

Estimation of genetic parameters for litter size in sheep: a comparison of a repeatability and a multivariate model

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Abstract

Genetic parameters were estimated for litter size in two prolific sheep breeds, i.e. the Zwartbles and the synthetic breed Swifter. Genetic parameters and breeding values for litter size in different parities were estimated using both a repeatability and a multivariate animal model. The estimated heritability from the repeatability model was 0.10 for the Zwartbles and 0.12 for the Swifter. For the multivariate model, heritability of litter size in first, second and third parity was 0.05, 0.07 and 0.10 for the Zwartbles and 0.09, 0.12 and 0.09 for the Swifter. Genetic correlation for litter size in Swifter was 0.81 between parity 1 and 2 and 0.99 between parity 2 and 3. For the Zwartbles genetic correlations were all very close to unity. Environmental correlations between litter size in subsequent parities were not constant over parities. Phenotypic variance in litter size in both breeds was 0.309 in first parity and was almost 50% higher in later parities. Based on the results it is recommended to apply a multiple trait model.

Keywords: genetic parameters, litter size, multiple trait, repeatability model, sheep.

Introduction

Litter size is an important component of productivity in sheep. Differences in litter size contribute more to total lamb-weight weaned per ewe than growth rate of individual lambs (Bradford, 1985). Litter size can be improved by within-breed selection and by combining prolific breeds in a cross breeding scheme. The Zwartbles and the Swifter are two prolific breeds of sheep which are used within The Netherlands. Both breeds are relatively fecund and have good meat production characteristics. The Swifter is a synthetic breed which originates from the Texel and the Flemish Milk sheep (Bekedam *et al.*, 1994). The objective in developing the Swifter was to combine the larger litter size of the Flemish Milk sheep with the outstanding meat production traits of the Texel sheep.

Selection on litter size requires knowledge of genetic parameters of litter size measured in different parities. The objective of this study was to estimate those genetic parameters in Zwartbles and Swifter sheep and to compare the estimates obtained by applying a repeatability model as compared with those for a multiple trait model.

Material and methods

Data were available for 14 514 Zwartbles and 48 275 Swifter litters collected by the breeding organizations

of these breeds. The data comprised litters born from 1986 to 1994 for the Swifter and from 1990 to 1994 for the Zwartbles. For each litter, the number of lambs born and the date of birth was recorded. Pedigree information from 1976 onwards was available on all ewes. For rams, ancestors born after 1978 for Zwartbles and after 1979 for Swifter were included in the pedigree. This resulted in 20 457 animals in the Swifter pedigree file and 7798 animals in the Zwartbles pedigree file.

The majority of litters were born from January to April each year. Litters born from June through November were excluded from the analysis because of possible effects of induced oestrus. This resulted in elimination of 2% of all litters for the Swifter and less than 1% for the Zwartbles. Effects of flock, month and year of birth were combined in a HYS class. Records from two subsequent months were combined in one HYS class in case the number of records was less than four. The number of lambings in parity four and higher was limited and therefore not included in the analysis.

After imposing the restrictions for lambing season, HYS class and parity, 8075 litters for the Zwartbles and 31 380 litters for the Swifter were available for analysis. The number of litters in each parity is given in Table 1.

Table 1 Average unadjusted litter size and number of litters in different parities

Parity	Litter size				No. of litters	
	Zwartbles		Swifter		Zwartbles	Swifter
	Mean	s.d.	Mean	s.d.		
1	1.64	0.576	1.68	0.590	3433	13861
2	2.12	0.670	2.17	0.691	2951	11135
3	2.31	0.717	2.37	0.733	1691	6384
Overall	1.95	0.701	2.00	0.718		

Preliminary analysis using least-squares methods on data regarding first and second parity was used to determine the fixed effects to be included in the model. Two methods were used for estimating the genetic parameters. First a repeatability model was applied which combined the information available for all three parities into one set of parameters. Secondly a multiple trait model was applied which also estimated the correlation between the three parities, resulting in parameter estimates for the three parities separately.

The repeatability model was constructed as follows:

$$Y_{ijkl} = HYS_i + p_j + a_k + M_k + e_{ijkl}$$

where Y_{ijkl} is litter size in the l th litter of animal k , HYS_i the fixed effect of the i th herd-year-season, p_j the fixed effect of the j th parity, a_k the random additive genetic effect of the k th animal $\sim(0, A\sigma_a^2)$, M_k the random effect due to common environmental effect for all litters of the k th animal $\sim(0, I\sigma_m^2)$ and e_{ijkl} the residual (environmental) effects pertaining to record $Y_{ijkl} \sim(0, I\sigma_e^2)$. Matrix A is the matrix with additive genetic relationships between animals, σ_a^2 , σ_m^2 and σ_e^2 are variance due to additive genetic effects, common environmental effects and residual effects. Progeny of a ewe with multiple litters share a common genetic (a_k) and a common environmental effect (M_k). The residual effects as well as the

common environmental effects are assumed to be uncorrelated and have a common variance.

The multivariate model for litter size was defined as:

$$Y_{ij} = HYS_i + a_j + e_{ij}$$

where Y_{ij} is litter size of ewe j , HYS_i the fixed effect of the i th herd-year-season, a_j the random additive effect of the j th animal (ewe) and e_{ij} the residual effect. For estimation of genetic parameters the restricted maximum likelihood technique was used by applying the *REML* programs version 3.1 (Groeneveld and Kovac, 1990) and *VCE* version 3.1 (Groeneveld, 1994).

Results

The unadjusted mean litter size per parity hardly differed between the breeds (Table 1). The average litter size as well as the standard deviation increased with parity number. The difference in standard deviation between first and second parity is twice as large as the difference between second and third parity.

Estimation of genetic parameters

Estimated parameters for both breeds from the repeatability model are given in Table 2.

The variance due to common environmental effects was estimated to be zero for the Zwartbles and accounted for proportionately 0.02 of the variation in litter size for the Swifter. Heritability estimated from the repeatability model was 0.10 (s.e. 0.12) for the Zwartbles and 0.12 (s.e. 0.007) for the Swifter.

Results from the multivariate model showed that genetic correlations among litter size in different parities are high in Swifter (Table 3) as well as Zwartbles (Table 4). The phenotypic variance clearly increased with parity in both breeds (Table 2). Heritability of litter size was found to be different

Table 2 Variance components for litter size from the repeatability model and the multiple trait model (standard errors in parentheses)

	Repeatability model		Multiple trait model	
	Zwartbles	Swifter	Zwartbles	Swifter
Environmental variance (σ_e^2)				
Parity 1	0.347 (0.005)	0.334 (0.002)	0.293 (0.008)	0.282 (0.003)
Parity 2			0.382 (0.011)	0.369 (0.005)
Parity 3			0.418 (0.019)	0.424 (0.007)
Additive genetic variance (σ_a^2)				
Parity 1	0.039 (0.005)	0.046 (0.003)	0.016 (0.007)	0.026 (0.002)
Parity 2			0.027 (0.011)	0.052 (0.004)
Parity 3			0.048 (0.02)	0.040 (0.006)

Table 3 Genetic parameters for litter size of the Swifter using a multivariate model (heritabilities on the diagonal, genetic correlations above and environmental correlations under the diagonal)

	Parity 1	Parity 2	Parity 3
Parity 1	0.09 (0.007)	0.81 (0.008)	0.88 (0.008)
Parity 2	0.04	0.12 (0.01)	0.99 (0.003)
Parity 3	0.08	0.12	0.09 (0.012)

Table 4 Genetic parameters for litter size of the Zwartbles using a multivariate model (heritabilities on the diagonal, genetic correlations above and environmental correlations under the diagonal)

	Parity 1	Parity 2	Parity 3
Parity 1	0.05 (0.022)	1.00 (0.007)	1.00 (0.007)
Parity 2	0.06	0.07 (0.026)	1.00 (n.e.)
Parity 3	-0.04	0.10	0.10 (0.042)

n.e. = not estimated.

between breeds. For the Zwartbles, the heritability increased with parity, while a trend is absent for the Swifter. The genetic correlation between litter size in second and third parity is very close to 1.0 in both breeds. The genetic correlation between first and second parity was 1.0 for the Zwartbles. For the Swifter, however, it was 0.81.

Discussion

The methods for estimating genetic parameters used in this study assume the trait under consideration to have a continuous distribution. Litter size, however, has a discrete distribution which implies that a threshold model would have been a more appropriate choice. Olesen *et al.* (1994) have shown that the assumption of a continuous distribution is justified. They estimated the heritability of litter size in sheep, using linear, threshold and Poisson models. All models performed similarly with respect to goodness of fit, predictive ability and ranking of sires. Heritability was highest for the threshold model. Spearman's rank correlations between sire solutions from the linear model and the threshold model were 0.998 and 0.997, indicating that the rankings were nearly identical.

Heritabilities estimated in this study are within the range of heritabilities previously estimated in different breeds of sheep. De Graaf *et al.* (1985) estimated heritabilities for litter size in Texel sheep ranging from 0.17 to 0.20 in parity 1 to 4. Genetic correlations were 0.675 between parity 2 and 3 and 0.617 between parity 2 and 4. They used univariate

sire models for litter size within parity and estimated genetic correlations from the predicted breeding values. Olesen *et al.* (1994) applied a linear sire model and estimated the heritability of litter size to be 0.20 and 0.12, using data on 1-year-old ewes. Other estimates for the heritability of litter size have been summarized from the literature by Gonzalez in 1982, as referred to by Bradford (1985). In that study an average heritability of 0.10 was found with the median class ranging from 0.05 to 0.10.

In the repeatability model the proportion of variance due to common environmental effects (c^2) ranged from 0 in the Zwartbles to 0.02 in Swifter (Table 2). The environmental correlations between litter size in different parities estimated with the multivariate model ranged from 0.04 to 0.12 in Swifter and -0.04 to 0.10 in Zwartbles (Tables 3 and 4). These results indicate that the general assumption of constant environmental correlation between parities in the repeatability model in this case is not justified.

In the present study two models were used for estimating the genetic parameters for litter size in sheep, the repeatability model and the multivariate model. The repeatability model is easier to apply on a large scale because it requires knowledge of a smaller number of parameters and is less computationally demanding. Disadvantage is that the model assumes the three parities to be the same trait, i.e. equal variances in all parities, genetic correlations of unity between parities and equal environmental correlations. In the present analysis, a clear difference in variance between parities was found. The multiple trait model treats the parities as different traits and thus allows for the variances of the three parities to differ (Henderson, 1988). A problem with this type of model is the higher demands regarding computer facilities and usually a larger data set is required for estimating genetic and phenotypic correlations.

The genetic correlations for litter size between parities for the Swifter ranged 0.807 to 0.99 (Table 3) while for Zwartbles all genetic correlations were estimated to be 1.0 (Table 4). In case of the Zwartbles it can be concluded that the litter size in the three parities can be looked at as being genetically the same trait for which the variance is dependent on parity. For the Swifter, correlations deviate more from unity and consequently it is less appropriate to treat observations in different parities as the same trait. When looking at the variance components, genetic as well as environmental, there is a clear increase from parity one to three in both breeds.

Roehe and Kennedy (1995) compared selection on a repeatability and multiple trait animal model for

reproduction traits measured in different parities of sows. They concluded that the use of a multiple trait model was most appropriate. The breeding values of animals present in 1994 were used to illustrate the differences between selection based on the breeding values estimated from both models. Selection of animals with the highest breeding values estimated from the repeatability model would on average result in the selection of older animals than selection based on breeding values from the multiple trait model. The main reason for the selection of older animals is the increase in variance in litter size with parity.

To meet the requirements of the repeatability model regarding the equal variances, rescaling the observations in the different parities to a common variance is one option. Meuwissen *et al.* (1996) indicated that correction for heterogeneous variance should take into account the effects of fixed effects on the observations. They developed a method for prediction of breeding values which simultaneously corrects for the phenotypic heterogeneous variances. In this procedure, heritabilities are assumed to be homogeneous. This procedure can be viewed as an alternative for the multiple trait model provided that the genetic correlations and heritabilities justify the assumption of a single trait with homogeneous heritability.

Conclusion

The genetic parameters for litter size estimated in the present study were of similar size as found in the literature. Variance components (genetic and environmental) differed over parities. Genetic correlations between litter size over parities were equal to one for the Zwartbles, but not completely for the Swifter. Environmental correlations were not

constant over parities as assumed in the repeatability model. Therefore application of a multiple trait model is most appropriate.

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