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Original paper

ESTIMATION OF THE VARIANCE COMPONENTS OF THE SOW LITTER SIZE TRAITS USING REML METHOD - REPEATABILITY MODEL

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Abstract

Variance components for sow litter size traits were estimated using the REML method. Number of live born piglets (NBA), number of still born piglets (NSB), number of total born piglets (NTB) and number of weaned piglets (NW) were treated as traits which repeated several times during sow lifetime - repeatability model. Results of the fertility of Swedish Landrace sows realized on three pig farms in the Republic of Serbia were presented in four data sets DS1 (farm 1), DS2 (farm 2), DS3 (farm 3) and DS23 (farms 2 and 3 together). Fixed part of the model for litter size traits at farrowing (NBA, NSB and NTB) included parity, mating season as year-month interaction, litter genotype and weaning to conception interval as class effects. The age at farrowing was modelled as a quadratic regression nested within parity, whereas preceding lactation length was included as linear regression. In case of NW the model included parity, weaning season as yearmonth interaction, number of piglets in litter subsequent to crossfostering and litter genotype as class effects. The age at farrowing was included into the model in the same way as in case of previous traits. Random part of the model was the same for all analysed traits and represented as effect of common environment in litter where sows had been born, permanent effect of environment in sows' litters and direct additive genetic effect. Heritability of NBA varied between 0.050 (DS2) and 0.076 (DS3), NSB between 0.004 (DS3) and 0.027 (DS2), NTB between 0.065 (DS2) and 0.073 (DS3) and of NW between 0.010 (DS2) and 0.028 (DS1). Share of permanent environment of sow in phenotypic variance was higher than share of litter effect and mostly lower than share of direct genetic effect.

Key words: heritability, litter size traits, pigs, variance components

Introduction

In order to achieve maximum accuracy in evaluation of breeding value of sows for litter size traits, it is necessary to estimate as accurately as possible their variance components. For that purpose, it is necessary to determine the most optimal mixed model for analysis. That means to include all class, regression and random effects which influence variation of

mentioned traits. Determining of these effects is based on knowledge of the biology of pig fertility.

The litter size traits, at least most of them, are low hereditary traits which impedes their improving through selection. On the other hand, direct additive genetic effect is the the most common source of variation in relation to other variance components (random effects). Another problem related with improvement of litter size traits through selection is fact that those traits can be under negative maternal effect, and they can only be measured in sows after first farrowing which effects prolonging of the generation interval. Also, undesirable correlation between litter size and some important carcass quality traits which for a long time have been in the center of attention in pig selection (i.e. back fat thickness) is well known. Mentioned litter size traits are expressed several times during a lifetime of breeding females. It can cause dilemma whether these traits should be approached as traits which repeat several times during lifetime (repeatability model) as suggested by Logar (2000) or as specific traits (multi trait model) as presented by Tholen et al. (1998).

Residual Maximum Likelihood method (REML) is mostly applied for estimation of variance components of production traits in pigs which enables the most objective estimation of parameters using information deriving from the matrix of animal relationship.

The objective of this study was to estimate variance components of litter size traits, based on reproduction performance realized on three pig farms in the Republic of Serbia, as follows: number of live born piglets (NBA), number of still born piglets (NSB), number of total born piglets (NTB) and number of weaned piglets (NW) for the purpose of selecting traits which would be included into aggregate genotype in estimation of the breeding value of sows. This is extremely important for building of modern selection system in pig production. Radojković et al. (2012) stated that despite the great genetic progress in the last two decades in terms of production traits of pigs, biological limits have not been reached. Traits are still characterized by significant phenotypic and genetic variability, which, in addition to heredity, variable in different traits, provides the basis for the expectation that conventional selection will enable continuous improvement of production performance of pigs for significant number of years to come.

Materials and methods

Litter records of Swedish Landrace sows (the largest pig breed population in Serbia) collected over a period of 13 years on three pig farms (farm 1, 2 and 3) in the Republic of Serbia were analysed in this study. Data sets from mentioned farms have been marked as DS1 (farm 1), DS2 (farm 2), DS3 (farm 3) and as DS23 when analysed data included a combination of fertility records from farms 2 and 3. In Table 1 the structure of analysed data and used pedigree files per farm is presented.

Average number of litters per sow, as well as average number of selected sows per litter, was approximately similar on all farms, indicating rather equal structure of analysed data sets.

Pedigree files were done for three generations. Share of ancestors in total number of animals in pedigree file was the lowest in case of DS1 (14.39%), and highest in case of DS3 (32.86%). Only in DS3 is the number of base animals greater than 15%, this pulls the base animal percentage in the combined dataset.

Parameter	DS1	DS2	DS3	DS23
No. of litters	11014	6757	8452	15209
No. of sows	2803	1826	2235	4061
Average no. of litters per sow	3.93	3.70	3.78	3.74
No. of sires	192	127	157	204
No. of litters from which sows are				
selected	2022	1344	1617	2636
Average no. of sows per common				
litter	1.39	1.36	1.38	1.54
Total no. of animals				
in pedigree file	3274	2559	3329	5023
No. of animals with records	2803	1826	2235	4061
No. of ancestors	471	733	1094	962
No. of base animals	330	374	728	808
(percentage, %)	(10.07%)	(14.61%)	(21.87%)	(16.09%)

Table 1. Structure of data sets and pedigree files (second part of table)

Based on presented number of sires, averagely selected sows per litter and number of ancestors in pedigree, the presence of strong genetic relation between farms 2 and 3 is noticeable since significant number of Swedish Landrace boars was used on both farms. This was reason why variance components of analysed traits were also determined based on data from both farms together, as well as separately for each farm.

In Table 2 the number of analysed data, average values and phenotypic variability of litter size traits in analysed DS are presented.

Trait	Data set	No. of records	X	SD	min	max	CV
Number of live	DS1	11014	9.13	2.66	0	19	29.14
born piglets	DS2	6757	9.76	2.78	0	20	28.49
(NBA)	DS3	8452	9.76	2.89	0	20	29.66
	DS23	15209	9.76	2.84	0	20	29.15
Number of still	DS1	11014	0.77	1.21	0	14	156.78
born piglets	DS2	6757	0.68	1.05	0	11	154.31
(NSB)	DS3	8452	0.52	0.96	0	15	182.51
	DS23	15209	0.59	1.00	0	15	168.83
Number of total	DS1	11014	9.90	2.84	1	20	28.69
born piglets	DS2	6757	10.44	2.90	1	20	27.78
(NTB)	DS3	8452	10.29	2.96	1	20	28.75
	DS23	15209	10.36	2.93	1	20	28.33
Number of	DS1	11014	7.83	2.38	0	14	30.45
weaned piglets	DS2	6757	8.68	1.83	0	13	21.09
(NW)	DS3	8452	8.53	2.36	0	13	27.71
	DS23	15209	8.60	2.14	0	13	24.94

Table 2. Descriptive statistics for litter size traits according to analysed data sets

Analysed traits of litter size showed no significant differences between farms, in regard to average, or parameters of phenotypic variability. Only the average NW in DS1 was lower compared to the other farms.

Variance components of studied traits and share of single variance components in the phenotypic were estimated using the method of Residual Maximum Likelihood - REML. Application of REML method for estimation of dispersion parameters is necessary due to fact that sample representing the basis for estimation is not random, but is a population under selection. During determination of variance parameters using REML method analysed traits were treated as traits which repeat several times during a production lifetime (repeatability model). In such treatment of the litter size traits, a confounding problem involving maternal effect can occur but it is successfully solved by inclusion of the litter in which animals were born as a random effect in the model (Andersen, 1998; Logar, 2000; and Lukovic et al., 2004).

Special method of data preparation enabled simultaneous application of two different models used for analysis of the variability of litter size traits at birth (NBA, NSB and NTB) in litters of primiparous and older sows. This approach is a consequence of the fact that in the litters of primiparous sows two very important effects are not expressed, duration of previous lactation and period from previous weaning to conception.

In preparation of data, in reference to the effect of duration of previous lactation, real values of this parameter (in litters of older sows) were substituted with deviation from the average value for duration of lactation on farm (real value of the parameter minus average value), and in primiparous sows, for this parameter value 0 was included. When duration of lactation is included into the model as linear regression effect, it means that in primiparous sows this effect is not present, whereas for other parities, the effect of this factor on other traits of litter size at birth is normally analysed.

The effect of duration of period from weaning to conception on size of subsequent litter was studied as a fixed effect with categorical classes. According to previous findings relating to specific expression of this effect on litter size traits at birth, as well as distribution of frequency of this parameter, duration of this period was divided into 10 classes, as suggested by Lukovic et al. (2003), in the way presented in Table 3.

Class	1	2	3	4	5	6	7	8	9	10
Duration (days)	<4	4	5	6	7	8	9	10-23	24-32	>32

Table 3. Classes of duration of the period from weaning to conception

In the results pertaining to fertility realized in the first farrowing, for duration of period from weaning to conception, it was necessary to include any value besides those presented in Table 3. In that case, in analysis of variance of studied traits for fertility results for first farrowing, forming of unit vector occurs, since the same values appear. The model practically ignores this effect (since in this case there is no variability – it is not possible to calculate variance, i.e. it is equal 0) in primiparous sows, whereas in case of results of realized fertility in latter parities this effect is taken into consideration without any disturbances.

In scalar notation, used models for estimation of variance components of litter size traits at birth (NBA, NSB and NTB) by REML method are presented in equation (1):

$$\begin{bmatrix} y_{1ijklmno} \\ y_{2ijklmno} \end{bmatrix} = \mu + P_i + S_j + LG_k + b_{1i}(x_{ijklmno} - \overline{x}) + b_{2i}(x_{ijklmno} - \overline{x})^2 + \\ + \begin{bmatrix} 0 \\ WC_l + b_3(z_{ijklmno} - \overline{z}) \end{bmatrix} + l_m + p_{ijklmno} + a_{ijklmno} + e_{ijklmno} \end{bmatrix}$$
(1)

where $y_{qijklmno}$ represents NBA, NSB or NTB in litters of primiparous sows (y = 1) or older sows (y = 2). Class effects in the models were: parity (P_i), mating season as interaction of year and month (S_j), litter genotype (LG_k) and interval from weaning to conception (WC_i). Age of the sow at farrowing was modelled as square regression effect nested between parities ($x_{ijklmno}$), whereas duration of previous lactation was included as a linear regression effect ($z_{ijklmno}$). Random part of the models is presented through the effect of common environment in the litter where sows were born (l_m), permanent effect of the environment in sows' litters ($p_{ijklmno}$) and direct additive genetic effect ($a_{ijklmno}$). Previous analyses showed a negligible estimate for the maternal effect which was reason for exclusion of this effect from the models. This effect was probably not expressed because on every farm equalization of litters was done by crossfostering of piglets.

Model used for estimation of variance components of NW is presented in equation (2):

$$y_{ijklmno} = \mu + P_i + S_j + LG_k + R_l + b_{1i}(x_{ijklmno} - \overline{x}) + b_{2i}(x_{ijklmno} - \overline{x})^2 + l_m + p_{ijklmno} + a_{ijklmno} + e_{ijklmno}$$

$$(2)$$

where $y_{ijklmno}$ represents NW. Indications of the effects have the same meaning as in equation (1) except S_j which in this case is the effect of weaning season as an interaction between year and month. The model also included as a fixed effect, the number of reared piglets in litter (R_l), i.e. number of piglets in litter after equalization. The purpose for inclusion of this effect into the model was to diminish the effect of equalization procedure on variability of NW, as well as on objectivity of calculated parameters of dispersion. The statistical significance of systematic influences which have been included in the models and coefficients of determination were shown in the paper presented by Radojković et al. (2007).

For estimation of phenotypic and genetic variances of analysed traits by REML method, as well as establishing the percentage share of individual variance components in phenotypic variance, was used program package "VCE-5" (Kovac et al., 2002). Previously fixed part of the model was analysed using procedures of the program package "SAS/STAT" (SAS Inst. Inc., 2001).

Results and discussion

The shares of individual variance components in the phenotypic variance for NBA are presented in Table 4.

As presented in equations (1 and 2), direct additive genetic effect of the animal, effect of common litter environment and effect of permanent environment which sows provide to

their litters are included as random effects within mixed model used for estimation of parameters using REML method in all traits.

Data set	$\hat{\sigma}^2_{Ph}{}^*$	$\hat{h}^2 \pm se_{(\hat{h}^2)}$	$\hat{l}^2 \pm se_{(\hat{l}^2)}$	$\hat{p}^2 \pm se_{(\hat{p}^2)}$
DS1	6.389	0.055 ± 0.004	0.027 ± 0.005	0.038 ± 0.006
DS2	7.224	0.050 ± 0.004	0.018 ± 0.004	0.053 ± 0.007
DS3	7.744	0.076 ± 0.008	0.012 ± 0.004	0.058 ± 0.007
DS23	7.584	0.064 ± 0.008	0.028 ± 0.005	0.048 ± 0.007

 Table 4. Estimation of the share of individual variance components in the phenotypic variance for number of live born piglets (NBA)

DS23 7.584 0.064 \pm 0.008 0.028 \pm 0.005 0.048 \pm 0.007 * - $\hat{\sigma}_{Ph}^2$: estimates of phenotypic variance; \hat{h}^2 : estimates of the heritability; \hat{l}^2 : estimates of the common

litter effect; \hat{p}^2 : estimates of the effect of permanent environment

Values of heritability coefficients varied from 0.050 (DS2) to 0.076 (DS3) and it can be stated that they were rather uniform in studied DS. Presented interval of values of heritability coefficients obtained in this research is very close to values shown by Kim (2001); Noguera et al. (2002); Chen et al. (2003); Stella et al. (2003); Vukovic (2003); and Holm et al. (2004). Higher values of studied parameter were presented by Logar (2000); Hannenberg et al. (2001); Peskovicova et al. (2002); Lukovic et al. (2004); Holm et al. (2005); Radojković et al. (2005); Lukovic et al. (2007); Ibanez-Escriche et al. (2010); Pandey and Singh (2010); and Wolf (2010).

The effect of litter in which sows were born explained from 1.2 % (DS3) to 2.8 % (DS23) of total variability of studied trait. Although the share in total variability of NBA explained by this effect was small, in certain cases (DS1) it was almost 50 % of direct additive genetic effect, which justified its inclusion in the model. Results obtained in this research are in accordance with results presented by Logar (2000); Lukovic et al. (2004) and Lukovic et al. (2007).

Share of the effect of sow permanent environment in total variability of NBA varied in interval from 0.038 (DS1) to 0.058 (DS3). Part of phenotypic variance explained with this effect was considerably high, in case of DS2 even higher than direct additive genetic effect. In concordance to results obtained in this research are results relating to influence of this effect on variation of studied trait presented by Logar (2000); Vukovic (2003); Stella et al. (2003); Wolf et al. (2005); Lukovic et al. (2004); Lukovic et al. (2007) and Wolf (2010). Somewhat higher values were presented by Hanenberg et al. (2001); Damgaard et al. (2003); Chen et al. (2003) and Barbosa et al. (2010), whereas Peskovicova et al. (2002) established lower value.

Estimation of the share of individual variance components in total variability of NSB established based on different data sources is presented in Table 5.

Heritability of studied trait varied within 0.004 (DS3) and 0.027 (DS2), and it was in accordance with results obtained in application of this method by Kim (2001) and Vukovic (2003), whereas Hannenberg et al. (2001) established slightly higher value for the studied parameter.

The effect of common litter environment explained a very small part of total variability of studied trait in the interval from 0.4 % (DS3) to 2.0 % (DS1), whereas the effect of

permanent environment of sows explained a slightly higher share which varied from 1.5 % (DS1) to 3.1 % (DS2) of total NSB variability.

Data set	$\hat{\sigma}^2_{Ph}{}^*$	$\hat{h}^2 \pm se_{(\hat{h}^2)}$	$\hat{l}^2 \pm se_{(\hat{l}^2)}$	$\hat{p}^2 \pm se_{(\hat{p}^2)}$
DS1	1.378	0.025 ± 0.003	0.020 ± 0.003	0.015 ± 0.004
DS2	1.070	0.027 ± 0.005	0.006 ± 0.003	0.031 ± 0.005
DS3	0.884	0.004 ± 0.003	0.004 ± 0.003	0.025 ± 0.006
DS23	0.967	0.016 ± 0.003	0.004 ± 0.002	0.028 ± 0.004

 Table 5. Estimation of share of variance components in the phenotypic variance for number of still born piglets (NSB)

* - $\hat{\sigma}_{Ph}^2$: estimates of phenotypic variance; \hat{h}^2 : estimates of the heritability; \hat{l}^2 : estimates of the common

litter effect; \hat{p}^2 : estimates of the effect of permanent environment

In Table 6 the share of individual variance components in the phenotypic variance of NTB is presented.

Direct additive genetic effect explained from 6.5% (DS2) to 7.3% (DS3) of total variability of studied trait which are lower values compared to results presented by Logar (2000); Marios et al. (2000); Kim (2001); Hannenberg et al. (2001); Serenius et al. (2003); Vukovic (2003); Wolf et al. (2008); Barbosa et al. (2010) and Schneider et al. (2012).

The effect of common litter environment was lower than the direct additive genetic effect and its share in total variability of NTB varied in the interval from 0.015 (DS3) to 0.034 (DS23), which is in accordance with results presented by Logar (2000); Marios et al. (2000) and Bolet et al. (2001).

 Table 6. Estimation of the share of individual variance components in the phenotypic variance for number of total born piglets (NTB)

Data set	$\hat{\sigma}^2_{Ph}{}^*$	$\hat{h}^2 \pm se_{(\hat{h}^2)}$	$\hat{l}^2 \pm se_{(\hat{l}^2)}$	$\hat{p}^2 \pm se_{(\hat{p}^2)}$
DS1	7.293	0.066 ± 0.007	0.032 ± 0.005	0.040 ± 0.005
DS2	7.846	0.065 ± 0.011	0.025 ± 0.009	0.030 ± 0.011
DS3	8.022	0.073 ± 0.007	0.015 ± 0.007	0.065 ± 0.011
DS23	8.009	$\textbf{0.067} \pm 0.008$	0.034 ± 0.005	0.041 ± 0.005

* - $\hat{\sigma}_{Ph}^2$: estimates of phenotypic variance; \hat{h}^2 : estimates of the heritability; \hat{l}^2 : estimates of the common

litter effect; \hat{p}^2 : estimates of the effect of permanent environment

Share of permanent effect of sow in the phenotypic variance of studied trait was lower than additive effect, but higher than the effect of litter, and varied in the interval from 0.030 (DS2) to 0.065 (DS3). Similar results in regard to share of this effect in total variability of NTB were obtained by Logar (2000); Kim (2000) and Wolf (2010). Contrary to mentioned authors Hannenberg et al. (2001); Damgaard et al. (2003) and Barbosa et al. (2010) established higher share of this effect compared to the values interval presented in this research, whereas the value of this parameter presented by Vukovic (2003) was lower.

Phenotypic variances, heritability as well as individual shares of other random effects in total variability of NW established based on analysed data sets are presented in Table 7.

 Table 7. Estimation of the share of individual variance components in the phenotypic variance for number of weaned/ reared piglets (NW)

Data set	$\hat{\sigma}^2_{Ph}{}^*$	$\hat{h}^2 \pm se_{(\hat{h}^2)}$	$\hat{l}^2 \pm se_{(\hat{l}^2)}$	$\hat{p}^2 \pm se_{(\hat{p}^2)}$
DS1	2.384	0.028 ± 0.005	0.007 ± 0.003	0.019 ± 0.006
DS2	1.593	0.010 ± 0.004	0.002 ± 0.002	0.041 ± 0.006
DS3	1.739	0.013 ± 0.005	0.002 ± 0.002	0.018 ± 0.006
DS23	1.674	0.011 ± 0.003	0.012 ± 0.005	0.017 ± 0.004

* - $\hat{\sigma}_{Ph}^2$: estimates of phenotypic variance; \hat{h}^2 : estimates of the heritability; \hat{l}^2 : estimates of the common

litter effect; \hat{p}^2 : estimates of the effect of permanent environment

Heritabilities of studied trait were extremely low and varied in the interval from 0.010 (DS2) to 0.028 (DS1) what is in accordance with results obtained by Radojković et al. (2011). Obtained values of this parameter were lower than values established using this method procedure on data sets proportional in regard to scope of data used in the analysis by Kim (2001); Chen et al. (2003); Vukovic (2003); Radojković et al. (2005) and Pandey and Singh (2010). Even though the effect of number of reared piglets in litter after equalization (R_1) was included in applied model for genetic analysis of this trait, such attempt did not enable overcoming of the problem caused by equalization in analysis. With this model, in practice, the genetic variability of the ability of sow to rear certain number of piglets was estimated, and not the number of reared piglets in the narrow sense of the term.

The effect of litter explained only from 0.2 % (DS2 and DS3) to 1.2 % (DS23) of total variability.

Share of permanent effect of sows in total variability of NW was, with the exception of DS1, higher than direct additive effect and varied in the interval from 0.017 (DS23) to 0.041 (DS2), which is in concordance with the result presented by Chen et al. (2003). Slightly higher share of this effect in phenotypic variance of studied trait was established by Kim (2001), whereas Vukovic (2003) established lower value.

Conclusion

Share of additive genetic component of heritability in total phenotypic variability was the highest of all analysed variance components of litter size traits at farrowing (NBA, NSB and NTB), whereas in case of NW it was lower than the effect of permanent environment of sow which she provides to litters. Presented values of heritability varied within the limits of values which in application of REML method were also established by other authors except for NW whose deviance may be the consequence of litter (except in NSB, DS1) and mainly lower than share of direct genetic effect (except in cases: NBA, DS2; NSB, DS2, DS3 and DS23; NW, DS2, DS3, DS23). Share of phenotypic variability of studied traits which was explained by the effect of litter and permanent environment was within the limits of values presented in literature.

Based on share of individual variance components in the phenotypic variability, objectivity of estimated dispersion parameters as well as objectivity in determination of phenotypic values of analysed traits, it can be emphasized that NBA or NTB are most acceptable traits for inclusion into aggregate genotype in estimation of sows' breeding value.

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