



Estimation of Genetic Parameters for Four Reproduction Component Traits in Two Chinese Indigenous Pig Breeds*

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ABSTRACT : The reproduction component traits are important components of sow efficiency. The objective of this study was to evaluate the phenotypic and genetic parameters of four reproduction component traits (age at puberty (AP), preweaning number dead (PND), weaning to service interval (WSI), and intra-individual SD in litter size (IISDLS)) of sows in two Chinese indigenous pig breeds. Available reproductive records including 22,591 piglets born from 2,054 litters by 574 Jiangquhai sows and 464 Meishan sows were used in this investigation. A set of mixed models and restricted maximum likelihood methodology were used for the multiple trait analyses of these traits. The results showed that the estimates of heritabilities (\pm standard error) for AP, PND, WSI and IISDLS were 0.40 ± 0.05 , 0.06 ± 0.03 , 0.20 ± 0.02 and 0.09 ± 0.03 in Jiangquhai sows, and 0.35 ± 0.06 , 0.05 ± 0.03 , 0.18 ± 0.03 and 0.10 ± 0.04 in Meishan sows, respectively. There was moderate genetic correlation between AP and WSI, while there were low genetic correlations between the other pairwise traits. The genetic correlations were positive for most of the pairwise traits, except for the one between AP and IISDLS. The results indicated that all traits except for AP were difficult to make genetic improvement by traditional selection methods due to low heritabilities and the favorable improvement of AP might result in unfavorable changes of IISDLS due to the trend of genetic antagonism. (**Key Words :** Sow, Reproduction Component Trait, Heritability, Genetic Correlation)

INTRODUCTION

The reproductive performance of the sow is one of the key factors affecting production profitability of the pig industry (Jiang et al., 2002). In studies on porcine reproduction performance over past years, the main efforts were focused on estimating genetic parameters or dissecting molecular architecture controlling genetic variation of litter size (Rothchild et al., 1996; Short et al., 1997; Vincent et al., 1998; Zhu et al., 2001; Lukovic et al., 2007), and few researchers gave high attention to other reproduction component traits in practice. Nevertheless, it has been gradually accepted that some reproduction component traits

are important components affecting sow efficiency, which make valuable or potential contributions to production profitability. Obviously, there is much importance attached to in-depth research of the phenotypic and genetic characteristics of reproduction component traits.

The reproduction component traits of sows can be generally classified into two different types: the direct and the indirect component traits. The former usually comprises the basic physiological or directly recorded characters such as number of corpus luteum or ovulation rate, placental surface area, fetal weight, number of mummies, gestation length, etc. The latter mainly accommodates the statistically transformed secondary traits, e.g., variation of piglets weight at birth or weaning, variation of litter size across parities of a sow, number of live piglets per sow per annum and other statistical indicators derived from the former or litter size. It is obvious that the indirect component traits reveal the variation, consistency or stability of individual performance or annual production efficiency. There are also other possible ways in which reproduction component traits affect profitability of pig production. For instance, the more unfavorable reproduction component traits require more human, financial and material resources in organization and

* This work was supported by Key Project of National Basic Research and Developmental Plan (2006CB102105) of China, National Natural Science Foundation of China (30571328), and National High Technology Research and Development Program (2007AA10Z148).

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Received October 1, 2007; Accepted February 15, 2008

Table 1. Summary of available data from Jiangquhai and Meishan sows

Variables	JQH	MS
Genetic groups No.	12	8
Dams No.	574	464
Litters No.	1,108	946
Piglets No.	12,342	10,249

JQH = Jiangquhai sows, and MS = Meishan sows.

The same abbreviations were used in the following Tables.

management of the pig industry, and even might lead to the lower yield of other inheritably related economic traits. From a viewpoint of economics, we suggest that the reproduction component traits with potential influence on production efficiency should be considered as the breeding objective when planning the future new pig breeding program. As usual, most of the reproduction traits are low heritability traits and difficult to genetically improve by using traditional selection methods, which essentially rank the order of selection indexes or estimated breeding values of individuals in a breeding population. It is necessary to reveal whether or not the secondary reproduction component traits are of as low heritability as the ordinary reproduction traits.

Jiangquhai and Taihu pigs are two types of Chinese indigenous pig breeds with eximious reproduction performance. Especially Meishan pigs, one of seven sub-breeds of Taihu pigs which are very well known to the world, have been widely used in the construction of resource populations for QTL mapping studies (Sato et al., 2003; Houston et al., 2005; Lee et al., 2005). Comparing with other breeds, besides the highest litter size, these two breeds have many other prominent characters such as sound mothering ability, good adaptability to crude diet, good anti-disease competence, excellent meat quality etc. (Zhang, 1986; Zhang, 1991). They are acknowledged as excellent maternal genetic material to improve the reproduction performance of other low yield breeds. In our previous studies, the detailed characteristics of litter size, litter weight at birth and individual weight at weaning of these two breeds were investigated (Ding et al., 1999; Zhu et al., 2000; Ge et al., 2001). However, other interesting reproduction component traits have not been explored until now. The aim of this study was to estimate the phenotypic and genetic parameters of four reproduction component traits of these two pig breeds, which included age at puberty (AP), preweaning number dead (PND), weaning to service interval (WSI), and intra-individual SD in litter size (IISDLS).

MATERIALS AND METHODS

Management and feeding

Sows of Jiangquhai and Meishan pigs in this

investigation came from the State Conservation Farm in Jiangsu province of China. The management and feeding conditions of the two breeds were similar. Pigs were raised in housed conditions and all adult sows were kept in separate pens. Immature replacement gilts ate without confinement and the adult sows were maintained under controlled-feeding conditions and fed daily at ~2.8 kilogram per sow. All sows were fed with farm-special designed powdered diets. The energy level in the diet varied from 11.7 to 12.5 MJ/kg and crude protein varied from 11.5 to 14.5% according to the fallow, gestation and lactation period of sows. Drinking water was available constantly. In addition, green vegetables were supplied daily on a small-scale. Under the farm management systems, the lactation period of Jiangquhai pigs continued until 45 days, while Meishan pigs continued until 30 days. In this study, the management and feeding systems were fairly constant throughout the period of original data production.

Data preparation

After editing the original data set, all available reproduction records of two breeds including 22,591 piglets born in 2,054 litters by 1,038 multiparous sows (574 Jiangquhai sows and 464 Meishan sows) were obtained to measure AP, PND, WSI and IISDLS. All the pedigree information was traced back according to the pedigree records, and sire group numbers, dam numbers and concrete kindred structures of each breed were available in detail. A brief description of raw data and pedigree records is presented in Table 1.

All analytical traits in this investigation were measured or calculated according to the edited records. AP was defined as the days from birth to the first emergence of detectable estrus time in the gilt. The estrus times were confirmed and recorded by experienced veterinary technical staff. PND was defined as the total number of dead or lost piglets during lactation, which was denoted by the discrepant numbers between piglets at weaning and piglets born alive when the midway cross-fostering did not happen. WSI was defined as the days from weaning time to the next successful service time. There was no artificial control of sows' estrus in the farm management system and the weaning time and successful service time were extracted from the raw data records. IISDLS, namely the index of the stability of litter size among parities of a specific individual, was defined as the standard deviation of litter sizes from all parities of a sow. The formula for calculating IISDLS was as follow:

$$\text{IISDLS} = \sqrt{\frac{\sum_{i=1}^n (X_i - \bar{X})^2}{n}}$$

Where, n was the total number of parities of a sow; X_i

was the litter size of i^{th} parity; and \bar{X} was the average of litter sizes from all parities of a sow. Thereinto, litter size was the number born alive because the total number born in the raw data set was recorded fragmentarily in the earlier period.

Statistical and genetic analyses

Descriptive statistics of AP, PND, WSI and IISDLS included the test of normality, significance test of difference for breeds and the estimates of other conventional statistical parameters. Based on the kurtosis and skewness coefficients, the D'Agostino-Pearson test for normality was used to evaluate the data sets. The statistical difference of four traits between two breeds was detected based on the Student's t -test technique, and hereinto both PND and WSI were the total average of all parities of an individual in a simple consideration. The main statistical analyses were performed by the PROC UNIVARIATE procedure in the SAS software package (SAS Inst. Inc., Cary, NC).

Genetic parameters were estimated using the restricted maximum likelihood (REML) algorithm applied to a multiple-trait mixed model. To lighten computation burden, before the final mixed model was solved, four traits were analyzed firstly with a single-trait model to determine significant factors as well as their first-order (two-way) interactions. The candidate factors included year-season, house number, mating type (pure mating and cross mating, only for PND), age (covariate for IISDLS), and number born alive (covariate for PND and WSI). House number was excluded for all traits, mating type for PND was also excluded, and no significant interactions were found. In addition, one-way ANOVA analyses were performed to adjust the class levels of year-season to new levels following the criterion that different classes without statistically significant difference were incorporated into the same class. The significant fixed effects, confirmed by the aforementioned analyses, and random effects were then included in the mixed model for multiple-trait analysis of the four traits. The mixed models of AP, PND, WSI and IISDLS were respectively as following:

$$y_{ijl} = YS_i + G_j + a_l + e_{ijl} \quad (1)$$

$$y_{ijkl} = YS_i + G_j + P_k + a_l + e_{ijkl} \quad (2)$$

$$y_{ijkl} = YS_i + G_j + P_k + b_1(NBA)_{ijkl} + a_l + e_{ijkl} \quad (3)$$

$$y_{ijl} = YS_i + G_j + b_2(AGE)_{ijl} + a_l + pe_l + e_{ijl} \quad (4)$$

Where, y was the observation; YS was the fixed effect of the adjusted year-season; G was the fixed effect of genetic

group; P was the fixed effect of parity; b_1 was a fixed regression coefficient of y on number born alive (NBA) of the sow in which the measurement was observed; b_2 was a fixed regression coefficient of y on age (AGE) of the sow in which the measurement was observed; a was the random additive genetic effect of sow; pe was the permanent environment effect of sow; and e was the random residual term. The effects of animal, permanent environment and residual were assumed random with zero means and variances $A \otimes G_0$, $I \otimes P_0$ and $I \otimes R_0$, where I was identity matrix; A was additive genetic relationship matrix between animals; and G_0 , P_0 and R_0 were (co)variance matrices of the traits for additive genetic, permanent environment and residual effects, respectively. The models were rewritten in a general matrix form:

$$y = X\beta + Za + Wp + e$$

Where, y was the observation vector, β was the vector of fixed effects, a was the vector of animal genetic effect, p was the vector of permanent environmental effects (only for IISDLS), and e was the vector of residuals. Matrices X , Z , W were corresponding incidence matrices.

In solution of models, the convergence criterion was set to 1.0×10^{-8} . The standard errors of genetic parameters were calculated using the estimated standard errors of corresponding (co)variance components based on the standard error propagation rules. Referenced to the studies (Bai et al., 2006; Oh et al., 2006), the free MTDFREML programs were used to run the models for obtaining the genetic (co)variances and corresponding standard errors (Boldman et al., 1997). All analyses of each breed were performed separately.

RESULTS

Phenotypic traits

Table 2 depicts descriptive statistics and distribution characteristics of the phenotypic values of the four traits. All traits except for PND were significantly different statistically between the two breeds. There existed a trend for AP and WSI of Jiangquhai sows to be earlier or shorter than Meishan sows, while the opposite applied for IISDLS between the two breeds. None of the D'Agostino-Pearson tests was statistically significant, and all the p -values exceeded the critical point to accept the hypothesis H_0 at the 0.5% level. The test results suggested that the distributions of data of all traits in each breed were approximately true of a normal distribution and data transformation was not required before subsequent model solutions, although logarithmic transformation had been involved when analyzing the weaning to first service interval in previous

Table 2. Descriptive statistics of age at puberty, preweaning number dead, weaning to service interval, and intra-individual SD in litter size

Parameters	AP		PND		WSI		IISDLS	
	JQH	MS	JQH	MS	JQH	MS	JQH	MS
Minimum	38	64	0	0	2.5	3	1.02	1.00
Maximum	128	115	5.2	4	18	22	6.75	6.34
Mean	84.82A	96.61B	1.38	1.25	4.88a	5.92b	3.84A	3.22B
p-value of t-test	0.00		0.14		0.01		0.00	
SD	16.25	13.62	1.45	1.44	4.12	5.02	1.25	1.02
Kurtosis	-0.47	0.54	0.36	0.23	1.34	1.24	-0.13	0.02
Skewness	-0.20	-0.08	0.45	-0.63	1.92	1.22	0.64	0.72
p-value for distribution	0.42	0.39	0.60	0.52	0.10	0.05	0.56	0.23

SD = Std. deviation; AP = Age at puberty (day), PND = Preweaning number dead (No.), WSI = Weaning to service interval (day) and IISDLS = Intra-individual SD in litter size (No.), respectively. p-values of *t*-test denoted the statistical significance of phenotypic difference of means between two breeds. p-value for distribution denoted D'Agostino-Pearson test for deviation of an empirical frequency distribution from normal distribution ($p < 0.05$ indicating significant deviation).

studies (ten Napel et al., 1995; Imboontaa et al., 2007).

Heritabilities

The heritabilities of the analyzed traits ranged between 0.05 and 0.40 in two breeds (Tables 3 and 4). The highest heritability was found for AP, whereas the trait PND had the lowest heritability. In total, the heritability estimates were moderate for AP, while low were for the other traits. The heritability estimates of AP, PND and WSI were approximately in agreement with previous other reports (ten Napel et al., 1995; Sterning et al., 1998; Zhang et al., 2000; Damgaard et al., 2003; Holm et al., 2004; Mesa et al., 2006), but to our knowledge there are no reference literature for the novel trait IISDLS.

Phenotypic and genetic correlations

The results of phenotypic and genetic correlations are given in Table 3 and 4 for Jiangquhai and Meishan sows, respectively. Correlations on a phenotypic scale were inferred to be low judging from the present results, and especially a negative correlation was shown between AP

and IISDLS and the correlation between AP and PND was close to zero in both breeds; it needs to be further confirmed whether there are similar trends in other pig breeds. On a genetic scale, a relatively high positive correlation existed between AP and WSI, and this estimate fell within the range of a previous study (Sterning et al., 1998). Conversely, the estimate of AP had a low negative association with that of IISDLS, which indicated a low genetic antagonism between this pair of traits. In addition, the genetic correlations of AP with PND and WSI with IISDLS were also low. In summary, there were low to moderate genetic correlations between analytical traits in the two breeds, and most of the genetic correlations were positive except for the negative ones between AP and IISDLS.

DISCUSSION

Although litter size is a pivotal economically important trait, the reproduction performance of the sow is generally measured by using other economic-related indicators rather than directly by using litter size. Such economic indicators,

Table 3. Heritabilities, phenotypic and genetic correlations for age at puberty, preweaning number dead, weaning to service interval, and intra-individual SD in litter size in Jiangquhai sows

	AP	PND	WSI	IISDLS
AP	0.40±0.05	0.03±0.10	0.38±0.07	-0.12±0.09
PND	0.04	0.06±0.03	0.24±0.08	0.21±0.10
WSI	0.14	0.07	0.20±0.02	0.09±0.08
IISDLS	-0.15	0.12	0.16	0.09±0.03

Figures on the diagonal were the heritabilities (\pm standard error), figures upper off-diagonals were genetic correlations (\pm standard error), and figures lower off-diagonals were phenotypic correlations. This note also applies to Table 3.

Table 4. Heritabilities, phenotypic and genetic correlations for age at puberty, preweaning number dead, weaning to service interval, and intra-individual SD in litter size in Meishan sows

	AP	PND	WSI	IISDLS
AP	0.35±0.06	0.12±0.12	0.36±0.09	-0.10±0.10
PND	0.02	0.05±0.03	0.20±0.09	0.26±0.12
WSI	0.12	0.10	0.18±0.03	0.16±0.09
IISDLS	-0.17	0.13	0.11	0.10±0.04

e.g., the number of produced pigs per sow per annum, were tightly dependent on several reproduction component traits such as precocity for first service success, lactation length, weaning to service (estrus) interval, piglet mortality, etc. (Aumaitre et al., 1976; Damgaard et al., 2003). Much of the variation of reproduction component traits is due to management and environmental effects (Britt, 1986; Tantasuparuk et al., 2000; Damgaard et al., 2003); but Martinat Botte et al. (1985a, 1996b) and Tholen et al. (1996) considered that genetic variation also exists because many of these traits differ among breeds and breed crosses. Under controlled management and environment conditions, genetic factors could play a key role in determining the actual performance. Given these, it is worthwhile to investigate the phenotypic and genetic characters of reproduction component traits in a modern pig industry.

This research was mainly intended to estimate the phenotypic and genetic parameters of four reproduction component traits of Jiangquhai and Meishan sows, so as to primarily evaluate their breeding importance in improving reproductive merit of other low yield breeds. In Table 2, the phenotypic characteristics of AP, PND, WSI and IISDLS in Jiangquhai and Meishan sows were comparatively revealed. Difference between the two breeds was found on the phenotypic scale. Puberty of Jiangquhai sows was much earlier than for Meishan sows, and the dates of the earliest arrival at puberty differed by 26 days. In general, earlier puberty can remarkably reduce the feeding cost of sows. Arrival at puberty one month earlier can save 120 kg feed and increase productivity by 5-8 piglets per year (Legault, et al., 1984). In our opinion, the favorable allele for earlier puberty in the genome of Jiangquhai pigs provides a valuable resource for improving modern commercial pig breeds. Compared with low yield breeds, sows of prolific breeds usually have an earlier arrival at puberty, and this leads to a misconception that the age at puberty is essentially associated with prolificacy. In our previous report, the mean litter sizes of Jiangquhai and Meishan sows in all parities were severally 12.2 and 12.4 piglets per litter without statistically significant difference (Zhu et al., 2000), but, in this investigation, the age at puberty of the two breeds significantly differed by almost half of a month (Table 2). This result suggests that the age at puberty and prolificacy have no inevitable association in nature, which, of course, needs further confirmation in other pig breeds. Pre-weaning number dead, related to genetic and environmental (nutrition and management) factors, is an important source of economic loss to the pig industry. Piglet death mainly occurs during early lactation of sows, and there is a very high genetic correlation between piglet number of early and later periods of lactation (Su et al., 2007), in which 60% of pre-weaning number dead occurs in

the first 3 days approximately. In this research, although the lactation of Jiangquhai sows was longer, PND of Jiangquhai sows was very close to that of Meishan sows, without statistically significant difference. Considering that piglet death rarely occurs in later lactation, we deduce there is no inheritable difference of PND between the two breeds. In a physiological consideration, the longer the lactation of the sow, the more mature the follicular development after parturition. Given this, we speculated that the phenotypic difference of WSI was mainly caused by the lactation of Jiangquhai sows being postponed 15 days longer, rather than by the heritable difference of the two breeds. In practice, the stable production of sows much lightens the spending of management resources in farms. On the SD scale, IISDLS provides a measurement of the stability of litter size among parities of a specific individual. Obviously, it is of high importance to investigate this trait. In this investigation, we reported the first example, to our knowledge, of the novel trait IISDLS in pigs and the phenotypic parameters of the two breeds provide a future reference for the research of other pig breeds.

In the estimation of genetic parameters, we conducted a preliminary analysis before final solution of the linear mixed model. The preliminary analysis showed that the estimation based on the unadjusted classes of fixed effects resulted in the large undervaluation of the genetic variance component, which brought the known moderate heritability for AP nearly to zero (data not shown). Without doubt, the results based on adjusted class levels were more close to the true value. For AP, PND, WSI and IISDLS, the result of adjustments was that the class levels of year-season decreased from 74 to 26, 31, 28 and 19 in Jiangquhai sows and from 56 to 18, 23, 21 and 14 in Meishan sows, respectively. In general, the estimated heritabilities were low for reproduction or reproduction-related traits of sows. In our investigation, the final results of heritabilities showed that all analyzed traits except for AP are low heritability traits, and this means that a large component of variation of these traits was determined by environmental factors. The genetic correlation estimates between the four reproduction component traits had the same sign in both breeds. All the estimates of genetic correlations were positive and low, except for the moderate favorable ones between AP and WSI and the slightly unfavorable ones between AP and IISDLS. Incidentally, the estimated correlations had high standard errors, and we thought the low heritabilities of the studied traits were probably the cause of high standard errors. In the literature, many studies have investigated similar traits related to puberty, piglet loss and farrowing or weaning to estrus interval of sows, although the measurement scales in different studies might be a little various to a certain trait in the same biological sense.

Presumably, for differently measured traits with the same biological meaning, the correlations between them may differ on a phenotypic scale but be near on a genetic scale. In this investigation, the estimated genetic correlations between AP, PND and WSI were actually in approximate accordance with previous results. For example, Holder et al. (1993) found that younger pigs at puberty had a shorter weaning to estrus interval, and this conclusion was in agreement with the estimates of positive genetic correlation between AP and WSI.

It is well accepted that knowledge of genetic parameters is the basis for genetic improvement in an advanced breeding program and for successful selection (Logar et al., 1999). The estimates of genetic parameters in this study reveal that only age at puberty could easily make genetic improvement by traditional selection methods. At the same time, although not significant, the trend of genetic antagonism between age at puberty and intra-individual SD in litter size hints that integrated performance measures should be considered, because the favorable improvement of age at puberty might result in unfavorable changes of intra-individual SD in litter size. Additionally, most reproduction component traits have low heritabilities, which means that breeders have to take much more effort if using the traditional breeding programs or consider the alternative molecular breeding programs such as marker-assisted selection (MAS) in order to meet the purpose of successful genetic improvement.

ACKNOWLEDGMENT

This research was supported by Key Project of National Basic Research and Developmental Plan (2006CB102105) of China, National Natural Science Foundation of China (30571328), and National High Technology Research and Development Program (2007AA10Z148). We also thank two anonymous reviewers for providing the useful modifying suggestions to improve the quality of this article.

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