

Uniformity in birth weight is heritable in Norwegian White Sheep

P. Sae-Lim¹, J.H. Jakobsen² & H.A. Mulder³

¹ Nofima AS, PO Box 210, 1431 Ås, Norway

² Norwegian Association of Sheep and Goat Breeders, PO Box 104, 1431 Ås, Norway

jj@nsg.no (Corresponding Author)

³ Wageningen University & Research Animal Breeding and Genomics, PO Box 338, 6700 AH Wageningen, The Netherlands

Summary

Birth weight is an optimum trait where very high and very low birth weights are undesirable as they may cause issues, such as dystocia, stillbirths and diminished lamb vigor. Due to economic and welfare concerns, selection for more uniform birth weight is therefore desirable at all litter sizes. If uniformity in birth weight is heritable, selection against very high and very low birth weights can be conducted. The aim of the current study was to investigate if direct and maternal genetic variances in uniformity in birth weight exist in Norwegian White Sheep (NWS). Data composed birth weights of 136,992 NWS lambs born between 2000 and 2017 and corresponding sire-maternal grand sire pedigree. The double hierarchical generalized linear mixed model (DHGLM) was fitted. The direct and maternal heritability for uniformity of birth weight were 0.08 and 0.11, respectively, and larger than for many other uniformity traits in livestock. Furthermore, the direct (57.8%) and maternal (69.4%) genetic coefficients of variation for uniformity were substantial, revealing large potential for selection for more uniform birth weight in NWS lambs. Genetic correlations between direct and maternal genetic effects on birth weight and uniformity were 0.39 and 0.12, respectively, indicating that that selection for more uniform birth weight may reduce the average birth weight genetically.

Keywords: sheep, birth weight, uniformity, maternal genetic effect, DHGLM

Introduction

The economy of a sheep enterprise can be improved by marketing more lambs per ewe, which may be achieved by an improvement of proportion of lambs surviving the period just before and right after birth. Birth weight is an optimum trait where very high birth weights and very low birth weights are undesirable as they may cause issues, such as dystocia, stillbirths and diminished lamb vigor (e.g. Dwyer, 2008). Neonatal mortality is considered as a welfare concern of the lamb, and difficult lambings are considered as poor welfare for the ewe. Due to economic and welfare concerns, uniformity of birth weight is therefore desirable at all litter sizes. If the uniformity in birth weight is heritable, selection against very high and very low birth weights can be conducted. Different procedures have been used to model uniformity. The double hierarchical generalized linear mixed model (DHGLM) (Rönnegård *et al.*, 2010) has earlier been applied to birth weight in pigs (Sell-Kubiak *et al.*, 2015) and to litter size in sheep (Cottle *et al.*, 2016), but never to birth weight in sheep. Birth weight of a lamb is affected by both direct and maternal genetic effects. Likewise, direct and maternal genetic effects may also affect uniformity in birth weight of a lamb. The aim of the current study was to apply a sire-maternal grandsire (sire-mgs) DHGLM to birth weight in sheep, and

to investigate if uniformity of birth weight is heritable in Norwegian White Sheep.

Material and methods

Data Description

Data were extracted from the Norwegian Sheep Recording System. The original dataset contained ~2.2 million birth weight records obtained during the time span from 2000 to 2017. Data were edited such that flocks should be genetically connected to other breeding flocks with a value of at least 0.055 (Lewis *et al.*, 2005). Only flocks with at least 50 birth weights during each of the 18 consecutive years were included. Further, sire of the lamb should be known and have sired at least 10 lambs with a birth weight in the dataset. After editing, the dataset contained 136,992 birth weight records of lambs sired by 3730 sires. The s-mgs pedigree file contained 10,208 animals.

Statistical Model

A sire-mgs DHGLM was used to estimate (co)variance components for birth weight and its uniformity. In order to facilitate convergence, the observed birth weight was standardized to a mean of zero and a variance of 1. The model was defined as:

,

where y is a vector of observations of standardized birth weights (stdwt) for the i^{th} individual. \mathbf{y} is the vector of response variables for the residual variance, where y_i is the squared residual of the i^{th} stdwt record, h_i is the diagonal element in the hat-matrix of \mathbf{y} , and σ^2 is the estimated residual variance of the i^{th} observation in the previous iteration (Felleki *et al.*, 2012). \mathbf{X} , \mathbf{Z} , and \mathbf{Q} are the incidence matrices corresponding to vectors of \mathbf{b} (fixed effects), \mathbf{u} (random genetic effects of s or mgs) and \mathbf{pe} (permanent environmental effects). \mathbf{u}_v ($\mathbf{u}_{s,v}$) and \mathbf{u}_{mgs} ($\mathbf{u}_{mgs,v}$) were assumed to follow: $\mathbf{u} \sim N(\mathbf{0}, \mathbf{G})$, where the \mathbf{G} is the sire-mgs (co)variance matrix. The sire-mgs DHGLM was fitted in ASReml until the log-likelihood has converged (Gilmour *et al.*, 2014). The λ was estimated to be close at the boundary of zero and thus the λ was excluded from the final sire-mgs DHGLM. Details of the conversion from the sire-mgs model to the animal model as well as computation of the genetic parameters are listed in the Appendix.

Results and Discussion

(Co)variance components for birth weight obtained in the sire-mgs DHGLM are listed in Table 1, along with the (co)variance components converted to the animal DHGLM with variances for direct and maternal additive genetic effects, permanent environment, residual and phenotypic variances. Lastly, heritabilities and genetic correlations are listed in the last column of Table 1.

Table 1. Variance components estimated in the sire-mgs DHGLM, variance components converted to the animal model with direct (d) and maternal (m) effects, and the corresponding heritability (h) and genetic correlation (r) after conversion of variances from the exponential scale (exp) to the additive scale.

Sire-mgs DHGLM	Animal DHGLM	Animal model	Genetic Parameters	
0.0177	0.0707	0.0736	0.123	
0.0019	-0.0279	0.0019	-0.320	
0.0242	0.1069	0.1007	0.175	

0.0086	0.0344	0.043
0.0028	-0.0061	-0.028
0.0028	-0.0061	0.062
0.0045	0.0157	0.077
0.0273	0.1090	0.111
-0.0040	-0.0706	0.392
0.0284	0.1570	-0.058
		0.0388
		0.3604
		0.5754
		-0.057
		0.121
		-0.540

Heritability and GCV

The estimate was low (0.077) but higher than those reported in the previous studies in livestock ($h^2 = 0.028$: min = 0.006 and max = 0.047; reviewed by Hill and Mulder (2010)) and higher than the estimates of h^2 for birth weight in pigs (0.008 to 0.01) (Sell-Kubiak *et al.*, 2015). The estimate of 0.111 was relatively high, suggesting that uniformity of birth weight is not only affected by the additive genetic effects of lambs but to a large degree also affected by the additive genetic effects of the ewe. Furthermore, we found substantial h^2 (57.8%) and h^2 (69.4%), suggesting that both direct and maternal genetic effects have high potential for response to selection for more uniform birth weight of lambs relative to the trait mean. Our estimates are, however, in the upper range of, or even greater than GCV from the previous studies in livestock and aquaculture species (mean = 40.6%: min = 30.0% and max = 58.0%; (Hill and Mulder, 2010; Sae-Lim *et al.*, 2015).

Genetic correlation

Genetic correlations varied from slightly negative to slightly positive (Table 1). For the direct effect, the r was 0.39, indicating that selection for larger birth weight in lambs will result in a larger variation in lamb birth weight. For the maternal effect, the r was 0.12, suggesting that maternal effect on birth weight and its uniformity are weakly correlated. This correlation is lower than the estimates ($r = 0.55$ to 0.62) of maternal effects in birth weight in pigs (Sell-Kubiak *et al.*, 2015). The genetic correlation between direct and maternal genetic effects on birth weight uniformity was -0.54, which suggests an antagonistic relationship between direct and maternal effects of uniformity. It is however known that estimation of genetic correlations between direct and maternal genetic effects may be biased (Bijma, 2006), and also that genetic correlations between mean and uniformity may have large standard errors (Mulder *et al.*, 2013).

Conclusion

Maternal genetic effects are important in sheep and therefore DHGLM was in this study extended to a sire-mgs DHGLM. Uniformity in birth weight is heritable in Norwegian White Sheep revealing possibilities for genetic improvement of the trait. Genetic correlations between direct genetic effects of mean and direct genetic effects of variance was weakly positive, indicating that selection for more uniform birth weight may reduce the average birth weight genetically.

List of References

- Bijma, P. 2006. Estimating maternal genetic effects in livestock. *J. Anim. Sci.* 84: 800-806.
- Cottle, D.J., A.R. Gilmour, T. Pabiou, P.R. Amer, & A.G. Fahey. 2016. Genetic selection for increased mean and reduced variance of twinning rate in Belclare ewes. *J. Anim. Breed. Genet.* 133: 126-137.
- Dwyer, C.M. 2008. The welfare of the neonatal lamb. *Small Rumin. Res.* 76: 31-41.
- Felleki, M., D. Lee, Y. Lee, A.R. Gilmour, & L. Rönnegård. 2012. Estimation of breeding value for mean and dispersion, their variance and correlation using double hierarchical generalized linear models. *Genet. Res.* 94: 307-317.
- Gilmour, A.R., B.J. Gogel, B.R. Cullis, S.J. Welham & R. Thompson. 2014. ASReml User Guide Release 4.1. VSN International Ltd, Hemel Hempstead, UK (available at: www.vsnl.co.uk)
- Hill, W. & H. Mulder. 2010. Genetic analysis of environmental variation. *Genet. Res.* 92: 381-395.
- Kriese, L.A., J.K. Bertrand & L. L. Benyshek, 1991. Age adjustment factors, heritabilities and genetic correlations for scrotal circumference and related growth traits in Hereford and Brangus bulls. *J. Anim. Sci.* 69: 478-489.
- Lewis, R.M., R.E. Crump, L.A. Kuehn, G. Simm, & R. Thompson. 2005. Assessing connectedness in across-flock genetic evaluations. *J. Anim. Sci.* 83 (Suppl. 1): 101
- Mulder, H., P. Bijma, & W. Hill. 2007. Prediction of breeding values and selection response with genetic heterogeneity of environmental variance. *Genetics* 175: 1895-1910.
- Mulder, H.A., L. Rönnegård, W.F. Fikse, R.F. Veerkamp & E. Strandberg. 2013. Estimation of genetic variance for macro- and micro-environmental sensitivity using double hierarchical generalized linear models. *Genet. Sel. Evol.* 45: 23
- Rönnegård, L., M. Felleki, F. Fikse, H.A. Mulder, & E. Strandberg. 2010. Genetic heterogeneity of residual variance-estimation of variance components using double hierarchical generalized linear models. *Genet. Sel. Evol.* 42. 10.1186/1297-9686-42-8
- Sae-Lim, P., A. Kaue, M. Janhunen, H. Vehviläinen, H. Koskinen, B. Gjerde, M. Lillehammer, & H. A. Mulder. 2015. Genetic (co) variance of rainbow trout (*Oncorhynchus mykiss*) body weight and its uniformity across production environments. *Genet Sel. Evol.* 47: 46.
- Sell-Kubiak, E., P. Bijma, E.F. Knol & H.A. Mulder. 2015. Comparison of methods to study uniformity of traits: Application to birth weight in pigs. *J. Anim. Sci.* 93: 900-911.

Appendix

Calculation of genetic parameters

The genetic (co)variance components of the sire-mgs DHGLM were converted to the corresponding direct (d) and maternal (m) components using the principle of conversion of a bivariate sire-mgs model as shown in Kriese *et al.* (1991):

$$= \quad (1)$$

The direct variance (σ^2_d) and maternal variance (σ^2_m) components of uniformity in equation (1) were on the exponential scale (*exp*) and they were subsequently converted to the additive scale following the conversion equations derived by Mulder *et al.* (2007):

$$\text{and } \sigma^2_{\text{res}} = \quad (2)$$

where σ^2_{res} is the residual variance of standardized birth weight from the univariate animal model.

The direct (h^2_d) and maternal (h^2_m) heritabilities of uniformity were calculated as:

$$= \quad \text{and} \quad = \quad (3)$$

where σ^2_{res} and σ^2_{res} is the squared phenotypic variance of standardized birth weight from the univariate animal model.

The genetic correlation on the exponential scale is expected to be equal to the genetic correlation on the additive scale. Hence, all genetic correlations were calculated on the exponential scale.

To understand the genetic potential for response to selection related to the trait mean, the direct genetic coefficient of variation (CV_d) for uniformity was calculated as $CV_d = \frac{\sigma_d}{\mu}$. Similarly, the maternal genetic coefficient of variation (CV_m) for uniformity was calculated as $CV_m = \frac{\sigma_m}{\mu}$.