Genetic Correlations Between Milk Production and Health and Fertility Depending on Herd Environment

J. J. Windig,¹ M. P. L. Calus, B. Beerda, and R. F. Veerkamp

Animal Sciences Group, Wageningen University and Research, Division Animal Resources Development, 8200 AB Lelystad, The Netherlands

ABSTRACT

High milk production in dairy cattle can have negative side effects on health and fertility traits. This paper explores the genetic relationship of milk yield with health and fertility depending on herd environment. A total of 71,720 lactations from heifers calving in 1997 to 1999 in the Netherlands were analyzed. Herd environment was described by 4 principal components: intensity, average fertility, farm size, and relative performance indicating whether herds had good (poor) health and fertility despite a high (low) production. Fertility was evaluated by days to first service and number of inseminations (NINS); somatic cell score was used as a measure of udder health. Data were analyzed with a multitrait reaction norm model. Genetic correlation within traits across environments ranged from 0.84 to unity. Genetic correlations of the 3 traits with milk yield were antagonistic but varied over environments. Genetic correlation of milk yield with days to first service varied from 0.30 in small herds to 0.48 in herds with low average fertility. Correlations with NINS varied from 0.18 in large herds to 0.64 in high fertility herds, and with somatic cell score from 0.25 in herds with a high fertility relative to production to 0.47 in herds with a relative low fertility. Selection in environments of average value resulted in different predicted responses over environments. For example, selection for a decrease of NINS of 0.1 in an average production environment decreased milk yield by 35 kg in low production herds, but by 178 kg in high production herds. **Key words:** milk yield, health and fertility, herd environment, reaction norm model

INTRODUCTION

Breeding for increased production in dairy cattle has negative side effects on health and fertility traits (Pryce et al., 1997; Rauw et al., 1998; Sandoe et al., 1999;

Roxstrom et al., 2001). To counter these effects, new breeding goals and management tools have been recommended (Neave et al., 1969; Barkema et al., 1999; Eslemont, 2003; Pryce et al., 2004; Royal and Flint, 2004). Generally, management and genetic effects are considered separately. However, genetic parameters, such as genetic correlations between production and health, may change over environments. In other words, selection for an increase in production under one management system may lead to more health risks than under other management systems. Thus, management and genetics have to be integrated to develop an effective program for improvement of health and fertility.

Although selection for higher production may lead on average to more health and fertility problems, there can be considerable variation across herd environments. The phenotypic effect of herd environment (management and other environmental effects) on health and fertility and their relationship with milk production at a national scale was recently explored (Windig et al., 2005a,b). With increasing average production, days to first service (**DFS**) and **SCS** decreased, whereas the number of inseminations (**NINS**) increased. Within herds, increased production always led to lower fertility and higher **SCS**. The extent, however, depended on the herd environment. In herds with low average production or low average fertility, differences between high- and low-producing animals were relatively small.

In animal breeding, management and other environmental effects are generally accounted for by treating them as a fixed effect, often in the form of herd-year-season effects. This adjusts results to the average environment, but ignores the interaction among management, environmental effects, and the genetics of animals, or the effects on the genetic association among milk yield and health and fertility traits. Recently, reaction norm models that use random regressions to estimate genetic parameters for each environment separately have been explored (Calus et al., 2002; Calus and Veerkamp, 2003; Hayes et al., 2003). A further extension is to model the relationship between several traits across herd environments (Kolmodin et al., 2002; Oseni et al., 2004; Pollott and Greeff, 2004). By doing

Received September 6, 2005.

Accepted November 30, 2005.

¹Corresponding author: jack.windig@wur.nl

so, genetic correlations between production and health and fertility traits in different herd environments can be estimated.

Objective of this study was to analyze genetic relationships among milk yield and health and fertility traits across herd environments with a multitrait reaction norm model. The overall objective was to assess whether the risks of high milk production in relation to SCS and fertility depended on the herd environment, and what the effect of selection in a specific environment was on traits in the same environment and on traits in other environments.

MATERIALS AND METHODS

Test-Day and Insemination Data

Data were available for 147,835 first-lactation heifers calving between July 1997 and June 1999. Insemination, production, and SCC records were the same as in Calus et al. (2005) and editing steps followed their procedure. All animals were at least 75% Holstein-Friesian. Animals were selected if they calved at an age between 640 and 1,095 d. Editing steps for environmental parameters (see below) reduced the number of heifers to 116,727. All (grand)daughters of (grand)sires with less than 20 (grand)daughters in the edited data were deleted, reducing the number of animals to 87,375. Herd-year-season subgroups were formed based on the method of Crump et al. (1997) with a minimum of 5 animals per subclass, a minimum length of 30 d, and a maximum length of 365 d. Records of animals that could not be assigned to a group with at least 5 records or that were assigned to a group with less than 3 records for any of the traits were deleted. Additionally, (maternal grand)sires with progeny in less than 3 herd-year-season classes and herd-year-season classes with progeny of less than 3 (maternal grand)sires were deleted. These steps reduced the number of records to 71,270.

Herd Environment

The herds were described by 65 environmental variables, partly derived from production data (e.g., average kg of fat per cow) and partly from the annual national agricultural survey (e.g., area of the farm). These environmental variables were reduced with principal components analysis to 4 principal components (PC) by choosing the PC that explained more than 5% of the total variance in all traits (details in Windig et al., 2005b). The first principal component (PC1, explaining 10.34% of the total variance) was interpreted as production intensity. Environmental variables that contributed most to PC1 were herd averages of 305-d protein, milk, and fat yield. Some fertility indices that were

negatively correlated to production also contributed negatively to this PC. The second PC (PC2, 8.86%) was interpreted as fertility because all fertility herd averages had large contributions. Principal component 3 (7.20%) combined variables related to the size of the farm such as number of employees, total hours of work, number of animals, and area of land (hereafter designated "scale"). Principal component 4 (6.58%) was a combination of production and fertility, in which both production and fertility herd averages had positive contributions. Consequently, farms that had a high fertility despite high production received high scores, whereas farms that performed low on both production and fertility received low scores (hereafter, PC4 is designated "relative performance").

Analyzed Traits

For production, 305-d milk yield was used. Somatic cell count was converted to SCS by $SCS = \log_2(SCC/100,000) + 3$ (Ali and Shook, 1980), and was used as a health trait. It was defined as the average SCS across test days. Two fertility traits were considered: DFS and NINS. Days to first service was calculated as interval from calving to first service. Records for DFS were missing if DFS was <20 or >300. Number of inseminations was missing if NINS was 0 or >10. These editing steps were applied to exclude extremely long lactation records, records with extreme short gestations due to abortions, and records with errors.

Pedigree

All sires, paternal grand dams, and maternal grand-sires of animals with records in the data were included in the pedigree file. All male predecessors of those animals, available from the pedigree data, were also included. Identification of dams of bulls was included if a dam had 2 or more sons; otherwise, dams were included as base parents. A total of 1,754 animals were included in the relationship matrix.

Reaction Norm Model—Univariate Analysis

Variance components were estimated with a sire-maternal grandsire model. Fixed effects were included in the model for mean and herd-year-season subclass. Fixed regressions were included to account for age at calving and for breed of the cow. The influence of environmental parameters on additive genetic merit was modeled by applying a random regression for each (maternal grand)sire, representing its EBV, on values of a PC for the herd-years in which his (grand)daughters were producing. The incidence matrix of maternal

grandsire effects was laid over the matrix of sire effects; that is, if a bull had entries in the data both as sire and maternal grandsire, the breeding value when being a maternal grandsire was equal to half the breeding value when being a sire. To account for heterogeneous residual variances, the residual variance was estimated separately for groups of 9,000 animals with similar herd environments.

The applied model was

$$Y_{ijklm} = \mu + \text{FIXED} + \sum_{n=0}^p \beta_{n,i} \Phi_n(PC_k) + 0.5 \left(\sum_{n=0}^p \beta_{n,j} \Phi_n(PC_k) \right) + \varepsilon_{ijklm} \quad [1]$$

where Y_{ijklm} is the performance of animal m , with sire i , grand sire j , and herd environment k ; μ is the average performance over all animals; *FIXED* includes herd-year-season subclasses and second order polynomial regressions on age at calving and percentage of Holstein-Friesian, Dutch Friesian and Meuse-Rhine-Yssel genes; $\beta_{n,i}$ is coefficient n of the random regression on the orthogonal polynomials of PC scores of the daughters of sire i ; $\Phi_n(PC_k)$ ($n = 0$ to p) are the design values of the orthogonal Legendre polynomials of order p for the PC in environment k ; $\beta_{n,j}$ is coefficient n of the random regression on the orthogonal polynomials of PC scores of the maternal granddaughters of sire j ; and ε_{ijklm} is the residual effect of cow m in environment k within group of environments l .

The Legendre polynomials were restricted to a first-order polynomial, because of convergence problems for higher-order polynomials in the multivariate case, and because higher-order polynomials did not give a significantly better fit (see Calus et al., 2005). This definition of the genetic model resulted in estimated sire variances of intercepts and slopes and covariances between intercepts and slopes that model possible interactions between slopes and intercepts. From these (co)variances, sire variances within single environments could be calculated (Kirkpatrick and Heckman, 1989; Van Tienderen and Koelewijn, 1994; Kolmodin et al., 2002; Oseni et al., 2004). The (co)variances of intercepts and slopes depend on where the intercept is chosen (Van Tienderen and Koelewijn, 1994) and are difficult to interpret. Therefore, only (co)variances, heritabilities, and genetic correlations within and between environments, and their approximate standard errors are presented here.

Residual variances could not be calculated within single environments (i.e., herds) because they contained too few observations (generally in the range of 10 to 20). Instead, residual variances for groups of 9,000 indi-

viduals with similar herd environments were calculated. Groups were composed by ranking animals according to their PC values. The first group consisted of animals 1 to 9,000, the second of animals 4,501 to 13,500, the third of animals 9,001 to 18,000, and so on, until the last group of animals: 63,001 to 71,270 (i.e., the last group contained 8,270 animals instead of 9,000), resulting in 15 overlapping groups. To achieve this grouping, the model was run twice; once with animals 1 to 9,000, 9,001 to 18,000, 18,001 to 27,000, and so on grouped, and once with animals 4,501 to 13,500, 13,501 to 22,500, and so on grouped. The additive genetic (co)variances estimated in both runs were very similar and averaged to obtain final estimates. Heritabilities and genetic correlations (see below under multiple-trait model) were estimated for the average PC value of each group (hereafter referred to as $\mathbf{pc}_{\text{env}1}$ to $\mathbf{pc}_{\text{env}15}$). Heritabilities were calculated as 4 times the sire variance in $\mathbf{pc}_{\text{env}\#}$ divided by the sum of the residual variance of the corresponding herd environment group plus 1.25 times the sire variance. The factor 1.25 is explained by the fact that both effects for sires (1 times the sire variance) and maternal grand sires (0.25 times the sire variance) were included in the model.

In some cases, the model with intercept and slope did not converge. Then, a reduced model with intercept only was used, and changes in heritabilities were the result of changes in residual variance components only. All analyses were performed with ASREML (Gilmour et al., 2002). Statistical significance was evaluated by calculating approximate standard errors of heritabilities and genetic correlations rather than likelihood ratio tests for a significant difference from zero of the variances of intercepts and slopes. The latter depend on the definition of the intercepts. Moreover, nonconvergence prevented the estimation of likelihood ratios in a number of cases and the focus of interest in the present study is on (changes in) heritabilities and genetic correlations, not on intercepts and slopes of reaction norms.

Reaction Norm Model—Multiple Trait Analysis

To obtain genetic correlations of production with the other traits in different environments, the univariate random regression model was extended to a multiple trait analysis. The estimated covariance matrix (V) combined variances and covariances of the random regression of, for example, milk and DFS:

$$V = \begin{bmatrix} \sigma_{\beta_0}^2(\text{milk}) & \sigma_{\beta_0(\text{milk}),\beta_1(\text{milk})} & \sigma_{\beta_0(\text{milk}),\beta_0(\text{DFS})} & \sigma_{\beta_0(\text{milk}),\beta_1(\text{DFS})} \\ \sigma_{\beta_1(\text{milk}),\beta_0(\text{milk})} & \sigma_{\beta_1}^2(\text{milk}) & \sigma_{\beta_1(\text{milk}),\beta_0(\text{DFS})} & \sigma_{\beta_1(\text{milk}),\beta_1(\text{DFS})} \\ \sigma_{\beta_0(\text{DFS}),\beta_0(\text{milk})} & \sigma_{\beta_0(\text{DFS}),\beta_1(\text{milk})} & \sigma_{\beta_0}^2(\text{DFS}) & \sigma_{\beta_0(\text{DFS}),\beta_1(\text{DFS})} \\ \sigma_{\beta_1(\text{DFS}),\beta_0(\text{milk})} & \sigma_{\beta_1(\text{DFS}),\beta_1(\text{milk})} & \sigma_{\beta_1(\text{DFS}),\beta_0(\text{DFS})} & \sigma_{\beta_1}^2(\text{DFS}) \end{bmatrix} \quad [2]$$

with $\beta_{\#}$ being the random regression coefficients as defined in equation [1]. To obtain genetic correlations between the 2 traits in herd environments pc_1 to pc_{15} , the variance-covariance matrix was computed as $M'VM'$:

$$M = \begin{bmatrix} M_{\phi} & 0 \\ 0 & M_{\phi} \end{bmatrix} \text{ and } M_{\phi} = \begin{bmatrix} \Phi_0(pc_{env1}) & \Phi_1(pc_{env1}) \\ \Phi_0(pc_{env2}) & \Phi_1(pc_{env2}) \\ \vdots & \vdots \\ \Phi_0(pc_{env15}) & \Phi_1(pc_{env15}) \end{bmatrix} \quad [3]$$

where 0 is a 15×2 matrix of zeros and $\Phi_0(pc_{env\#})$ and $\Phi_1(pc_{env\#})$ are the design values of the first-order orthogonal Legendre polynomial for herd environment $\#$. In case the multiple trait analysis had difficulty with convergence, the variances of the traits and the covariance within the traits were fixed to the values of the univariate analyses. In that case, only the between-trait covariances (i.e., only the 4 covariances in the lower left hand corner of V) could vary. Inferences from the univariate analysis were also provided by the multitrait analysis. Results were very similar and only those of the multitrait analysis are presented, except for cases in which the multitrait analysis did not converge and the univariate analysis was used.

Selection Response

The implications of the dependency of estimated genetic parameters on the environment were analyzed by calculating the correlated response in SCS and the 2 fertility traits when selection for an increase in milk took place in pc_8 , which is the herd environment at or very close to the average of all herd environments. The correlated response is given by:

$$CR_Y = R_X r_A \frac{\sigma_{A,Y}}{\sigma_{A,X}}$$

where CR_Y = the correlated response in trait Y ; R_X is the direct response in trait X to selection; r_A is the additive genetic correlation between trait X and Y ; and σ_A is the genetic additive standard deviation (Falconer and Mackay, 1996). The correlated response was calculated for SCS and the fertility traits in pc_{env1} , pc_{env8} , and pc_{env15} . So for pc_{env8} , the response was in the same environment, whereas for pc_{env1} and pc_{env15} , the response was in another environment, and genetic correlations between traits and across environments were used. Correlated responses were also calculated for milk, when selection was directly for SCS, DFS, or NINS in pc_8 . The response for the directly selected trait was set to +1,000 kg of milk, -6 d for DFS, -0.1 for NINS, and -0.5 for SCS. These responses were chosen

so that the selection intensity, i , was about 2 phenotypic standard deviations, corresponding to approximately 5% of the animals selected in mass selection.

RESULTS

Phenotypic Changes

Phenotypically, traits varied over the 4 environmental axes (principal components), average production intensity, fertility, farm scale, and relative performance (Table 1). The range covered by the 4 PC for milk production and the health and fertility traits is given in Table 1. These traits varied least over PC3, which is better characterized by number of animals ranging from 28 (pc_{env1}) to 130 (pc_{env15}), with 57 animals in the average environment (pc_{env8}). A detailed analysis of the phenotypic changes was given in Windig et al. (2005b). Milk production decreased not only with decreasing production intensity and relative performance but also, albeit less so, with increasing fertility and scale (Table 1). Likewise, NINS decreased not only with increasing average fertility but also with decreasing production intensity and relative performance and slightly with increasing scale, whereas DFS increased with decreasing production intensity and slightly with increasing relative performance and decreasing scale. Changes in SCS were smallest for production intensity and largest for relative performance, decreasing with increasing intensity, fertility, and relative performance, and decreasing with scale.

These changes were accompanied by heterogeneous phenotypic variances (Table 1). Largest changes in variance were seen for DFS and NINS, which were more variable at lower production intensities, relative performance, and fertility. Changes in variance were less dramatic for milk and in opposite direction from the fertility traits, whereas changes in variance for SCS were relatively small. Generally higher variances occurred in environments with higher means, but opposite trends in means and variances were observed for SCS and for milk when relative performance was used as the environmental variable.

Univariate Analysis

Trends in additive genetic variances over environments (not shown) were generally similar to phenotypic variances. For DFS, the REML analysis did not converge for scale and relative performance, except when a fixed additive genetic variance over environments was assumed. Heritabilities were relatively constant because ratios of phenotypic and additive genetic variances were similar over environments. Highest heritabilities were found for milk (about 50%) and for SCS

Table 1. Variation in mean, phenotypic variance, and heritability across herd environments¹

	Production intensity (PC1)		Fertility (PC2)		Scale (PC3)		Relative performance (PC4)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
305-d milk								
Mean	7,417	6,777–8,159	7,554	7,670–7,406	7,670	7,877–7,396	7,496	7,135–7,999
Variance	9,766	0.78–1.19	9,901	1.15–1.06	10,007	1.05–0.97	10,018	1.10–0.91
h^2	0.49	0.98–1.08	0.51	0.77–1.05	0.50	1.06–0.93	0.49	0.98–1.03
SCS								
Mean	2.23	2.72–1.89	2.17	2.52–2.08	2.16	2.53–2.12	2.29	2.79–2.02
Variance	1.261	1.01–1.11	1.286	0.99–1.05	1.319	1.00–1.02	1.278	1.02–1.01
h^2	0.22	1.09–0.83	0.20	1.06–0.99	0.20	0.96–1.02	0.21	1.00–1.03
Days to first service								
Mean	88	109–74	88	94–85	89	90–87	87	86–92
Variance	1,040	1.79–0.61	965	1.26–0.94	985	0.96–1.04	985	1.07–0.92
h^2	0.09	0.87–1.01	0.09	0.92–1.06	0.08	1.09–1.00 ²	0.09	0.91–1.03 ²
No. of inseminations								
Mean	2.03	1.87–2.27	2.05	2.34–1.82	2.04	2.26–2.00	2.07	2.45–1.90
Variance	1.935	0.81–1.38	2.144	1.32–0.68	2.053	1.24–0.87	2.092	1.27–0.83
h^2	0.03	0.59–1.28	0.03	1.15–0.97	0.03	0.97–1.03	0.03	0.81–1.19

¹Animals were ranked according to environmental values (principal components, PC) and grouped into 15 environmental groups (pc_{env1} to pc_{env15}). Mean = mean phenotypic value, Variance = total (phenotypic) variance. Mean = value in herd environments with average environmental value (pc_{env8}), range = value in pc_{env1} – value in pc_{env15} .

²Variable additive genetic variance model did not converge. Changes in heritabilities are entirely due to variable residual variances over herd environments.

(20%), whereas heritabilities for the fertility traits were relatively low (9% for DFS and 3% for NINS). Trends for additive genetic variances of milk were opposite to trends in its phenotypic variance when herds were ranked by average fertility (PC2). Opposite trends for additive and phenotypic variances were also observed for SCS when herds were ranked by production (PC1). Consequently the heritabilities for these 2 trait–PC combinations showed the largest changes (Figure 1): 14.5 and 5.6%, respectively. Changes in heritabilities of fertility traits were smaller, but changes could be relatively large because the heritabilities themselves were smaller. Largest changes were seen for DFS–fertility, increasing from 8.4 to 9.7%, and for NINS–production intensity, where the heritability more than doubled from 1.9 to 4.2% with increasing intensity.

Genetic correlations within traits across environments (Table 2) were smaller, indicating more changes in ranking of breeding values for the 2 fertility traits than for milk production and SCS. For the combinations DFS–fertility, NINS–fertility, and NINS–scale, the genetic correlation between the extreme environments (pc_{env1} and pc_{env15}) was less than 0.9, whereas it was close to 0.9 for DFS–intensity. Other genetic correlations were mostly around 0.97, except for SCS–fertility, SCS–scale, and milk–relative performance, all of which were above 0.99. Analyses for DFS–scale and DFS–relative performance did not converge, probably due to lack of variation in additive variance across environments.

Multivariate Analysis

Genetic correlations between milk and SCS in the average environments varied around a mean of 0.35, whereas the genetic correlations between milk and DFS and milk and NINS tended to be somewhat higher (Table 3). These genetic correlations between the traits and milk in the same environment varied considerably over environments (Figure 2): milk with SCS from 0.25 to 0.47, with DFS from 0.30 to 0.48, and with NINS from 0.18 to 0.64. In some instances the genetic correlation with milk production in another environment was higher than the correlation with milk in its own environment (Table 3). For example, the genetic correlation between NINS and milk in low production herds was 0.21, whereas the genetic correlation between NINS in low production herds and milk in high production herds was 0.67.

Genetic correlations decreased with increasing relative performance, but there were no consistent trends for the other PCs (Figure 2). The trends of the correlations of milk with DFS and milk with SCS were similar, except over production levels. The trends of the correlations of milk with DFS tended to be opposite to the trends of the correlations of milk with NINS, except over relative performance. The genetic correlations of milk with NINS were the most variable. They were weakest (<0.2) in large herds, and strongest (>0.6) in small herds and high fertility herds. Genetic correlations of SCS with milk tended to change less than corre-

Figure 1. Change in heritabilities over herd environments. Herd environments measured as 4 different principal components: PC1 = production intensity (■), PC2 = fertility (▲), PC3 = scale (△) and PC4 = relative performance (○); x-axis shows PC score; y-axis shows heritabilities for A) milk; B) SCS; C) days to first service; and D) number of inseminations.

lations with DFS and NINS with milk, and were almost constant over herds ranked according to scale (PC3).

Selection Response

The estimated correlated responses to selection for an increase in milk production in average environments were constant over environments (Table 4). However,

the response in milk production differed substantially over environments with selection for DFS, NINS, and SCS in the average environment. For example, selection for a decrease in NINS of 0.1 in herds with average fertility caused a decrease in milk of nearly 111 kg in the same environment. However, in herds with low fertility this decrease was only 35 kg, whereas in herds with high fertility, the decrease was 178 kg. In general,

Table 2. Genetic correlations ($\pm$ SE) within traits between lowest and highest analyzed environments (pc_{env1} and pc_{env15})

	Trait ¹			
	305-d milk	SCS	DFS	NINS
Production intensity (PC1) ²	0.976 ($\pm$ 0.019)	0.985 ($\pm$ 0.027)	0.911 ($\pm$ 0.085)	0.970 ($\pm$ 0.157)
Fertility (PC2)	0.960 ($\pm$ 0.025)	0.997 (—) ³	0.883 ($\pm$ 0.097)	0.899 ($\pm$ 0.157)
Scale (PC3)	0.960 ($\pm$ 0.025)	0.998 ($\pm$ 0.015)	1.000 ⁴	0.841 ($\pm$ 0.153)
Relative performance (PC4)	0.998 ($\pm$ 0.009)	0.951 ($\pm$ 0.035)	1.000 ⁴	0.974 (—) ³

¹DFS = Days to first service; NINS = no. of inseminations.

²PC = Principal component.

³Bounding of variance components prevented calculation of standard errors.

⁴Model with heterogeneous additive (co)variances did not converge.

Table 3. Genetic correlations within and across environments between 305-d milk production and fertility traits (days to first service, DFS, and no. of inseminations, NINS) and SCS^{1,2}

		SCS			DFS			NINS		
		Low	Average	High	Low	Average	High	Low	Average	High
Milk	Production intensity (PC1)									
	Low	0.29	0.30	0.31	0.39	0.45	0.48	0.21	0.14	0.09
	Average	0.34	0.35	0.35	0.34	0.38	0.41	0.47	0.40	0.34
Milk	Fertility (PC2)									
	Low	0.39	0.37	0.36	0.48	0.48	0.48	0.32	0.28	0.18
	Average	0.35	0.34	0.33	0.33	0.37	0.39	0.53	0.47	0.43
Milk	Scale (PC3)									
	Low	0.35	0.37	0.40	0.30 ³	0.30 ³	0.30 ³	0.60	0.64	0.68
	Average	0.33	0.35	0.38	0.35 ³	0.35 ³	0.35 ³	0.39	0.43	0.47
Milk	Relative performance (PC4)									
	Low	0.47	0.46	0.45	0.42 ³	0.42 ³	0.42 ³	0.34	0.35	0.36
	Average	0.37	0.36	0.36	0.36 ³	0.36 ³	0.36 ³	0.28	0.30	0.32
	High	0.27	0.26	0.25	0.30 ³	0.30 ³	0.30 ³	0.21	0.24	0.26

¹Animals were ranked according to environmental values (principal components, PC) and grouped into 15 environmental groups (pc_{env1} to pc_{env15}). For each PC–trait combination, 9 correlations are given. Correlations with milk in the same environment are shown on the diagonal (boldface). Top rows show correlation of traits with milk in low environment (pc₁), middle rows show correlation with average environment (pc₈), and bottom rows show correlation with high environment (pc₁₅).

²Approximate standard errors for SCS on average 0.066 (ranging from 0.048 to 0.082), for DFS 0.089 (0.071 to 0.107) and for NINS 0.113 (0.095 to 0.130).

³Variable additive genetic (co)variance model did not converge. Variation in genetic correlations is entirely due to variable additive genetic variance over environments of milk only.

selection to reduce SCS or improve fertility decreased milk production and vice versa. Selection for reduced SCS led to a decrease in milk especially in high production herds and herds with a low relative performance. Selection for shorter DFS caused a large decrease in low production and low fertility herds, whereas the largest decreases in milk caused by selection for less NINS occurred in high production, high fertility, and small herds. On the other hand, selection for an increase in milk had an especially high correlated response for NINS in low fertility herds.

DISCUSSION

The relationships between milk yield and the fertility traits and SCS varied considerably over herd environments. Generally in dairy cattle breeding little importance is given to genotype $\times$ environment interaction. Genetic correlations in production across environments tend to be close to unity; consequently, reranking of sires is rare or absent. Heterogeneity of variances is the most common effect of genotype $\times$ environment interaction observed, but methods have been developed to account for these when estimating breeding values (e.g., Meuwissen et al., 1996). Strong correlations across environments are also observed in this study, although for the fertility traits, somewhat lower values down to 0.84 were observed. However, this may not be taken

as an indication that genotype $\times$ environment was not important. Genetic correlations between traits varied more (Figure 2) so that in combination with heterogeneous variances (Table 1), the responses to selection in an average environment differed widely across environments (Table 4). The implication is that it is difficult to weigh the relative importance of different traits when breeding values are based on another environment.

Variable genetic variances and heritabilities have been reported before. The trend observed when no variable residual variances were allowed was that heritabilities of production traits increased with production levels (e.g., Hill et al., 1983; Veerkamp and Goddard, 1998; Hayes et al., 2003). This trend was also observed with heterogeneous residual variances (Kolmodin et al., 2002; Raffrenato et al., 2003). Kolmodin et al. (2002) reported that heritabilities increased for days open with increasing herd averages for days open. Likewise, in the current study, the heritability for milk increased with increasing production levels and heritability of NINS was higher in the environment with more inseminations, i.e., the low fertility environment, and in the high production environment. Heritability of DFS, however, was higher in the high fertility environment in which DFS itself was lower. There was no consistent trend over all trait–environment combinations.

Relative performance was the fourth principal component in which average fertility and SCS were evalu-

Figure 2. Trends in genetic correlations between 305-d milk production and SCS (○), days to first service (▲), and number of inseminations (■); x-axis shows principal components (PC) score; y-axis shows genetic correlations for A) production intensity; B) fertility; C) scale; and D) relative performance.

ated relative to average production. Thus, herds in which the fertility was high and SCS was low despite a high production received a high score. Whereas, herds in which the fertility was low, SCS high, and production was low received a low score. There was a consistent trend in genetic correlations over herds differing in relative performance. In herd environments in which the relative performance was low, genetic correlations with milk were stronger (i.e., less favorable). Phenotypically, the herds with low scores for relative performance had the highest SCS levels and lowest fertility. The strong genetic correlations in these herds indicated stronger trade-offs between production and fertility or health. Possibly, management and genetics were not well matched in these herds. Raffrenato et al. (2003) also reported less favorable correlations in low production environments.

Apart from the genetic correlations along the relative performance axis, there were no consistent trends in correlation–environment combinations. The trend in

genetic correlations of milk with DFS was opposite to the trend with NINS for herd environment measured as production, fertility, and scale. Kolmodin et al. (2002) reported stronger genetic correlations of days open with milk both in lower production and higher fertility herds. Furthermore, in our study, it was found that the trends in response to selection in the average environment generally agreed with the trends in genetic correlations with milk in the same environment.

Depending on the environment in which selection takes place, strong correlated responses may occur over the entire environmental range or be more restricted. For example, if selection took place in low fertility herds for an increase in milk, a relatively strong response in DFS would have occurred not only in low fertility herds but also in average and high fertility herds (Table 3). On the other hand, whereas selection for a decrease in NINS in high fertility herds would have resulted in a relatively strong response in milk in high fertility herds itself, the response in low fertility herds would have

Table 4. Correlated responses to selection in the average environment for an increase in milk of 1000 kg or a decrease in days to first service (DFS), number of inseminations (NINS), and SCS¹

Selection in average environment for	Correlated response of	Response environment	Principal component			
			PC1	PC2	PC3	PC4
Milk: +1,000 kg	DFS	Low	7.2	4.8	4.4	4.7
		Average	6.2	4.9	4.5	4.7
		High	5.1	5.1	4.5	4.6
Milk: +1,000 kg	NINS	Low	0.11	0.25	0.16	0.10
		Average	0.14	0.17	0.15	0.11
		High	0.16	0.13	0.16	0.12
Milk: +1,000 kg	SCS	Low	0.27	0.26	0.24	0.28
		Average	0.26	0.25	0.26	0.27
		High	0.25	0.24	0.28	0.26
DFS: -6 d	Milk	Low	-193	-201	-183	-100
		Average	-190	-168	-117	-81
		High	-147	-134	-36	-61
NINS: -0.1	Milk	Low	-35	-72	-183	-100
		Average	-111	-134	-117	-81
		High	-178	-198	-36	-61
SCS: -0.5	Milk	Low	-176	-233	-269	-327
		Average	-233	-229	-243	-247
		High	-298	-209	-214	-167

¹Animals were ranked according to environmental values (principal components, PC) and grouped into 15 environmental groups (pc_{env1} to pc_{env15}). The average environment is pc_{env8}. Correlated responses are given for pc_{env8} itself and for pc_{env1} (=low) and pc_{env15} (=high). PC1 = production intensity, PC2 = fertility, PC3 = scale, and PC4 = relative performance.

been relatively weak. With selection for an increase in milk, the genetic correlations indicated that NINS would have increased (i.e., fertility would have decreased) especially if selection had taken place in small herds, herds with a high fertility, and herds with a high production (Table 3). This increase would not only have occurred in herds in the same environment, but also in large herds, herds with a low production, and herds with low fertility. Consequently, it may be interesting to change the environment in which selection takes place depending on the breeding goals. Variable genetic correlations may also influence the relative importance of traits in indices used for selection. Calus et al. (2005) showed that the relative importance of fertility to yield traits could double across environments and that possible reranking based on a total merit index occurred.

From a biological viewpoint, one may interpret strong genetic correlations as trade-offs between, for example, fertility and milk production. Trends in correlations for PC1, PC2, and PC3 were, however, opposite for NINS and DFS. These traits are clearly 2 different aspects of fertility from the genetic viewpoint. One possible reason is that DFS depends on the farmer's decision when to inseminate, whereas NINS depends on the cow. However, the farmer will base his decision more on the phenotypic value for milk production than on the genotypic value. Days to first service and NINS also differ from a physiological viewpoint: DFS depends on heat

detection, which is determined by estrus expression levels, whereas insemination success depends, among other things, on quality of embryos (personal communication, T. van der Lende, Wageningen UR, Lelystad, The Netherlands). Estrus levels were lower in high-producing cows (Lopez et al., 2004) whereas embryo quality was shown to be better in nonlactating cows than in lactating cows (Sartori et al., 2002). Thus, although both DFS and NINS were negatively related to production, a simple trade-off between fertility and milk production is an oversimplification.

Variation in herd environment was measured in the current study using principal components. The first 4 PC explained about 33% of the total variance in all traits. Thus, a substantial part of the variation in the environmental variables was not explained by the principal components. For example, some soil types were not associated with high or low production, fertility, or farm size. By limiting the analysis to the first 4 PC, only that part of the variation in the environment covered by several correlated environmental variables was analyzed in this study. Therefore, an underlying environmental parameter, such as production intensity influencing several environmental variables, could be uncovered. However, one should keep in mind that other uncorrelated environmental variables could still be of interest. These variables can be analyzed as a single trait describing herd environment.

Generally, herd environments have been measured using a single trait (e.g., Calus and Veerkamp, 2003; Hayes et al., 2003), often in the form of the herd average of the trait itself that was being analyzed (e.g., Kolmodin et al., 2002). Both methods—PC analysis and single environmental variables—have their merits. Principal components have the disadvantage that they may be difficult to interpret. In the current study, the first 4 PC were relatively straightforward, but higher-order PC were not. Single-trait herd averages as the environmental variable is the logical method if there is a specific question about the effect of an environmental parameter. For example, Berry et al. (2003) found that genetic variance for BCS increased with improving silage quality. A disadvantage of single-trait environmental variables is that the response might be to a correlated environmental variable instead of the variable itself; for example, the herd average of DFS was strongly correlated to the herd average of production. If there was a trend in genetic correlations over DFS herd levels; this might or might not have been due to production effects. With a PC analysis, all correlated variables are combined into new variables. In the current study, DFS and milk yield along with other production or production-related variables were combined into the first PC, and DFS and other fertility or fertility-related variables into the second PC. Thus, with a PC analysis, effects of overall combined effects such as overall fertility or relative performance are evaluated.

The use of a dependent variable, such as milk production of individual animals, in the explanatory variable such as average herd milk production, is sometimes seen as a disadvantage in reaction norm models. This concern is partially alleviated by the use of PC in which the explanatory variable consists of more than the dependent variable alone. Moreover, Calus et al. (2004) showed that the definition of environmental parameters including or excluding information from animals themselves in own herd averages hardly influenced estimation of genetic parameters.

Reaction norms provide the opportunity to estimate genetic parameters for an infinite number of environments. In practice, however, estimation of parameters should be restricted to the range of environments for which sufficient data are available. One reason is that if a function is extended into environments without data, it is assumed that the trend (e.g., increasing variances) is the same over the whole range. A change in a trend cannot be detected if data are missing. Unless the estimated reaction norms run parallel, polynomial models inevitably result in larger variances in extreme environments (Stearns et al., 1991). If this is not the case many data points in the extreme environments are required to counter this effect. This study restricted

the estimation of the genetic parameters to the range of the environment of the 4,500th animal to the 67,500th animal, with animals ranked according to the environmental values, so that enough data around these points were available for reliable estimation. The disadvantage is that one restricts the results to the less extreme environments. For example, average 305-d production along PC1 (production intensity) varied in this study from 6,500 to 8,500 kg. In more extreme environments genetic correlations might be more extreme, but a reliable estimate of these correlations cannot be provided.

For the estimation of heritabilities, a second reason for restricting the environmental range for which estimations were made was that residual variances also varied over environments. Because data for a single animal are generally restricted to one environment only, one cannot estimate residual variances of reaction norm components. In this study, variation in residual variances was estimated by grouping animals based on the environments in which they were measured. This can only be done with sufficiently large groups. Small group sizes result in unstable residual variances. When group sizes were halved, residual variances varied from one extreme to the other over short stretches of the environmental range. Working with overlapping groups further smoothed the sudden jumping of residual variances across environments.

CONCLUSIONS

Genetic correlations between milk and fertility traits and SCS differed considerably over environments. Consequently, the response in one trait to selection for another trait also differed over environments. Furthermore, if selection took place in one environment, but the response occurred in another environment, responses were different. It is important to take into consideration the environment in which breeding values and genetic correlations are determined when the effect of milk production on health and fertility traits and selection on these traits is evaluated.

ACKNOWLEDGMENTS

We thank NRS (Gerben de Jong), who provided the production and fertility data set for this study; Alterra Wageningen UR (Edo Gies), who provided data from the national agricultural survey; and two anonymous reviewers for comments on earlier versions of the manuscript. This study was financially supported by the Ministry of Agriculture, Nature and Food (Programme 414 “maatschappelijk verantwoorde veehouderij”f).

REFERENCES

- Ali, A. K. A., and G. E. Shook. 1980. An optimum transformation for somatic cell concentration in milk. *J. Dairy Sci.* 63:487–490.
- Barkema, H. W., Y. H. Schukken, T. Lam, M. L. Beiboer, G. Benedictus, and A. Brand. 1999. Management practices associated with the incidence rate of clinical mastitis. *J. Dairy Sci.* 82:1643–1654.
- Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2003. Estimation of genotype $\times$ environment interactions, in a grass-based system, for milk yield, body condition score, and body weight using random regression models. *Livest. Prod. Sci.* 83:191–203.
- Calus, M. P. L., P. Bijma, and R. F. Veerkamp. 2004. Effects of data structure on the estimation of covariance functions to describe genotype by environment interactions in a reaction norm model. *Genet. Sel. Evol.* 36:489–507.
- Calus, M. P. L., A. F. Groen, and G. de Jong. 2002. Genotype $\times$ environment interaction for protein yield in Dutch dairy cattle as quantified by different models. *J. Dairy Sci.* 85:3115–3123.
- Calus, M. P. L., and R. F. Veerkamp. 2003. Estimation of environmental sensitivity of genetic merit for milk production traits using a random regression model. *J. Dairy Sci.* 86:3756–3764.
- Calus, M. P. L., J. J. Windig, and R. F. Veerkamp. 2005. Associations among descriptors of herd management and phenotypic and genetic levels of health and fertility. *J. Dairy Sci.* 88:2178–2189.
- Crump, R. E., N. R. Wray, R. Thompson, and G. Simm. 1997. Assigning pedigree beef performance records to contemporary groups taking account of within-herd calving patterns. *Anim. Sci.* 65:193–198.
- Esslemont, R. J. 2003. The costs of poor fertility and what to do about reducing them. *Cattle Pract.* 11:237–250.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. 4th ed. Longman Group, Harlow, UK.
- Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2002. *AS-REML Reference Manual*, NSW Agriculture, Orange, Australia.
- Hayes, B. J., M. Carrick, P. Bowman, and M. E. Goddard. 2003. Genotype $\times$ environment interaction for milk production of daughters of Australian dairy sires from test-day records. *J. Dairy Sci.* 86:3736–3744.
- Hill, W. G., M. R. Edwards, M. K. A. Ahmed, and R. Thompson. 1983. Heritability of milk yield and composition at different levels and variability of production. *Anim. Prod.* 36:59–68.
- Kirkpatrick, M., and N. Heckman. 1989. A quantitative genetic model for growth, shape, reaction norms, and other infinite-dimensional characters. *J. Math. Biol.* 27:429–450.
- Kolmodin, R., E. Strandberg, P. Madsen, J. Jensen, and H. Jorjani. 2002. Genotype by environment interaction in Nordic dairy cattle studied using reaction norms. *Acta Agric. Scand. A Anim. Sci.* 52:11–24.
- Lopez, H., L. D. Satter, and M. C. Wiltbank. 2004. Relationship between level of milk production and estrous behavior of lactating dairy cows. *Anim. Reprod. Sci.* 81:209–223.
- Meuwissen, T. H. E., G. de Jong, and B. Engel. 1996. Joint estimation of breeding values and heterogeneous variances of large data files. *J. Dairy Sci.* 79:310–316.
- Neave, F. K., F. H. Dodd, R. G. Kingwill, and D. R. Westgarth. 1969. Control of mastitis in dairy herds by hygiene and management. *J. Dairy Sci.* 52:696–707.
- Oseni, S., I. Misztal, S. Tsuruta, and R. Rekaya. 2004. Genetic components of days open under heat stress. *J. Dairy Sci.* 87:3022–3028.
- Pollott, G. E., and J. C. Greeff. 2004. Genotype $\times$ environment interactions and genetic parameters for fecal egg count and production traits of Merino sheep. *J. Anim. Sci.* 82:2840–2851.
- Pryce, J. E., M. D. Royal, P. C. Garnsworthy, and I. L. Mao. 2004. Fertility in the high-producing dairy cow. *Livest. Prod. Sci.* 86:125–135.
- Pryce, J. E., R. F. Veerkamp, R. Thompson, W. G. Hill, and G. Simm. 1997. Genetic aspects of common health disorders and measures of fertility in Holstein Friesian dairy cattle. *Anim. Sci.* 65:353–360.
- Raffrenato, E., R. W. Blake, P. A. Oltenacu, J. Carvalheira, and G. Licitra. 2003. Genotype by environment interaction for yield and somatic cell score with alternative environmental definitions. *J. Dairy Sci.* 86:2470–2479.
- Rauw, W. M., E. Kanis, E. N. Noordhuizen-Stassen, and F. J. Grommers. 1998. Undesirable side effects of selection for high production efficiency in farm animals: A review. *Livest. Prod. Sci.* 56:15–33.
- Roxstrom, A., E. Strandberg, B. Berglund, U. Emanuelson, and J. Philipsson. 2001. Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish red and white dairy cattle. *Acta Agric. Scand. A Anim. Sci.* 51:7–14.
- Royal, M. D., and A. P. F. Flint. 2004. Genetic improvement of dairy cattle fertility. *Cattle Pract.* 12:21–29.
- Sandoe, P., B. L. Nielsen, L. G. Christensen, and P. Sorensen. 1999. Staying good while playing God - The ethics of breeding farm animals. *Anim. Welf.* 8:313–328.
- Sartori, R., R. Sartor-Bergfelt, S. A. Mertens, J. N. Guenther, J. J. Parrish, and M. C. Wiltbank. 2002. Fertilization and early embryonic development in heifers and lactating cows in summer and lactating and dry cows in winter. *J. Dairy Sci.* 85:2803–2812.
- Stearns, S., G. de Jong, and B. Newman. 1991. The effects of phenotypic plasticity on genetic correlations. *Trends Ecol. Evol.* 6:122–126.
- Van Tienderen, P. H., and H. P. Koelewijn. 1994. Selection on reaction norms. Genetic correlations and constraints. *Genet. Res.* 64:115–125.
- Veerkamp, R. F., and M. E. Goddard. 1998. Covariance functions across herd production levels for test day records on milk, fat, and protein yields. *J. Dairy Sci.* 81:1690–1701.
- Windig, J. J., M. P. L. Calus, G. de Jong, and R. F. Veerkamp. 2005a. The association between somatic cell count patterns and milk production prior to mastitis. *Livest. Prod. Sci.* 96:291–299.
- Windig, J. J., M. P. L. Calus, and R. F. Veerkamp. 2005b. Influence of herd environment on health and fertility and their relationship with milk production. *J. Dairy Sci.* 88:335–347.