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A preliminary investigation into genotype x environment interaction in South African Holstein cattle for reproduction and production traits

F.W.C. Neser¹, J.B. van Wyk¹ & V. Ducrocq²

¹ Department of Animal, Wildlife and Grassland Sciences, UFS, P.O. Box 339, Bloemfontein, 9300, South Africa; ²INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78302 Jouy-en-Josas, France

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Abstract

The purpose of the study was to investigate a possible genotype by environment interaction in first calf South African Holstein cows for both production and reproduction traits. Data from 100 975 cows on a total mixed ration (TMR) and 22 083 pasture based cows were used. These cows were the progeny of 4 391 sires and 84 935 dams produced over a period of 11 generations. Traits analysed were milk production (corrected to a 305-day equivalent) and age at first calving (AFC). Both were recorded over a period of 30 years from 1980 - 2010. Production or AFC in each environment (TMR vs. pasture) was treated as a separate trait. Bivariate analyses, fitting an animal model using the ASREML software, were used to obtain genetic correlations between the traits measured in each environment. The fixed factors included were a concatenation of breeder-keeper-year for both milk production and AFC and age at first calving which was fitted as a linear regression for milk production. The random part consisted of the direct additive effects only. The genetic correlation for milk production measured in the two different environments was 0.90 (0.027) and that of age at first calving 0.28 (0.12). The heritability estimates for milk production were 0.23 (0.008) under the TMR system and 0.32 (0.015) for the pasture based system, while the estimates for AFC were 0.063 (0.005) and 0.055 (0.009), respectively. The rather large-scale effect in the heritability $(0.23 \rightarrow 0.32)$, as well as the correlation of less than one for milk production between the two environments, indicates that a G x E may exist. However, the low genetic correlation between the two environments for AFC is much more real and indicates that G x E should be taken into account when sire selection is performed.

Keywords: Age at first calving, milk production, total mixed ration, pasture

*Corresponding author: neserfw@ufs.ac.za

Introduction

Genotype x environment interaction (G x E) in dairy cattle is a contentious issue that is usually ignored in genetic evaluations. It can, however, play a significant role in the accuracy of breeding values in different environments, if it exists, with a negative impact on genetic response when it is ignored. In South Africa two main production environments exist. The majority of cows in milk recording are kept under a total mixed ration (TMR) system. There are, however, a significant number of herds that utilize a pasture-base system for milk production. Currently, many bulls are used in both these systems without regard of any possible change of rank that may occur between these systems if a genotype x environment interaction exists.

Genotype by environment interaction can be described by inclusion of an interaction term in the traditional quantitative genetic model. Another approach is to define the phenotypic expression in various environments, as separate traits and estimate the genetic correlation between those traits.

The purpose of the study was thus to investigate a possible genotype by environment interaction in first calf South African Holstein cows for both production and reproduction traits by treating the traits in each environment as separate traits.

Materials & Methods

Data from 100 975 cows on a TMR system and 22 083 pasture based cows were used in the analysis. These cows were the progeny of 4391 sires and 84 935 dams produced over a period of 11 generations, in 277 herds. Traits analysed were first lactation milk production (corrected to a 305-day equivalent) and age at first calving (AFC). Both were recorded over a period of 30 years from 1980 - 2010.

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Trait	n	Mean ± SD	Minimum	Maximum	CV%
Milk production (kg)					
Total mixed ration	100 975	8221 ± 2452.0	126	17 510	29.83
Pasture	22 083	6366 ± 1279.0	1 456	11 430	20.09
AFC (days)					
Total mixed ration	100 975	820.4 ± 115.7	463	1 325	14.10
Pasture	22 083	857.9 ± 110.7	444	3 449	12.90

Table 1 Descriptive statistics of data used after editing for the first lactation milk production and age at first calving (AFC) in the analysis

n = number of records; SD = standard deviation; CV% = coefficient of variation.

Production or AFC in each environment (TMR vs. pasture) was treated as separate traits. A concatenation of breeder-keeper-year was fitted as a fixed effect for both production and AFC, while age at first calving was fitted as a linear regression for milk production. Two trait animal models were fitted, which allowed the calculation of relevant genetic correlations between traits measured in each environment, together with their appropriate standard errors. This was obtained using the ASREML program (Gilmour et al., 2009).

The bivariate model used in the estimation of genetic (co)variances for both milk production and AFC were:

$$\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix} = \begin{bmatrix} X_1\beta_1 \\ X_2\beta_2 \end{bmatrix} + \begin{bmatrix} Z_1g_1 \\ Z_2g_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Where Y_i is a n \times 1 vector of records for the i^{th} trait; i=1 to 2 for milk production on a TMR system and milk production in a pasture system or AFC on a TMR system and AFC in a pasture system. X_i is a n \times p incidence matrix that relates data to the unknown vector of location parameters β_i . The vector β contains breeder-keeper-year as a fixed effect for both milk production and AFC and age at first calving as a linear regression for milk production. The incidence matrix Z_i relating to unknown random vectors of the direct breeding value g_i (i=1 to 2) to Y_i . The unknown vector e_i contains the random residuals due to environmental effects specific to individual records. The random genetic effects were assumed to have a mean of zero and variances (VARg):

$$VARg \begin{bmatrix} g_1 \\ g_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2g_1 & A\sigma g_1g_2 \\ A\sigma g_2g_1 & A\sigma^2g_2 \end{bmatrix}$$

where A represents the numerator relationship matrix with rank equal to the number of animals in the pedigree ($n = 213\ 089$) used in the analysis. The random residual effects were assumed to have a mean of zero and variances (VARe).

VARe
$$\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} E\sigma^2e_1 & E\sigma e_1e_2 \\ E\sigma e_2e_1 & E\sigma^2e_2 \end{bmatrix}$$

where E represents an identity matrix with rank equal to the number of animals with records (n = 123 058).

Results and Discussion

Statistics describing first lactation milk production (kg) and age at first calving (AFC) (days) in the two different environments are presented in Table 1. Milk production differed between the two environments. A first-lactating Holstein cow on a TMR feeding system produced on average 1855 kg more milk per 305-day lactation period than her counterpart under a pasture feeding system. For age of first calving the difference between the two production systems was 37.5 days in favour of the TMR system.

Parameter estimates for production and reproduction traits measured in the two different environments are presented in Table 2. In the case of milk production, heritability estimates obtained from a wide range of dairy populations ranged from 0.17 to 0.29 (Weller & Ezra, 2004; Mostert *et al.*, 2006; Maiwashe *et al.*, 2008; De Ponte Bouwer *et al.*, 2013). The estimate of the present study for TMR (0.23) generally accords well with the range of literature values cited. The corresponding estimate of 0.32 for the population from the pasture based feeding system is higher than these respective values.

The heritability estimates for AFC were much lower than those in previous reports (0.22; Allaire & Lin, 1980), (0.16; Moore *et al.*, 1992), (0.38; Ojango & Pollott, 2001) but similar to estimates less than 0.10 (Moore *et al.*, 1991; Mäntysaari *et al.*, 2002; Nilforooshan & Edriss, 2004) and even as low as 0.02 (VanRaden & Klaaskate, 1993).

Table 2 Estimates of (co)variance components and ratios (SE in brackets), as well as direct heritability (in bold on the diagonal), genetic correlations (below the diagonal) and phenotypic correlations (above the diagonal) obtained from the two-trait analysis

Parameters	Milk production		Age at first calving		
	Total mixed ration	Pastures	Total mixed ration	Pastures	
Variances					
Direct additive	360 270	274 361	438.45	452.79	
Error	1 179 070	571 718	6 514.28	7 769.35	
Phenotypic	1 539 340	846 079	6 952.70	8 222.10	
(Co) variance ratios					
Milk production					
Total mixed ration	0.23 (0.008)	0.90 (0.027)			
Pastures	282 487	0.32 (0.015)			
Age at first calving					
Total mixed ration			0.063 (0.005)	0.28 (0.12)	
Pastures			126.49	0.055 (0.009)	

The genetic correlation for first lactation milk production measured in the two different environments was 0.90 (0.027) and that of age at first calving 0.28 (0.12). Veerkamp et al. (1994) reported no interaction between genotype and feeding system for milk production traits. The value of 0.90 was high compared with the estimate of 0.60 between the 305-d milk yields of Luxembourg and Tunisian Holstein populations (Hammami et al., 2009). Weigel et al. (2001) found high genetic correlations (>0.80) between milk yields across 17 Interbull country members. The reported estimates were higher than 0.90 between countries with predominantly grazing systems (i.e. Ireland, Australia, New Zealand). Genetic correlations were also higher than 0.91 between countries with high milk production (USA, Canada, Belgium, The Netherlands and Italy). Correlations between remaining Interbull members ranged between 0.8 and 0.9. On the other hand, studies on G x E between countries with different climatic conditions and production systems (Stanton et al., 1991; Costa et al., 2000; Ojango & Pollott, 2002) are limited. In these studies, genetic correlations between countries suggest the existence of G x E for milk yield in Holsteins. In general most of the estimates reported were high (>0.80) showing little or no evidence for a significant G x E in milk production. Almost all the within-country analyses, according to a review by Hammani et al. (2009), reported only a scaling effect for milk yield with large heterogeneity of variances and in some case heterogeneity of heritability estimates was observed.

Mee (2012), in a review on reproductive issues arising from different management systems (zero grazing and pasture based), reported variable results for genotype x environment interaction in reproduction traits for dairy cattle. Studies in Brazil and Columbia (Ceron-Munoz *et al.*, 2004), the Netherlands (Calus *et al.*, 2005), Australia (Fulkerson *et al.*, 2008) and in the UK (Haskell *et al.*, 2007; Strandberg *et al.*, 2009) found G x E interactions when reproduction between different herd management systems were compared. Other studies on reproduction performance under different production environments in the UK (Pryce *et al.*, 1999), Canada (Boettcher *et al.*, 2003), Ireland (Buckley *et al.*, 2003), the USA (Kearney *et al.*, 2004) and

Australia (Haile-Mariam *et al.*, 2008), in contrast, found no G x E. This, according to Mee (2012) reflects the variety of herd management systems, the variation in methods used to describe reproductive performance and the limitations of some study designs.

Conclusions

The rather large scale effect in the heritability $(0.23 \rightarrow 0.32)$ as well as the correlation of less than one for milk production between the two environments indicates that a G x E may exist. However, the low genetic correlation between the two environments for AFC is much more real and indicates that G x E should be taken into account when sire selection is done. Breeders should select animals within environmental conditions, comparable to where candidate animals are intended to perform.

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