in Landrace and for STAY12 and STAY23 in Large White but was positive at later parities in both breeds. This difference might be associated with the change in the genetic correlations with NBA and MWB over parity and the fact that total litter weight at weaning, which has a positive genetic correlation with LWB, was considered at selection for sows in this population (Ogawa et al., 2019c).

3.5 | General discussion

We estimated genetic parameters for binary traits relating to sow stayability at different parities in purebred Landrace and Large White pigs of a single Japanese pig breeding company, using several different models. We also estimated the variance components by using Models 1, 3, and 5 in AIREMLF90 software (Misztal et al., 2002), and the results were similar (Tables S2, S3, and S4), whereas the REML estimates were diverged when using Model 4 in Large White. Heritability estimates obtained by using Model 1 were low in both breeds and at all parities (Table 2), and the random regression model analysis with Model 4 could not give reliable results (Table S1). These facts indicate the difficulty in binary-trait analysis and the fact that efficiently improving sow stayability by direct selection would be difficult (Aasmundstad et al., 2014; Hong et al., 2019; Le et al., 2016;

TABLE 4 Estimated genetic correlations ± standard errors (SEs) and 95% confidence intervals in parentheses of sow stayability traits with litter traits at farrowing by using a two-trait linear animal model (Model 5)

Trait	STAY12	STAY23	STAY34	STAY45	STAY56	STAY67
Landrace						
NBA	0.159* ± 0.082 (−0.013 to 0.309)	0.321** ± 0.067 (0.188 to 0.458)	0.584** ± 0.057 (0.475 to 0.697)	0.548** ± 0.064 (0.415 to 0.670)	0.595** ± 0.086 (0.420 to 0.741)	0.422** ± 0.089 (0.247 to 0.585)
NSB	−0.234** ± 0.083 (−0.388 to −0.070)	−0.201** ± 0.084 (−0.377 to −0.053)	−0.060 ± 0.088 (−0.218 to 0.124)	−0.070 ± 0.080 (−0.225 to 0.096)	−0.232** ± 0.099 (−0.422 to −0.043)	−0.484** ± 0.104 (−0.659 to −0.263)
SVB	0.334** ± 0.081 (0.158 to 0.475)	0.246** ± 0.076 (0.095 to 0.391)	0.152* ± 0.094 (−0.040 to 0.335)	0.197** ± 0.088 (0.017 to 0.375)	0.328** ± 0.086 (0.168 to 0.493)	0.524** ± 0.105 (0.330 to 0.708)
LWB	−0.214** ± 0.085 (−0.407 to −0.060)	0.160** ± 0.059 (0.039 to 0.275)	0.442** ± 0.065 (0.325 to 0.574)	0.475** ± 0.062 (0.343 to 0.598)	0.467** ± 0.083 (0.314 to 0.622)	0.168* ± 0.100 (−0.036 to 0.355)
MWB	−0.514** ± 0.079 (−0.681 to −0.369)	−0.277** ± 0.062 (−0.404 to −0.157)	−0.236** ± 0.068 (−0.357 to −0.100)	−0.082* ± 0.068 (−0.214 to 0.056)	−0.165* ± 0.093 (−0.364 to 0.003)	−0.395** ± 0.094 (−0.563 to −0.232)
Large White						
NBA	−0.014 ± 0.107 (−0.212 to 0.194)	0.144* ± 0.081 (−0.012 to 0.288)	0.479** ± 0.085 (−0.302 to 0.656)	0.363** ± 0.071 (0.229 to 0.513)	0.431** ± 0.104 (0.249 to 0.677)	0.556** ± 0.098 (0.381 to 0.754)
NSB	−0.430** ± 0.085 (−0.573 to −0.256)	−0.212** ± 0.083 (−0.360 to −0.039)	−0.138* ± 0.092 (−0.309 to 0.033)	−0.270** ± 0.085 (−0.443 to −0.104)	−0.293** ± 0.092 (−0.464 to −0.102)	−0.352** ± 0.124 (−0.597 to −0.119)
SVB	0.474** ± 0.115 (0.248 to 0.661)	0.248** ± 0.085 (0.085 to 0.410)	0.197** ± 0.096 (0.005 to 0.376)	0.346** ± 0.088 (0.177 to 0.527)	0.355** ± 0.134 (0.135 to 0.701)	0.506** ± 0.126 (0.260 to 0.743)
LWB	−0.360** ± 0.082 (−0.506 to −0.187)	−0.052 ± 0.072 (−0.186 to 0.088)	0.229** ± 0.079 (0.076 to 0.391)	0.182** ± 0.070 (0.043 to 0.332)	0.216** ± 0.105 (0.030 to 0.450)	0.235** ± 0.113 (0.025 to 0.463)
MWB	−0.555** ± 0.078 (−0.693 to −0.394)	−0.347** ± 0.066 (−0.469 to −0.209)	−0.453** ± 0.080 (−0.602 to −0.298)	−0.313** ± 0.076 (−0.469 to −0.168)	−0.361** ± 0.091 (−0.530 to −0.173)	−0.446** ± 0.108 (−0.655 to −0.235)

Note: See Table 1 for abbreviations of trait names.
*The absolute value of the estimate was greater than SE.
**The absolute value of the estimate was greater than 2 SE.

López-Serrano et al., 2000; Poulsen et al., 2020; Serenius et al., 2006; Tholen et al., 1996).

As far as we know, this is the first study to estimating genetic correlations of sow stayability with NSB, SVB, LWB, and MWB. Genetic correlations with other traits have been estimated (Hong et al., 2019; Le et al., 2016; López-Serrano et al., 2000; Tholen et al., 1996). Associations with maternal performance and mothering ability, within-litter variation of piglet birth weight and pattern of litter size variation over parity, and resilience indicators should also be investigated (Damgaard et al., 2003; Dobrzański et al., 2020; Gäde et al., 2008; Poulsen et al., 2020).

Factors affecting stayability can be divided into voluntary and involuntary. The latter affects "functional" stayability (e.g., Abe et al., 2020; Oliveira et al., 2020; Valencia-Posadas et al., 2017), which might be a trait to be truly improved. However, it is often difficult to use detailed information about reasons for culling. As a compromise, an indirect evaluation of sow functional stayability could be performed, for example by including the effects of NBA and other indicators possibly relating to voluntary culling in analytical model (Poulsen et al., 2020). In many cases, the final goal of improving sow lifetime productivity is a crossbred population. Previous studies have analyzed the stayability of crossbred sows (Abell et al., 2016; Engblom et al., 2009; Engblom et al., 2016; Poulsen et al., 2020; Serenius et al., 2006). From this perspective,

further study will be needed to improve sow lifetime productivity (e.g., Bijma & van Arendonk, 1998; Steyn et al., 2021; Wientjes & Calus, 2017).

4 | CONCLUSION

We estimated low heritability of sow stayability in Landrace and Large White populations of a single Japanese pig breeding company, irrespective of model (linear or threshold), breed (Landrace or Large White), and parity (first to seventh). Estimated genetic correlations of sow stayability among parities differed between breeds and models (two-trait linear–linear model and single-trait random regression linear model). Estimated genetic correlations of sow stayability with traits relating to farrowing performance (NBA, NSB, SVB, LWB, & MWB) were considered to reflect of the content of decision making by farmers. In particular, the genetic correlation with NBA was promising in many cases, indicating that improving NBA does not readily inhibit sow stayability.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

ORCID

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 at the end of this article.

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