Estimation of Variance Components for Litter Size in the First and Later Parities in Improved Jezersko-Solcava Sheep

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Summary

Aim of this study was to estimate variance components for litter size in Improved Jezersko-Solcava sheep. Analysis involved 66,082 records from 12,969 animals, for the number of lambs born in all parities (BA), the first parity (B1), and later parities (B2+). Fixed part of model contained the effects of season and age at lambing within parity. Random part of model contained the effects of herd, permanent effect (for repeatability models), and additive genetic effect. Variance components were estimated using the restricted maximum likelihood method. The average number of lambs born was 1.36 in the first parity, while the average in later parities was 1.59 leading also to about 20% higher variance. Several models were tested in order to accommodate markedly different variability in litter size between the first and later parities: single trait model (for BA, B1, and B2+), two-trait model (for B1 and B2+), and single trait model with heterogeneous residual variance (for BA). Comparison of variance components between models showed largest differences for the residual variance, resulting in parsimonious fit for a single trait model for BA with heterogeneous residual variance. Correlations among breeding values from different models were high and showed remarkable performance of the standard single trait repeatability model for BA.

Key words

sheep, litter size, variance components, heterogeneity

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Aim

Improved Jezersko-Solcava sheep is a traditional aseasonal meat-type sheep breed of considerable importance for Slovenian sheep production. This breed was established with the introgression of Romanov breed in a part of local Jezersko-Solcava breed in Slovenia in order to increase its litter size. Today, this is the most numerous sheep breed in Slovenia. Litter size is a trait of great economical importance in lamb meat production, because it directly affects profitability. Direct selection on litter size is limited due to low heritability (Matos et al., 1997) and consequently slower genetic improvement is obtained. Nevertheless, selection on litter size is included in many breeding programs in the world, in some cases also as the main breeding objective (e.g., Baelden et al., 2005). The aim of this study was to estimate variance components for litter size in the first and later parities in Improved Jezersko-Solcava sheep in Slovenia in order to provide necessary parameters for routine genetic evaluation.

Material and methods

Data for Improved Jezersko-Solcava sheep were retrieved from breeding program in Slovenia for the period from 1994 to 2010. Raw data contained 66,082 records for 12,969 Improved Jezersko-Solcava sheep. Data set contained information about the number of lambs born, parity, age at lambing, lambing date, herd, and animal identification. Records for: parities larger than 10, herds with less than 15 animals, and litter size reported as 0 were excluded from the analysis. If the number of lambs born was larger than 3, the number of lambs born was set to 3. Season of lambing was defined as month within the year. Seasons with less than 20 animals were joined to the previous or next season to improve data structure. Final data set contained 60,948 records. Based on this data a pedigree file was created using all available relationship information between animals and contained 14,248 animals.

Analysis was performed for the number of lambs born in all parities (BA), the number of lambs born in the first parity (B1), and the number of lambs born in later parities (B2+). The first step was to develop fixed part of model using GLM procedure in SAS (SAS, 2004). Criteria for choice of effects in the fixed part of model were significance, coefficient of determination, and degrees of freedom. Coefficient of determination was the highest for the model with the effect of season (as year-month interaction) and the effect of age at lambing (as quadratic regression) nested within parity. Dispersion parameters were estimated using restricted maximum likelihood method as implemented in VCE (Groeneveld et al., 2008). The random part of model included the effect of herd, additive genetic (animal) effect, permanent environmental effect (for repeatability models analysing BA and B2+), and residual. In order to accommodate markedly different variability of litter size between the first and later parities several models were used: single trait model (for BA, B1, and B2+), two-trait model (for B1 and B2+), and single trait model with heterogeneous residual variance (for BA). All models can be written in general matrix form as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_h h} + \mathbf{Z_p p} + \mathbf{Z_a a} + \mathbf{e} \cdot$$

where $\mathbf{y}$ is a vector of phenotype observations for the number of lambs born; $\mathbf{b}$ is a vector of unknown parameters for fixed effects (season and age within parity); $\mathbf{h}$, $\mathbf{p}$, and $\mathbf{a}$ are vectors of unknown parameters for herd, permanent effect, and additive genetic (animal) effect, respectively; $\mathbf{e}$ is vector of residuals; while $\mathbf{X}$, $\mathbf{Z_h}$, $\mathbf{Z_p}$, and $\mathbf{Z_a}$ are design matrices linking phenotype records with corresponding parameters. Model assumptions were:

$$E(\mathbf{y}) = \mathbf{Xb}, \quad \mathbf{h} \mid \mathbf{H} \sim N(\mathbf{0}, \mathbf{H}), \quad \mathbf{p} \mid \mathbf{P} \sim N(\mathbf{0}, \mathbf{P}),$$
$$\mathbf{a} \mid \mathbf{G} \sim N(\mathbf{0}, \mathbf{G}), \quad \mathbf{e} \mid \mathbf{R} \sim N(\mathbf{0}, \mathbf{R}),$$

where $\mathbf{A}$ is numerator relationship matrix. In the case of single trait models $\mathbf{H} = \mathbf{I}\sigma_h^2$, $\mathbf{P} = \mathbf{I}\sigma_p^2$, $\mathbf{G} = \mathbf{A}\sigma_a^2$, and $\mathbf{R} = \mathbf{I}\sigma_e^2$, while in the case of two-trait model:

$$\mathbf{H} = \oplus_{i=1}^{n} \mathbf{H}_{0,i}, \mathbf{P} = \mathbf{I}\sigma_p^2, \mathbf{G} = \mathbf{A} \otimes \begin{pmatrix} \sigma_{a_{B1}}^2 & \sigma_{a_{B1},a_{B2+}} \\ & \sigma_{a_{B2+}}^2 \end{pmatrix}, \mathbf{R} = \oplus_{i=1}^{n} \mathbf{R}_{0,i},$$

$$\mathbf{H}_0 = \begin{pmatrix} \sigma_{h_{B1}}^2 & \sigma_{h_{B1},h_{B2+}} \\ & \sigma_{h_{B2+}}^2 \end{pmatrix}, \mathbf{R}_0 = \begin{pmatrix} \sigma_{e_{B1}}^2 & \sigma_{e_{B1},e_{B2+}} \\ & \sigma_{e_{B2+}}^2 \end{pmatrix},$$

where $\oplus$ and $\otimes$ denote Kornecker and direct sum matrix products, respectively; $\mathbf{H}_{0,i}$ denotes a selection of parts of $\mathbf{H}_0$ for the i-th animal as some animals might have records for B1 and/or B2+. Assumptions for the single trait model with heterogeneous residual variance were the same as for the standard single trait models except:

$$\mathbf{R} = \mathbf{R}_{B1} \oplus \mathbf{R}_{B2+} = \mathbf{I}\sigma_{e_{B1}}^2 \oplus \mathbf{I}\sigma_{e_{B2+}}^2$$

In this study, the phenotypic variance for the number of lambs born was decomposed into the following components: herd, animal and residual. In the case of analysing repeated records (for BA and B2+) animal component was further decomposed into the additive genetic part (=breeding value) and permanent effect, that partly covers dominance and the other effects associated with particular animal that cannot be attributed to genetics. Variance components were estimated using several models in order to accommodate markedly different variability of litter size between the first and later parities caused by the discrete nature of a count trait. Theoretically, the threshold model (Wright, 1934) would be more appropriate for the analysis of litter size in sheep, but computationally simpler model with Gaussian (normal) distribution was used, which should serve as a good (the best linear) approximation.

The baseline model was a single trait (repeatability) model where all records of one animal were analysed as one trait (BA). This model was then applied separately for the first parity only (B1) and later parities (B2+). With this we obtained separate estimates for variance components for B1 and B2+. In order to capture correlated information among these two traits a two-trait model was employed in the next step. Estimates from two-trait model should be more precise, especially for the B1 trait, but not markedly different than from a single trait analysis. The estimate of additive genetic correlation would provide a criterion upon which decision could be taken if a two-trait analysis of B1 and B2+ is warranted in comparison to a single trait analysis of BA.

Results and discussion

Analysed data set contained 60,934 records for litter size with 10,244 first parity records and 50,690 records for later parities (Table 1). The average number of lambs born was lower in the first parity (1.36) than in later parities (1.59) as expected

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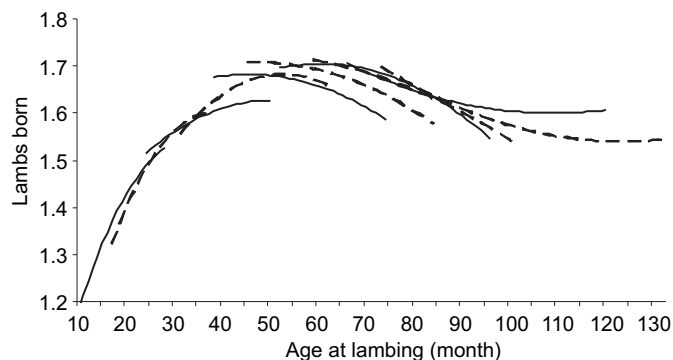Agric. conspec. sci. Vol. 76 (2011) No. 4

Table 1. Descriptive statistics and distribution for the number of lambs born in all parities (BA) and separately for the first parity (B1) and later parities (B2+)

Lambs born	N	Mean	SD[1]	Single	Twins	Triplets+
All parities (BA)	60,934	1.55	0.61	45.1	46.2	8.7
Parity 1 (B1)	10,244	1.36	0.51	60.4	37.6	2.0
Parity 2+ (B2+)	50,690	1.59	0.62	42.4	47.7	9.9

[1] Standard Deviation

Figure 1. Effect of age within parity on the number of lambs born as described with nested quadratic regression

due to the differences in the age of animals. Variability of litter size was also smaller in the first parity - standard deviation was about 20% smaller than for later parities. Given that litter size is a count trait with discrete distribution the rise of variability after the first parity can be attributed to the rise in mean. The distribution of litter size for the first parity was 60.4% for singles, 37.6% for twins and 2.0% for triplets and more. After the first parity the distribution shifted considerably towards twins (47.7) and to some extent to triplets and more (9.9), which explains the rise in variability.

The number of lambs born increased sharply up to the fourth parity and only slightly decreased after (Figure 1). Slight decrease after the peak could be attributed to the senescence of animals, but also to the effect of selection as animals with low production are being culled each year. Within parity the effect of age at lambing was noticeable. For the first four parities the increase in age at lambing was associated with considerable increase in litter size. After the fourth parity this effect was not so strong or even negative (opposite). The change of litter size with parity and age is related with physiological status of animals. Our results are in agreement with other studies, e.g., Maria and Ascaso (1999)

reported that litter size in different breeds increased with the advancement of age and parity up to the fourth parity.

Variance component estimates for the baseline model (single trait analysis of BA; Table 2) showed that chosen effects of herd, animal (additive genetic effect and permanent effect) are important sources of variability in BA. Herd effect accounted for 10%, permanent effect for 3%, and additive genetic effect accounted for 5% (= h^2_{BA}) of variability in BA. These estimates are in accordance with the literature on this subject (e.g. Matos et al., 1997). Analysis of variance for B1 resulted in smaller estimate for herd variance and residual variance, while additive genetic variance was a bit higher ($\sigma^2_{a_{B1}}$ =0.024 lambs[2]), but not markedly. Smaller estimates for B1 are expected due to the smaller phenotypic variance in the first parity, which is also the reason that heritability for this trait (B1) was higher (h^2_{B1} =0.10). Analysis of variance for B2+ resulted in larger estimates for all components except for

Table 2. Variance component estimates (±standard error and the corresponding ratio to phenotypic variance or correlation bellow the estimate) for the number of lambs born in all parities (BA) and separately for the first parity (B1) and later parities (B2+) with different models

	Component			
	Herd	Permanent	Animal	Residual
	All parities – single trait model			
BA	0.036 ± 0.004	0.009 ± 0.001	0.018 ± 0.002	0.285 ± 0.002
	0.10	0.03	0.05	0.82
	Parity 1 - single trait model			
B1	0.021 ± 0.003	—	0.024 ± 0.004	0.204 ± 0.004
	0.08		0.10	0.82
	Parity 2+ - single trait model			
B2+	0.041 ± 0.005	0.009 ± 0.002	0.018 ± 0.002	0.300 ± 0.002
	0.11	0.02	0.07	0.79
	Parity 1 & Parity 2+ - two-trait model			
B1	0.021 ± 0.003	—	0.026 ± 0.003	0.202 ± 0.004
	0.08		0.10	0.82
B2+	0.040 ± 0.005	0.008 ± 0.002	0.021 ± 0.002	0.299 ± 0.002
	0.11	0.02	0.06	0.81
B1-B2+	0.027 ± 0.003	—	0.022 ± 0.002	—
	0.93		0.94	
	All parities - single trait model with heterogeneous residual variance			
BA	0.034 ± 0.004	0.009 ± 0.001	0.018 ± 0.002	0.205 ± 0.003
	0.13, 0.09	0.03, 0.02	0.07, 0.05	0.77
				0.300 ± 0.002
				0.83

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the additive genetic effect where the same value as in the analysis of BA was obtained ($\sigma^2_{a_{B2+}}$ =0.018 lambs², h^2_{B2+} =0.07). Higher values were expected due to larger phenotypic variance of B2+.

Estimates from the two-trait model analysis of B1 and B2+ were generally in concordance with the separate analyses of B1 and B2+ (Table 2). That is, variance component estimates were generally lower for the B1 than for the B2+ trait, except for the additive genetic effect. Additive genetic variance estimates were a bit larger ($\sigma^2_{a_{B1}}$ =0.026 lambs², h^2_{B1} =0.10; $\sigma^2_{a_{B2+}}$ =0.021 lambs², h^2_{B2+} =0.06) in comparison to separate analyses but not markedly. Estimated correlation between B1 and B2+ for the herd effect was high ($r_{h_{B1},h_{B2+}}$ =0.93) as well as for the additive genetic effect ($r_{a_{B1},a_{B2+}}$ =0.94). The latter value suggests that the number of lambs born in the first and later parities is the same trait from the genetic point of view. Separate analyses and two-trait analysis of B1 and B2+ showed the difference in variance components for B1 and B2+, but the difference is not very large except for the residual variance, where difference is substantial, e.g., estimates from two-trait analysis are $\sigma^2_{e_{B1}}$ =0.202 lambs² vs. $\sigma^2_{e_{B2+}}$ =0.299 lambs².

Given that: 1) the analysed trait has a discrete distribution, 2) the estimates from two-trait analysis showed high additive genetic correlation between B1 and B2+, and 3) markedly different variance estimates only for the residual effect we investigated the possibility of performing single trait repeatability model with heterogeneous residual variance. Such a model should accommodate the discrete nature of the analysed trait and provide a good approximation in comparison to the theoretically more appropriate threshold model. Computationally such a model would be very parsimonious as only one additional variance component needs to be estimated from the data. Since this component is linked directly to phenotype there is enough information for estimation leading to stable convergence. Variance component estimates from such a model were very similar to the estimates from baseline model for BA. In addition separate estimates of residual variance were obtained for the first parity ($\sigma^2_{e_{B1}}$ =0.205 lambs²) and later parities ($\sigma^2_{e_{B2+}}$ =0.300 lambs²), which were of similar value as estimates from two-trait analysis of B1 and B2+. Correspondingly the variance ratios were different for the first parity than for later parities, e.g., h^2_{B1} =0.07 and h^2_{B2+} =0.05.

Correlations between breeding values evaluated using different statistical models were generally high (Table 3). Single trait repeatability model for BA is the most often used model for genetic evaluation for litter size in sheep (e.g., Matos et al., 1997). The lowest correlation (0.972) with BA had B1, which is expected due to the smaller number of records for B1 and markedly different residual variances for BA and B1 (Table 2). Due to the same, but opposite facts, the correlation between breeding values of BA and B2+ increased to 0.989. Correlation between breeding values from BA and B1-B2+ analyses were 0.982. Separate and two-trait analyses of B1 and B2+ provided breeding values of very high correlations (>0.99). Breeding values from single trait repeatability model for BA with heterogeneous residual variance were highly correlated with breeding values from standard single

Table 3. Correlations between breeding values for the number of born lambs from different statistical models (BA – single trait model for all parities; B1 – single trait model for the first parity; B2+ - single trait model for later parities; B1-B2+ - two-trait model for the first parity and later parities; BAH – single trait model for all parities with heterogeneous residual variance in the first parity and later parities)

	BA	B1	B2+	BAH
B1	0.972			
B2+	0.989	0.992		
B1-B2+[1]	0.982	0.998	0.998	0.990
BAH	0.996	0.984	0.993	/

[1] B1-B2+ - average breeding value of B1 and B2+

trait repeatability model for BA (0.996) or B2+ (0.993) or two-trait analyses of B1 and B2+ (0.990), showing good performance of this parsimonious model. Given that a single trait model with heterogeneous residual variance provides a good approximation for the discrete nature of analyzed trait it is surprising that correlation with breeding values from the standard single trait model for BA is so high (0.996). This shows remarkably robust behavior of the standard model.

Conclusions

Genetic parameters are required for routine genetic evaluation. This study provides such estimates for litter size in the first and later parities in Improved Jezersko-Solcava sheep in Slovenia. Several models were fitted to account for marked change of variance between the first and later parities. The largest change was observed for residual variance, where higher values were found in later parities, while variances for other components did not change markedly and genetic correlation was very high. Correlations among breeding values from different models showed that the simplest model (single trait repeatability model) can be a parsimonious choice for routine genetic evaluation.

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