HETEROGENEOUS VARIANCES AND GENOTYPE × ENVIRONMENT INTERACTION IN A RANDOM REGRESSION TEST-DAY MODEL

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INTRODUCTION

Genotype × environment interaction (G×E) in dairy cattle has gained renewed interest because 1) the increasing importance of health, fertility and functional traits in breeding goals, 2) the need for modeling more subtle fluctuations in traits over time, 3) the trend towards international evaluations (Mark, 2004), 4) the knowledge available from methods such as reaction norm models to model G×E (Kolmodin, et al., 2002) and 5) practically due to increased computing capacity estimation of higher dimensional model become feasible. For a single trait, G×E can cause heterogeneous genetic variances across environments, and genetic correlations between a trait expressed in different environments being smaller than unity. The objective of this paper is to account for G×E in a test-day model for somatic cell score (SCS) by inclusion of a reaction norm, in order to account for fluctuations in variances over time and to predict selection responses for a range of environments.

MATERIAL AND METHODS

Model. Genetic sire effects were modelled by applying random regressions (**RR**) using Legendre polynomial coefficients representing 1) days-in-milk (DIM), to account for differences along the lactation curve, 2) the environment (in the example herd test-day bulk milk somatic cell count (BMSCC)), to account for differences across environments in expression of genetic variances, and 3) the interaction between DIM and the environmental parameter to account for specific lactation curves in different herd environments. The within lactation animal effect was modelled by applying RR (for each lactation separately) on both DIM and the environmental parameter, to account respectively for individual differences in lactation curves and variable variances over environments. The between lactation animal effect was modelled by random effects for each animal. Heterogeneous residual variances were included in the model for 25 groups based on increasing values for DIM and the environment. Residual covariances other than permanent environmental were assumed to be zero. Fixed effects were included in the model for mean, DIM by BMSCC group, year-season of calving, and herd test-day. Fixed regressions were included to account for age at calving within parity, breed of the cow, for DIM within parity, and for the interaction between DIM and herd test-day environment. All analyses were performed using ASReml (Gilmour, et al., 2002).

Data. Edits to data included a minimum of 20 records on each herd test-day for all herds. Records before 5 DIM and after 365 DIM were deleted, as well as records of animals with fewer than 5 test-day records. Additional editing steps deleted sires with fewer than 25 daughters, sires with daughters in fewer than 3 herd test-days and herd test-days with daughters

of fewer than 3 sires. Finally, herd test-days with fewer than 5 remaining records were deleted. For each herd test-day, BMSCC was calculated as average of all available SCC records on that herd test-day, weighted by individual milk production. Somatic cell score was calculated from SCC (SCS = $\log_2$(SCC/100,000)+3). The final data set included 344,029 test-day records of 24,125 cows in 461 herds on 13,563 herd test-days. The pedigree included 479 sire entrees of which 182 were sires with daughters in the data.

RESULTS

Model selection. Based on the log likelihood ratio test, the RRM that best fitted the data included a fourth order RR on DIM, and a first order RR on both the BMSCC and the interaction between BMSCC and DIM. Models with higher order RR on DIM and BMSCC did not converge. Differences in log likelihood were larger for pairs of models with increasing order on DIM, than models with and without a RR on the interaction between DIM and BMSCC.

The results show that the model was able to allow a variable pattern of the sire variance across DIM to be different in different environments (i.e. at different levels of BMSCC; Figure 1). In herds with low BMSCC, the sire variance increased across DIM, while in herds with high BMSCC, the sire variances decreased with increasing DIM. Estimated heritabilities did change considerably across DIM in herds with low BMSCC, but did not change across DIM in herds with high BMSCC (Table 1).

Table 1. Estimated heritabilities[a] of SCS on herd test-days with different bulk milk somatic cell count (×10^{-3} cells/mL) (BMSCC) and at different days in milk (DIM).

	DIM				
BMSCC	40	110	175	245	315
85	0.06	0.08	0.11	0.14	0.16
130	0.06	0.08	0.11	0.13	0.15
175	0.06	0.08	0.10	0.13	0.14
230	0.07	0.08	0.10	0.11	0.13
360	0.10	0.09	0.10	0.10	0.11

[a]Approximate standard errors of the heritabilities ranged from 0.01 to 0.03.

The model allowed genetic correlations for SCS to be different between all possible combinations of DIM and BMSCC (Table 2). The estimated genetic correlation between SCS in early (40 DIM) and late lactation (315 DIM), was comparable in herds with low and high BMSCC (0.56 and 0.43, respectively). However, the estimated genetic correlation between SCS in herd test-days with low (85,000 cells/mL) and high BMSCC (360,000 cells/mL), was lower early in lactation (40 DIM), compared to late in lactation (315 DIM) (0.72 and 0.92, respectively).

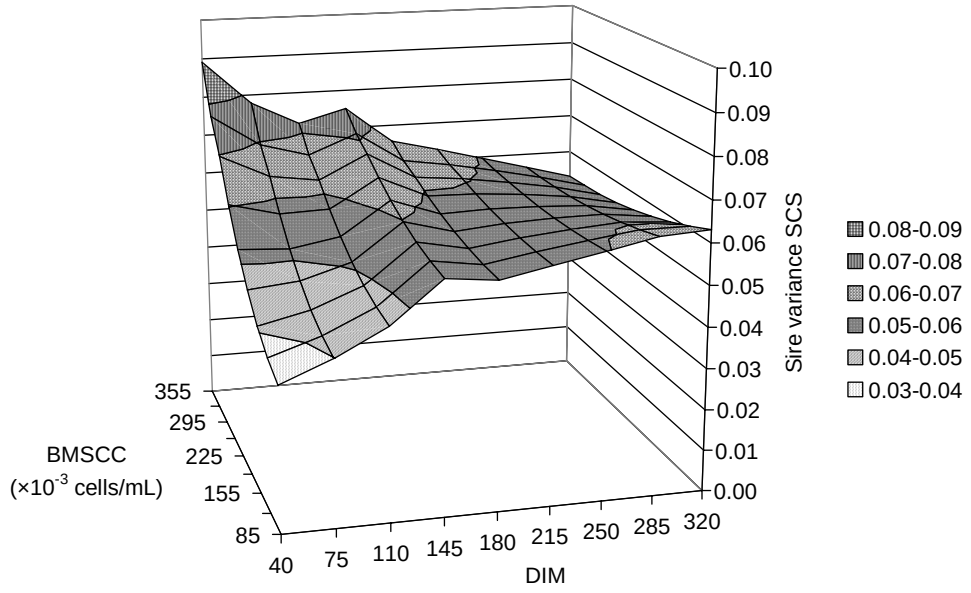

Figure 1. The pattern of sire variances for SCS across days in milk (DIM) at different levels of herd test-day bulk milk somatic cell count (BMSCC).

Table 2. Estimated genetic correlations[1] between SCS on herd test-days with different bulk milk somatic cell count (BMSCC) (×10^{-3} cells/mL), at 40 and 315 days in milk (DIM).

DIM		40			315		
	BMSCC	85	175	360	85	175	360
40	85	1.00					
	175	0.95	1.00				
	360	0.72	0.91	1.00			
315	85	0.56	0.53	0.42	1.00		
	175	0.60	0.56	0.43	0.99	1.00	
	360	0.65	0.60	0.43	0.92	0.96	1.00

[1]Approximate standard errors ranged from 0.01 to 0.13.

DISCUSSION

Modelling G×E by including a reaction norm in a random regression test-day model has the advantage that G×E effects are included in the estimated genetic parameters. The presented model allowed for genetic correlations between a trait in different environments to be smaller

than unity, as well as for heterogeneous genetic variances and heterogeneous heritabilities across environments. These three phenomena were in this study all found for SCS. The genetic correlations between SCS in different herd environments (i.e. between 0.72 and 0.92) were lower than estimates based on lactation records (Calus, et al., 2005), indicating that analysing data on test-day level reveals greater G×E effects compared to analyses on lactation records. Heterogeneous variances are usually corrected for as a way to increase accuracy of bull dam selection (Meuwissen, et al., 1996). In lactation models, suggested corrections scale records within herd-year groups according to their estimated variance (Meuwissen, et al., 1996). In the test-day model, however, the assumption is made that genetic variances depend on DIM. This means that the genetic variance applying for animals at different stages of lactation, in the same herd test-day, are different. However, genetic variance expressed as a result of G×E is expected to be the same for animals in the same herd test-day. Correction for heterogeneity of variance within environments would therefore be a challenge, as it has to be estimated to what extent the expressed genetic variance arises from interaction with the environment or stage of lactation. This problem can be circumvented by estimating effects of DIM and environment on the genetic variance simultaneously, as in the presented model. Other suggested test-day models that include a correction for heterogeneous variances across environments, did not allow the genetic correlation between environments to be lower than 1.0 (Lidauer and Mantysaari, 2002), or concluded that for milk yield the genetic correlation between different environments was not significantly different from unity (Gengler, et al., 2005). The present study, however, indicates that genetic correlations for SCS between different herd environments are at least early in lactation considerably lower than unity, and thus should be considered in methods to account for heterogeneity of variance.

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