Asian-Aust. J. Anim. Sci.
Vol. 20, No. 2 : 160 - 165
February 2007

www.ajas.info

Genetic Parameters for Litter Size in Pigs Using a Random Regression Model

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ABSTRACT : Dispersion parameters for the number of piglets born alive were estimated using a repeatability and random regression model. Six sow breeds/lines were included in the analysis: Swedish Landrace, Large White and both crossbred lines between them, German Landrace and their cross with Large White. Fixed part of the model included sow genotype, mating season as month-year interaction, parity and weaning to conception interval as class effects. The age at farrowing was modelled as a quadratic regression nested within parity. The previous lactation length was fitted as a linear regression. Random regressions for parity on Legendre polynomials were included for direct additive genetic, permanent environmental, and common litter environmental effects. Orthogonal Legendre polynomials from the linear to the cubic power were fitted. In the repeatability model estimate of heritability was 0.07, permanent environmental effect as ratio was 0.04, and common litter environmental effect as ratio was 0.01. Estimates of genetic parameters with the random regression model were generally higher than in the repeatability model, except for the common litter environmental effect. Estimates of heritability ranged from 0.06 to 0.10. Permanent environmental effect as a ratio increased along a trajectory from 0.03 to 0.11. Magnitudes of common litter effect were small (around 0.01). The eigenvalues of covariance functions showed that between 7 and 8 % of genetic variability was explained by individual genetic curves of sows. This proportion was mainly covered by linear and quadratic coefficients. Results suggest that the random regression model could be used for genetic analysis of litter size. (**Key Words :** Pigs, Litter Size, Random Regression Model, Genetic Parameters)

INTRODUCTION

There are several approaches to choice of method for genetic evaluation of litter size in pigs. They depend on genetic correlations between litter size in different parities, size of data set, capacity of computers etc. For traits like litter size the general question is whether to use a repeatability model or a multiple trait model. Many breeding programmes use a repeatability model for estimation of breeding values for litter size, mainly due to its simplicity (Alfonso et al., 1997). A repeatability model assumes complete genetic correlations between litter sizes in subsequent parities and a constant variance along the trajectory. Multiple trait analysis supposes subsequent observations to be different traits and may lead to more accurate genetic evaluation (Wang and Lee, 1999). Estimates of genetic correlations between parities were sometimes substantially lower than one, especially between the first and the later parities (Oh et al., 2006). The low correlations between parities indicate that partly different genes are responsible for litter size in different parities. However, multiple trait analyses were not always successful, mainly due to computational problems as a consequence of high genetic correlations in the last parities.

A recent approach in handling with longitudinal data or repeated observations has been the use of covariance functions and random regression model-RRM (Schaeffer and Dekkers, 1994). Litter size in pigs is measured more than once in a sow lifetime and could be considered as a longitudinal trait too. In pigs, RRMs were mainly used for feed intake and growth (Liu et al., 2002). Although, litter size differed from the growth traits, RRMs could be applied also for estimation of genetic parameters (Schaeffer, 2004). Main advantages of the RRMs in comparison to multiple trait models are smoother, less biassed (co)variance estimates as well as the possibility to predict covariance structure and breeding value of the animal at any point along the trajectory.

The aim of this paper was to estimate genetic parameters for number of piglets born alive (NBA) and to check the possibility of using RRM in order to increase accuracy of genetic evaluation for litter size.

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Received March 10, 2006; Accepted July 10, 2006

Table 1. Data and pedigree structure

Item	Data	Item	Pedigree
No. of litters	50,748	No. of animals with records	10,549
No. of animals	10,549	No. of ancestors	1,667
Litters per animal	4.81	No. of base animals	1,330
Animals per common litter	1.70	No. of sires	479

Table 2. Number of records, mean and standard deviation for number of piglets born alive (NBA), previous lactation length (LACT), and weaning to conception interval (WCI) by sow breed/line

Sow breed/line*	No. of records	NBA	LACT	WCI
SL	15,692	9.70±2.83	23.17±5.62	13.33±16.29
LW×SL**	830	9.96±2.79	24.21±5.99	12.08±15.64
SL×LW	15,989	9.94±2.85	24.11±6.59	13.85±16.82
LW	1,277	9.52±2.71	23.11±5.79	15.11±16.75
GL	10,396	9.32±2.68	23.52±5.74	12.90±15.95
GL×LW	6,564	9.75±2.83	24.39±7.08	13.78±16.46

* SL = Swedish Landrace, LW = Large White, GL = German Landrace; ** Sow breed given first.

MATERIALS AND METHODS

The data were obtained from the database of the pig recording system of the Croatian Livestock Center. Litter records from the first to the tenth parity from sows that farrowed between May 1992 and February 2005 were included. Besides identification number of sows and number of piglets born alive, individual records consisted of sow genotype, service sire, service sire breed, parity, mating season, age at farrowing, previous lactation length and weaning to conception interval. Records were excluded from analysis if data were outside the expected range (interval) obtained by examination of the data. Those records with previous lactation length longer than 60 days or previous weaning to conception interval longer than 80 days were deleted. Around 1% of records were removed for not meeting the above criteria. After data editing, a total of 50,748 records were used. The data and pedigree structure are presented in Table 1. The pedigree file was prepared for three generations.

Six sow breeds/lines were included in the analysis: Swedish Landrace (SL), Large White (LW), both crossbred lines between them-SL×LW and LW×SL, German Landrace (GL) and their crossbred line with Large White-GL×LW (Table 2). As expected, litter size was higher for crossbred sows. The previous lactation length did not differ greatly between the genotypes. The longest weaning to conception interval was recorded in the LW sows.

Choice of the fixed effects in the model for NBA is based on coefficient of determination, degrees of freedom, significance and proportion of variation explained by the effect studied, as well as simplicity and interpretation of the model. Significance of the effects was tested at the level of $p<0.05$ using the GLM procedure (SAS Inst. Inc., 2001). Fixed effects analysis showed that the following repeatability model (1) could be used for genetic evaluation of pigs.

$$\begin{aligned} y_{ijklmno} &= \mu + G_i + S_j + B_k + W_l + P_m \\ &+ b_{I\,m}\left(x_{ijklmno} - \bar{x}\right) + b_{II\,m}\left(x_{ijklmno} - \bar{x}\right)^2 \\ &- b_{III}\left(z_{ijklmno} - \bar{z}\right) + c_{ik} + p_m + a_m + e_{ijklmno} \qquad (1) \end{aligned}$$

where $y_{ijklmno}$ is NBA. Fixed effects in the model were: sow breed/line (G_i), mating season (S_j), service sire (B_k), weaning to conception interval (W_l), parity (P_m), age at farrowing ($x_{ijklmno}$), and previous lactation length ($z_{ijklmno}$). The weaning to conception interval was defined as a class effect with the following classes: 1-3, 4, 5, 6, 7, 8, 9, 10-23, 24-33, and 34-80 days. Three classes were considered for parity effect: the first for parity one, the second for parity two, and the third with later parities. Age at farrowing was modelled as a quadratic regression nested within parity class and previous lactation length was fitted as a linear regression. The random part of the repeatability model consisted of a common litter environmental effect (c), permanent environmental effect (p), and direct additive genetic effect (a). Preliminary analysis showed a negligible estimate for the maternal effect. Therefore, it was not included in the model.

In matrix notation the repeatability model can be written as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_c\mathbf{c} + \mathbf{Z}_p\mathbf{p} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \qquad (2)$$

where y is a vector containing NBA records, β is a vector of unknown parameters for fixed effects, c, p and a are vectors of parameters for common litter environmental, permanent environmental and direct additive genetic effect. X, Z_c, Z_p and Z_a are the corresponding incidence matrices. Finally, vector e presents the random residual. The

Table 3. Estimates of variances and ratios of phenotypic variance by repeatability model*

Variances	σ^2_{ph}	σ^2_a	σ^2_l	σ^2_p	σ^2_e
	7.468	0.519	0.074	0.325	6.549
Ratio in the phenotypic variance		h^2_a	l^2	p^2	e^2
		0.070	0.010	0.044	0.877

* σ^2_{ph}: phenotypic variance, σ^2_a: direct additive genetic variance, σ^2_l: common litter environmental variance. σ^2_p: permanent environmental variance. σ^2_e : residual variance, h^2_a: heritability, l^2: ratio of common litter environmental effect, p^2: ratio of permanent environmental effect. e^2: ratio of residual term.

following covariance structure (3) in the repeatability model was assumed:

$$\mathrm{var}\begin{bmatrix}\mathbf{a}\\ \mathbf{c}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathrm{A}\sigma_a^2 & 0 & 0 & 0\\ 0 & \mathrm{I}_c\sigma_c^2 & 0 & 0\\ 0 & 0 & \mathrm{I}_p\sigma_p^2 & 0\\ 0 & 0 & 0 & \mathrm{I}_e\sigma_e^2\end{bmatrix} \qquad (3)$$

where A is the numerator relationship matrix, I_c is identity matrix for common litter environmental effect. I_p is identity matrix for permanent environmental effect. I_e is identity matrix for residual. Covariances between random effects were assumed to be zero.

The following random regression model (4) with different order of Legendre polynomials was fitted:

$$\begin{aligned} y_{ijklmno} &= \mu + G_i + S_j + W_k + P_l + b_{II}\left(x_{ijklmno} - \bar{x}\right) \\ &+ b_{III}\left(x_{ijklmno} - \bar{x}\right)^2 + b_{III}\left(z_{ijklmno} - \bar{z}\right) \\ &+ \sum_{s=1}^{3}\sum_{m=0}^{k}\alpha_{sm}\Phi_m\left(p^*_{ijklmno}\right) + \varepsilon_{ijklmno} \end{aligned} \qquad (4)$$

The set of fixed effects used in RRM analysis for NBA included the same effects as in the repeatability model. The direct additive genetic effect, common litter environmental effect and permanent environmental effect were fitted as a random regression on parity using Legendre polynomials (LG). Orthogonal Legendre polynomials from linear (LG1) with two terms to cubic (LG3) with four terms were fitted. The standardized parity, with range from -1 to +1, was derived from (5) where p_{min} is the first and p_{max} the tenth parity.

$$p^* = \frac{2\left(p - p_{\min}\right)}{\left(p_{\max} - p_{\min}\right)} - 1 \qquad (5)$$

Matrix notation for random regression model is the same as for repeatability model (2). The following structure of covariances for RRM (6) was assumed:

$$\mathrm{var}\begin{bmatrix}\mathbf{a}\\ \mathbf{c}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{K}_{0a} & 0 & 0 & 0\\ 0 & \mathbf{I}_c\otimes\mathbf{K}_{0c} & 0 & 0\\ 0 & 0 & \mathbf{I}_p\otimes\mathbf{K}_{0p} & 0\\ 0 & 0 & 0 & \Sigma^{\oplus}\mathbf{R}_{0r}\end{bmatrix} \qquad (6)$$

where A is relationship matrix, K_{oa} is the covariance matrix for direct additive genetic effect, K_{oc} is the covariance matrix for common litter effect, K_{op} is the covariance matrix for permanent environmental effect, I_l and I_p are identity matrix, and R_{or} is residual matrix. Random effects and the residual were assumed to be independent and normally distributed. Covariances for NBA for every combination of two parities were calculated as shown in the case of direct additive genetic effect (7);

$$C_a = \Phi K_a \Phi^T \qquad (7)$$

where C_a is matrix of covariances and Φ is a matrix containing covariables for Legendre polynomials for parities.

Estimation of the covariance components in the repeatability and random regression model was based on Restricted Maximum Likelihood Method (REML) using the VCE5 software package (Kovac et al., 2002).

RESULTS AND DISCUSSION

Assuming complete genetic correlation between litter size in different parities, estimates of variance components and their ratios in the phenotypic variance were calculated using the repeatability model (Table 3). Within phenotypic variance, the largest part of variability belonged to residual variance (87.7%). About 12.3% of total variability was explained by random effects. The greater part of variability was explained by direct additive genetic effect (0.070), followed by permanent environmental effect (0.044), and the smallest proportion by the common litter environmental effect (0.010). Estimated phenotypic variance for NBA in the repeatability model (7.47) agreed with literature estimates (Ferraz and Johnson, 1993; Crump et al., 1997; Hanenberg et al., 2001). All of these estimates were obtained with repeatability models that included effects such as breed, parity, different contemporary groups, and seldom effects such as number of inseminations or sow birth period. Estimates also differed in number of data (between a few thousand and 200 thousand litter records). Some lower estimates of phenotypic variance for NBA (5.05 to 6.31) were reported by Chen et al. (2003) who included Landrace and Large White sows in their study, as did the authors mentioned above, but also litter records from Hampshire and Duroc sows. Besides breed difference, also reported by Chu (2005), pig losses accounted during

Table 4. Estimates of direct additive genetic (above diagonal) and phenotypic correlations (below diagonal) by random regression model

Parity	No. of records	Parity									
		1	2	3	4	5	6	7	8	9	10
1	10,324		0.896	0.772	0.726	0.725	0.729	0.710	0.656	0.544	0.337
2	8,080	0.123		0.973	0.947	0.927	0.896	0.850	0.800	0.744	0.645
3	7,208	0.122	0.132		0.993	0.973	0.935	0.886	0.847	0.825	0.783
4	6,116	0.115	0.128	0.150		0.992	0.963	0.923	0.893	0.882	0.849
5	5,138	0.106	0.118	0.141	0.152		0.990	0.965	0.944	0.932	0.883
6	4,220	0.101	0.110	0.134	0.150	0.160		0.993	0.980	0.963	0.890
7	3,415	0.095	0.101	0.127	0.148	0.165	0.185		0.996	0.977	0.888
8	2,698	0.082	0.090	0.117	0.140	0.159	0.183	0.204		0.989	0.905
9	2,060	0.070	0.088	0.119	0.143	0.163	0.186	0.209	0.216		0.957
10	1,489	0.051	0.087	0.123	0.145	0.158	0.174	0.192	0.201	0.227	

Table 5. Estimated variance components and proportions in the phenotypic variance for NBA by random regression model*

Parity	σ^2_{ph}	σ^2_a	σ^2_p	σ^2_l	σ^2_e	h^2_a	p^2	l^2	e^2
1	5.93	0.53	0.22	0.09	5.09	0.090	0.037	0.015	0.859
2	7.99	0.48	0.32	0.12	7.08	0.060	0.040	0.015	0.886
3	7.38	0.54	0.39	0.12	6.33	0.074	0.053	0.017	0.857
4	7.61	0.60	0.45	0.09	6.47	0.079	0.059	0.011	0.851
5	8.14	0.63	0.52	0.05	6.94	0.077	0.063	0.007	0.853
6	7.97	0.66	0.61	0.05	6.64	0.083	0.077	0.007	0.833
7	7.72	0.70	0.73	0.08	6.20	0.091	0.095	0.010	0.803
8	8.39	0.74	0.85	0.10	6.70	0.088	0.102	0.011	0.799
9	8.14	0.77	0.94	0.12	6.31	0.095	0.115	0.015	0.776
10	8.97	0.90	0.93	0.33	6.81	0.100	0.104	0.036	0.760

* σ^2_{ph}: phenotypic variance, σ^2_a: direct additive genetic variance, σ^2_p: permanent environmental variance, σ^2_l: common litter environmental variance, σ^2_e: residual variance. h^2_a: heritability. p^2: ratio of permanent environmental effect. l^2: ratio of common litter environmental effect, e^2: ratio of residual term.

the first two days may reduce the phenotypic variance for NBA (Kaplon et al., 1991), which could be one explanation for differences between studies.

Estimation of direct additive genetic effect (0.52) is higher than estimated in the study by Chen et al. (2003). A heritability estimate of 0.07 is lower than the average heritability estimate for NBA of 0.09 as reviewed by Rothschild and Bidanel (1998). The estimate of common litter environmental variance is the smallest of all variance components, as well as its ratio in the phenotypic variance that explains only 1% of the total variability. The small magnitude of this effect could be explained as a consequence of small full-sib size in the data, averaging only 1.7 animals which came from the same litter. More than 50% of the data consisted of single sow families. The estimate of permanent environmental variance was in agreement with Chen et al. (2003) who reported estimates of permanent environmental variances between 0.34 and 0.49. The estimate of permanent environmental effect as a ratio in the phenotypic variance was consistent with values reported by Logar et al. (1999) and Chen et al. (2003), but lower than estimates of 16 to 17% reported by Ferraz and Johnson (1993). Residual error variance as well as corresponding ratio in the phenotypic variance represents the largest part of variability.

Genetic correlations between litter sizes in different parities using RRM ranged from 0.34 to 0.99 (Table 4). The smallest genetic correlations were between the first and the later parities, and ranged between 0.90 and 0.34. Direct additive genetic correlations were highest between adjacent parities (0.90 to 0.99) and decreased as the interval between parities increased. Phenotypic correlations were much lower compared to genetic ones and ranged from 0.12 to 0.22, but showed a similar tendency to genetic correlations (Table 4).

Estimates of variances as well as ratios in the phenotypic variance for random effects obtained with the random regression model (Table 5) were slightly higher than those obtained using the repeatability model (Table 3). Except for the first parity, phenotypic variances by parities obtained with RRM were somewhat higher than in the repeatability model. Phenotypic variance ranged between 5.9 in the first parity and 9.0 in the tenth parity. Direct additive genetic variance as well as permanent environmental variance increased by parities. The smallest estimates of common litter environmental variances were noticed in the middle of the trajectory, in the fifth and sixth parity. Estimates of residual variance oscillated by parities, with the highest value in the second parity. Heritability estimates by parities ranged between 0.06 in the second parity and 0.10 in the tenth parity. Permanent environmental effect as a proportion in the phenotypic variance increased by parity and ranged from 0.04 to 0.11. Estimates of

Table 6. Eigenvalues with proportion (in brackets) of estimated covariance matrices of random regression coefficients for direct additive genetic effect with different Legendre polynomials (LG1-LG3)

Model	Eigenvalues			
	0th	1st	2nd	3rd
LG1	1.214 (92.46)	0.099 (7.54)		
LG2	1.192 (92.62)	0.088 (6.84)	0.007 (0.54)	
LG3	1.185 (93.30)	0.083 (6.54)	0.002 (0.16)	0.000 (0.00)

common litter environmental effect as a ratio were similar in magnitude (0.01) as in the repeatability model, except for the last parity. Estimates for residual variance as a ratio decreased by parities and ranged between 0.89 in the second parity and 0.76 in the tenth parity.

Direct additive genetic correlations obtained with RRM were somewhat lower than estimates obtained by Hanenberg et al. (2001) using a multiple trait model for the first six parities. They reported an increase from 0.79 between the first and the second parity to 0.96 between the fifth and the sixth parity. Generally, heritability estimates obtained with RRM were somewhat higher than those found in a univariate repeatability model. Estimates of direct additive genetic variances as well as heritabilities with RRM showed a decrease in the second parity. Similar findings of heritability decline in the second parity were reported by Hanenberg et al. (2001).

According to computing requirements for applied procedures of genetic evaluation of litter size, the repeatability model was the time-effective method of choice. With several measurements per animal, it requires less computational effort and less parameters to estimate than the random regression approach. However, if genetic correlations between litter sizes in different parities were lower and multiple trait analysis cannot be conducted due to computational problems, RRM could be preferred.

The eigenvalues for covariance matrices of the regression coefficients were calculated to quantify the relative contribution of higher terms in Legendre polynomials (Table 6). The eigenvalues of genetic covariance functions showed that the constant (zero) term accounted for between 92 and 93% of the additive genetic variability for NBA. This means that approximately 7 to 8% of variability was explained by the individual genetic curve of a sow. Eigenvalues of covariance functions also showed that quadratic Legendre polynomials with three coefficients are sufficient to model almost all variability for NBA. The proportion of direct additive genetic variance for higher terms was mainly covered by the linear coefficient (6.54 to 7.54).

In comparison to multiple-trait models, RRM is more correct from a statistical point of view, because it includes permanent environmental effect, which explained a substantial part of phenotypic variability. The repeatability model also includes permanent environment, but does not allow change of correlations between parities. RRM could be also more acceptable in definition of selection criteria. Between 7 and 8% of variability explained by individual curve could be interesting in selection for shape of production curve for litter size. Therefore, besides an increase in overall level of production (litter size), with inclusion of higher parities in the data set, RRM allows selection for persistency of litter size.

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