

Effect of Herd Environment on the Genetic and Phenotypic Relationships Among Milk Yield, Conception Rate, and Somatic Cell Score in Holstein Cattle

H. Castillo-Juarez,* P. A. Oltenacu,† R. W. Blake,†
C. E. Mcculloch,‡ and E. G. Cienfuegos-Rivas§

*Universidad Autónoma Metropolitana-Xochimilco,
Calzada del Hueso 1100, México 04960, Distrito Federal,

†Department of Animal Science, and

‡Biometrics Unit,

Cornell University, Ithaca, NY 14853

§Universidad Autónoma de Tamaulipas,
Ciudad Victoria, Tamaulipas, México

ABSTRACT

A total of 248,230 primiparous records of Holstein cows calving from 1987 to 1994 (daughters of 588 sires in 3042 herds) was used to evaluate potential genotype by environment interactions among mature equivalent milk yield, lactation mean somatic cell score, and conception rate at first service. Herds were classified into low and high environmental groups using three different criteria: standard deviation of herd mature equivalent milk yield, a combination of herd mature equivalent milk yield mean and standard deviation, and the herd mean of body weight at first calving divided by age at first calving. Genetic parameters were modeled by using multiple-trait linear mixed models and were fitted using the multiple-trait derivative-free software. Heritabilities for mature equivalent milk yield, lactation mean somatic cell score, and conception rate at first service were 0.221, 0.106, and 0.015 in low environment herds and 0.300, 0.093, and 0.009 in high environment herds, respectively. Genetic (and phenotypic) correlations between mature equivalent milk yield and lactation mean somatic cell score, mature equivalent milk yield and conception rate at first service, and lactation mean somatic cell score and conception rate at first service were 0.277, -0.417, and -0.209, (-0.049, -0.180, and -0.040) and 0.173, -0.318, and -0.144, (-0.087, -0.166, and -0.035) in low and high environment herds, respectively. The genetic correlations between pairs of traits were consistently smaller in high environment herds, suggesting that differences in management between the two environment levels lessened the antagonistic genetic association between the traits studied. A long-range plan for low environment herds should focus

on improving the level of management, which would greatly reduce the unfavorable correlated changes in lactation mean somatic cell score and conception rate at first service associated with the genetic improvement of mature equivalent milk yield.

(Key words: milk yield, conception rate, somatic cell score, management)

Abbreviation key: CR = conception rate at first service, MEM = mature equivalent milk, LMSCS = lactation mean SCS.

INTRODUCTION

Milk yield, reproductive performance, and health are important factors that determine profitability of dairy farms. High milk yield increases susceptibility to disease (25, 29) and reduces reproductive performance of cows (1, 13, 14). Mastitis decreases milk yield and quality and increases the risk of culling (3, 22); its economic impact is well documented (9, 12). The logarithmic transformation of milk somatic cell count into an SCS is highly correlated with mastitis, and it is as an indicator of the mammary health status (10). Selection against high SCS has been suggested to improve resistance to mastitis (23). Among the most common measures of reproductive performance, days to first service after calving, number of services per conception, and days open are highly influenced by management (7), whereas conception rate at first service (CR) is less dependent on management (13).

The phenotypic and genetic relationships between milk yield and reproduction and between milk yield and production disease have previously been shown to be antagonistic (11, 16, 26). It has also been shown that the phenotypic antagonistic relationship between milk yield and reproductive efficiency is inversely related to the level of management (11). However, another study (2) did not show differences among the genetic correla-

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Corresponding author: P. A. Oltenacu; e-mail:pao2@cornell.edu.

tions between milk yield and SCS from environments that were defined by herd average SCS.

The objective of this study was to evaluate the effect of herd environment on the genetic and phenotypic relationships among milk yield, conception rate, and SCS in primiparous Holstein cows. Accurate information regarding the interrelationships among these variables and their dependence on herd environment should prove useful for the design of effective breeding programs.

MATERIALS AND METHODS

Data and Edits

The data for this study were provided by the Animal Improvement Program Laboratory of the USDA. Only herds that had a size of every herd-year class between 50 and 500 records were included. All first lactation records with date of calving, SCS, mature equivalent milk production (MEM), and age at first calving between 18 and 36 mo were kept. Data were also restricted to sires with at least 50 daughter records for first calving.

The binary variable CR was set to zero if number of services was >1 or if number of services was equal to 1 but the second calving occurred >290 d after first breeding. The CR was set to unity if second calving was 260 to 290 d after first breeding. Culled cows and those that did not fit into either category were deleted from the data and may have introduced some bias. Age at first calving was calculated for every record. Maturity (MAT) was calculated as the ratio of body weight at first calving divided by age at first calving. Lactation mean of SCS (LMSCS) was defined as the average of up to 12 SCS test days as in Schutz et al. (19).

A total of 248,230 Northeast DHI Holstein records from cows calving from January 1987 to December 1994 remained after edits. The data represented 588 Holstein sires in 3042 herds. Means and standard deviations of variables considered in this study are presented in Table 1. The herd means and standard deviations for MEM, LMSCS, and CR are presented in Table 2.

Herd Classification

Herds were classified into either of two classes based on three criteria. The first criterion (C1) was based on MEM herd standard deviation with the high class representing the upper quartile (MEM herd SD ≥ 1737 kg) and the low class representing the lower quartile (MEM herd SD ≤ 1344 kg). The second criterion (C2) was based on a combination of MEM herd mean and MEM herd standard deviation.

Table 1. Descriptive statistics of the variables in the complete data set.

Variable	Mean	SD	Records (no.)
Mature equivalent milk (kg)	9916	1944	248,230
Conception rate at first service	0.504	0.500	248,230
Age at first calving	821	100	248,230
Age at second calving	1219	120	144,795
Lactation mean SCS	2.73	1.23	248,230
Body weight at first calving (kg)	570.3	22.6	246,719
MAT ¹ (kg/day)	0.704	0.109	246,719

¹MAT = Maturity measured as body weight at first calving divided by age at first calving.

To generate two classes with similar number of herds per class as when using C1, cut-off values for herd mean and herd standard deviation for MEM were set to upper 40% for MEM herd mean (≥ 9864 kg) and for MEM herd standard deviation (≥ 1621 kg) for high class and to lower 40% for MEM herd mean (≤ 9307 kg) and for MEM herd standard deviation (≤ 1479 kg) for low class.

A third criterion (C3) was based on the herd mean of MAT, a measure that depends mainly on nutritional management prior to production; the high class (MAT herd mean ≥ 0.733 kg/d) represented upper quartile, and the low class (MAT herd mean ≤ 0.638 kg/d) represented lower quartile.

The means and the standard deviations for each trait for high and low class as defined by the three classification criteria were very similar, and, hence, only the means and standard deviations for C2 classification criterion are shown in Table 3.

The number of records per sire, number of herds, and number of herd-year-season of calving combinations for the entire data set and for high and low environment class for each criterion are shown in Table 4.

The number of herds in low, medium, and high classes for two-way classification criteria combinations are shown in Table 5. The number of herds in each

Table 2. Herd means and herd standard deviations of selected variables in the complete data set.¹

Variable	Mean	SD
Herd mean for mature equivalent milk (kg)	9586	1159
Herd standard deviation for mature equivalent milk (kg)	1550	294
Herd mean for conception rate at first service	0.514	0.109
Herd standard deviation for conception rate at first service	0.492	0.025
Herd mean for lactation mean SCS	2.78	0.465
Herd standard deviation for lactation mean SCS	1.14	0.189

¹Number of herds = 3042.

Table 3. Descriptive statistics of the variables by herd environment.¹

Variable	Low level			High level		
	Mean	SD	Records (no.)	Mean	SD	Records (no.)
Mature equivalent milk (kg)	8450	1448	41,355	10,821	1946	87,090
Conception rate at first service	0.54	0.50	41,355	0.49	0.50	87,090
Age at first calving	867	106	41,355	793	88	87,090
Lactation mean SCS	2.90	1.24	41,355	2.67	1.22	87,090
Body weight at first calving (kg)	549.5	22.3	40,709	582.1	22.2	86,887
MAT ² (kg/day)	0.64	0.10	40,709	0.74	0.11	86,887

¹Herds with mature equivalent milk (MEM) herd mean ≤9307 kg and MEM herd standard deviation ≤1479 kg or with MEM herd mean ≥9864 kg and MEM herd standard deviation ≥1621 kg were assigned to the low or high environment class, respectively.

²MAT = Maturity measured as body weight at first calving divided by age at first calving.

diagonal represents the herds classified in the same class level by the two classification criteria. Table 5 shows that C1 and C2 classified about 70% of the herds in the same way, whereas only 54 and 48% of the herds are classified the same way by C2 and C3 and by C1 and C3, respectively. The number of herds consistently classified in low, medium, or high class by the three criteria was 306, 576, and 269, or about 38% of all herds.

Model and Analysis

The model used to estimate (co)variance components was a multiple-trait, linear, mixed sire model with equal design matrices. In matrix notation

$$Y = X\beta + Zu + e,$$

where **X** is a known indicator matrix accounting for the fixed effects of herd-year-season of calving, β is the unknown vector of fixed effects of herd-year-season of calving, **Z** is a known indicator matrix associating sire effects to the vector of observations **Y**, **u** is the vector

of unknown random sire effects, and **e** is the vector of residual random effects. Assuming normality we have

$$\begin{bmatrix} Y \\ u \\ e \end{bmatrix} \sim N \left(\begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix} \right),$$

where **V** = var (**Y**) = **ZGZ'** + **R**; **G** = var (**u**), the genetic (co)variance matrix; and **R** = var (**e**), the residual (co)variance matrix.

Three traits, MEM, LMSCS, and CR, were simultaneously analyzed.

A binary trait, CR, was included in a multiple-trait linear model in which the multivariate normal distribution of the traits is assumed because a normal approximation was adequate, given its mean (0.504) and the large number of records used in this study.

Matrix **A** contains the relationships among sires, sires of sires, and maternal grandsires of sires. Therefore, 588 sires were present in the data, but the number

Table 4. Number of records per sire,¹ number of herds, and number of herd-year-season of calving for complete data set and for low and high environmental classes for each herd classification criterion.²

Classification criteria	Environment class	Records per sire		Number of		
		Mean	SD	Herds	HYS ³	Records
All data	Complete	422.2	722.4	3042	63,416	248,230
C1	Low	70.4	131.9	763	13,992	41,383
	High	134.3	225.8	764	17,051	78,973
C2	Low	70.3	125.0	766	14,158	41,355
	High	148.1	253.5	759	17,793	87,090
C3	Low	71.2	148.6	759	13,495	41,879
	High	140.2	220.3	765	17,382	82,420

¹Number of sires = 588.

²Herd classification criteria: C1 = herds classified by mature equivalent milk herd standard deviation, C2 = herds classified by herd mean and herd standard deviation for mature equivalent milk, and C3 = herds classified by the ratio body weight at first calving divided by age at first calving.

³HYS = Herd-year-season of calving.

Table 5. Two-way classifications of herds by the three herd classification criteria.¹

C2	Number of herds											
	C1			C3	C1			C3	C2			
	L	M	H		L	M	H		L	M	H	
L	532	234	0	L	344	329	86	L	412	313	34	
M	231	1049	237	M	338	806	374	M	317	853	348	
H	0	233	526	H	81	381	303	H	37	351	377	

¹Herd classification criteria: C1 = Criterion 1: herds classified by mature equivalent milk herd standard deviation, C2 = Criterion 2: herds classified by herd mean and herd standard deviation for mature equivalent milk, C3 = Criterion 3: herds classified by the ratio body weight at first calving divided by age at first calving, L = low environment herd class, M = medium environment herd class (herds not included in low or high), and H = high environment herd class.

of animal effects (the size of **A**) included in this pedigree file was 717.

This sire model was used for the following analyses: a) complete data set, b) low environment class for every classification criterion, c) high environment class for every classification criterion, and d) low and high environment classes together for every classification criterion.

These analyses were performed to estimate the genetic (co)variance structure in the entire population (a), to estimate the genetic (co)variance structure within environment class (b) and (c), and to perform the likelihood ratio test (LRT) to compare a model with six (co)variances versus a model with 12 (co)variances, six for each environment (d).

If we define **G_o** as the symmetric matrix containing variances ($\sigma_{u_{ij}}^2$) and covariances ($\sigma_{u_{ij}}$) among the sire effects for the three traits, then

$$\text{Var} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{u}_3 \end{bmatrix} = \begin{bmatrix} \sigma_{u_{11}}^2 & \sigma_{u_{12}} & \sigma_{u_{13}} \\ & \sigma_{u_{22}}^2 & \sigma_{u_{23}} \\ \text{Symm} & & \sigma_{u_{33}}^2 \end{bmatrix} \otimes \mathbf{A} = \mathbf{G}_o \otimes \mathbf{A} = \mathbf{G},$$

where **u_j** is the vector of sire effects for trait j, while here and elsewhere \otimes is the Kronecker product.

A second model used was a bivariate trait linear mixed sire model with unequal design matrices and was used to estimate the genetic correlations between the same trait in low and high environment classes.

Here

$$\text{Var} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \begin{bmatrix} \sigma_{u_{11}}^2 & \sigma_{u_{12}} \\ \text{Symm} & \sigma_{u_{22}}^2 \end{bmatrix} \otimes \mathbf{A} = \mathbf{G}_o \otimes \mathbf{A} = \mathbf{G},$$

where **u_j** represents the vector of the sire effects for the same trait in the environment class j.

The strategy consisted of obtaining univariate estimates for genetic and residual (co)variances by using the multiple-trait derivative-free REML algorithm implemented by Boldman et al. (5) in MTDFREML software and by using them as starting values in the bivariate analysis. Also, bivariate (co)variance estimates were used as priors for the multiple-trait analysis.

The convergence criterion was attained when the variance of the simplex values was $\leq 10^{-9}$. It was assumed that global maximum was obtained when two restarts, by using previous converged values as starting values, produced convergence with no changes in the first three decimal places of the F-value (5).

Heritabilities for trait i were estimated as

$$\hat{h}_i^2 = 4\hat{\sigma}_{u_i}^2 / (\hat{\sigma}_{u_i}^2 + \hat{\sigma}_{e_i}^2),$$

where $\hat{\sigma}_{u_i}^2$ is the sire additive genetic variance for trait i, and $\hat{\sigma}_{e_i}^2$ is the residual variance for trait i.

With genetic variance $\hat{\sigma}_{g_{ii}}^2 = 4\hat{\sigma}_{u_i}^2$ and genetic covariance $\hat{\sigma}_{g_{ij}} = 4\hat{\sigma}_{u_{ij}}$, genetic correlations between traits i and j were estimated as $\hat{r}_{g_{ij}} = \hat{\sigma}_{g_{ij}} / (\hat{\sigma}_{g_{ii}} \cdot \hat{\sigma}_{g_{jj}})^{1/2}$.

The correlated response to selection was estimated as the regression of the breeding values of trait i on breeding values of trait j

$$\text{CR} = \hat{\beta}_{bv_i, bv_j} = \hat{r}_{g_{ij}} \left(\frac{\hat{\sigma}_{g_{ii}}}{\hat{\sigma}_{g_{jj}}} \right).$$

Comparing Genetic (Co)Variance Structures

Two approaches were considered to compare the genetic (co)variance structures, heritabilities, and genetic correlations between low and high management environments for the traits studied. First, a likelihood ratio

Table 6. Heritabilities of mature equivalent milk yield (MEM), lactation mean SCS (LMSCS), conception rate at first service (CR), and their genetic and phenotypic correlations for the complete data set¹

	MEM	LMSCS	CR
MEM	0.276 (0.01)	0.222 (0.025)	-0.413 (0.029)
LMSCS	-0.075	0.103 (0.004)	-0.153 (0.026)
CR	-0.173	-0.036	0.015 (0.001)

¹Heritabilities are on diagonal (bold), genetic correlations are above diagonal, and phenotypic correlations are below diagonal. Approximate standard errors are in parentheses.

test was used to compare the two G_o matrices from low and high environment classes (21). It is only an approximation because, although the two classes are environmentally independent, they share genes (same sires) so the complete independence assumption is not fulfilled. A significant test implies that (a) two separate models describe the genetic variation better than a single model (i.e., there are two different G_o matrices) and that (b) there exists genotype by environment interaction. Second, approximate standard errors for heritabilities and genetic correlations were calculated (17, 28) and used to assess differences between these parameters in high and low environment classes.

To determine whether sires were differentially used within environment classes, the PTA of sires from the entire data set were weighted by the number of daughters in each environment class and then the means were compared with a Student's *t*-test. Comparison of daughter frequency in the two classes was also used to test for differential use of sires with a chi-square test.

RESULTS AND DISCUSSION

General Results

The heritabilities and genetic and phenotypic correlations for the complete data set are presented in Table 6. These results are similar to other estimates (1, 2, 14, 20, 30). An antagonistic phenotypic and genetic association was found between MEM and CR and between LMSCS and CR, whereas the association between MEM and LMSCS was phenotypically favorable but genetically unfavorable.

Environmental Classes and the Genetic (Co)variance Structure

The effect of herd environment on the genetic (co)variance structure among the traits was similar, independent of the classification criteria used to stratify herds. This finding is not surprising given that a large propor-

Table 7. Heritabilities of mature equivalent milk yield (MEM), lactation mean somatic cell score (LMSCS), conception rate at first service (CR) and their genetic and phenotypic correlations within low and high herd environment class.¹

	MEM	LMSCS	CR	Class
MEM	0.300 (0.01)	0.173 (0.024)	-0.318 (0.036)	High
	0.221 (0.01)	0.277 (0.040)	-0.417 (0.042)	Low
LMSCS	-0.087	0.093 (0.004)	-0.144 (0.023)	High
	-0.049	0.106 (0.005)	-0.209 (0.050)	Low
CR	-0.166	-0.035	0.009 (0.001)	High
	-0.180	-0.040	0.015 (0.002)	Low

¹Herds with MEM herd mean ≤9307 kg and MEM herd standard deviation ≤1479 kg or with MEM herd mean ≥9864 kg and MEM herd standard deviation ≥1621 kg were assigned to the low or high environment class, respectively. Heritabilities are on diagonal (bold), genetic correlations are above diagonal, and phenotypic correlations are below diagonal. Approximate standard errors are in parentheses.

tion of the herds in the study are insensitive to the classification criteria used (Table 5). Therefore, only results using the C2 criterion are presented. No differential use of sires in the two classes was detected.

The heritabilities and genetic and phenotypic correlations for low and high environment classes are presented in Table 7, and sire and residual (co)variances for low and high environment classes are presented in Table 8. The likelihood ratio test shows that the genetic (co)variance structure is not the same for low and high environment classes (*P* < 0.001).

Table 8. Sire genetic and residual (co)variance components for mature equivalent milk yield (MEM), lactation mean SCS (LMSCS), and conception rate at first service (CR) within low and high herd environment classes.¹

	MEM	LMSCS	CR	Variance	Class
MEM	213,199.90	13.60336	-3.3421	Sire	High
	2,628,124.48	-176.88851	-133.72093	Residual	
	79,391.56	14.00671	-3.54521	Sire	Low
	1,356,825.55	-78.31094	-101.53432	Residual	
LMSCS		0.02898	-0.00056	Sire	High
		1.21180	-0.01871	Residual	
		0.03213	-0.00113	Sire	Low
		1.17946	-0.02017	Residual	
CR			0.00052	Sire	High
			0.23911	Residual	
			0.00091	Sire	Low
			0.23645	Residual	

¹Herds with MEM herd mean ≤9307 kg and MEM herd standard deviation ≤1479 kg or with MEM herd mean ≥9864 kg and MEM herd standard deviation ≥1621 kg were assigned to the low or high environment class, respectively. Variances are on diagonal (bold), and covariances are above diagonal.

A nonproportional change in genetic and residual variances for MEM was observed in the low versus high environment, leading to higher heritability in the high environment class, in agreement with other studies (4, 6, 24).

The heritabilities for LMSCS and CR did not differ for the high and low environment classes. Similar results were reported by Banos and Shook (2) for LMSCS by using herd average SCS as a criterion for defining environments.

Approximate standard errors for heritabilities and for genetic correlations ranged from 0.002 to 0.050. Based on these approximate standard errors, genetic correlations between MEM and LMSCS in the two environments were antagonistic and larger ($P < 0.10$) in low (0.277) versus high (0.173) herd environment. Similar results were obtained by Banos and Shook (2). Phenotypic correlations between MEM and LMSCS in low and high environments were small but favorable.

Genetic correlations between MEM and CR in the two environments were antagonistic and larger ($P < 0.20$) in low (−0.417) versus high (−0.318) herd environment. The phenotypic correlations between MEM and CR were also antagonistic but smaller, −0.180 and −0.166, in low and high environment classes.

The genetic correlations between LMSCS and CR in the two environments were negative and larger in low (−0.209) versus high (−0.144) herd environment. The phenotypic correlations between LMSCS and CR in the two environments were also negative but small and not different (−0.040 and −0.035).

A significant likelihood ratio test and statistically different genetic correlations between MEM and LMSCS and between MEM and CR in low and high environment classes reported in this study are indicative of genotype by environment interaction.

Genetic Correlations for the Same Trait Between Environments

The genetic correlations between the low and high environment classes for MEM, LMSCS, and CR were 0.975, 0.981, and 0.997, respectively, indicating that the breeding value and ranking of the sires for each of these traits would be the same in the two environment classes.

Correlated Responses to Selection for Milk

The expected correlated response in LMSCS and in CR for the entire population and for low and high herd environment classes when selection is practiced on MEM are shown in Table 9.

In the entire population, 1000 kg of genetic improvement in MEM is expected to be associated with a reduc-

Table 9. Expected correlated responses for lactation mean SCS (LMSCS) and conception rate at first service (CR), when selection is practiced on mature equivalent milk yield (MEM) by herd environment class and for the complete data set.¹

Class ²	LMSCS	Low/high ³	CR	Low/high ³
Low	0.1764		−0.0447	
		2.77		2.84
High	0.0638		−0.0157	
Complete data set	0.0995		−0.0311	

¹For every 1000 kg of MEM genetic gain.

²Herds with MEM herd mean ≤ 9307 kg and MEM herd standard deviation ≤ 1479 kg or with MEM herd mean ≥ 9864 kg and MEM herd standard deviation ≥ 1621 kg were assigned to the low or high environment class, respectively.

³Low/high represents the ratio of the expected correlated responses in the low and high environment classes for the traits studied.

tion in CR of 3.11%, or 6.17% of the average CR in this population. For the same genetic increase in FCM, Faust et al. (8) estimated a correlated decline of 11.9% in CR and an increase of 0.28 in number of services per conception, whereas Seykora and McDaniel (20) reported an increase of 5 to 10 d open. These results are also in agreement with findings by Studer (27), who reported a 25% decline in conception rates over the last 20 yr. However, Weller and Ezra (30) reported a phenotypic decrease in Israeli Holsteins for the inverse of the number of services to conception of 2.39% over 10 yr, but their estimate of the genetic trend was marginally positive, despite the negative phenotypic correlation between fertility and production.

The expected correlated response in CR was 4.47 and 1.57% in low and high environmental class, representing 8.63 and 3.22% of the current average CR in each group. Thus, superior management reduces the genetic deterioration of CR, which is close to three times larger in the low relative to high environment class (see Low/High in Table 9).

In the entire population 1000 kg of MEM genetic improvement is expected to cause an increase of 0.10 in LMSCS as a correlated response or 3.64% of the observed LMSCS average in this data. These results are consistent with other studies (15, 30) reporting that selection for milk has an unfavorable correlated response in SCS and in mastitis.

The expected correlated response in LMSCS was 0.176 and 0.064 in low and high environment classes, or 6.08 and 2.39% of the LMSCS average of each class. This finding indicated that good management reduces the genetic deterioration of LMSCS, even when this trait is not directly included in breeding programs.

CONCLUSIONS

Genetic correlation between environment classes for the same traits were near unity, indicating that MEM,

LMSCS, and CR are genetically equivalent traits across environment classes as defined in this study. Consequently, breeding values and ranking of sires are expected to be the same in the two environment classes for each trait studied.

Antagonistic genetic associations were found in the general population between MEM and SCS and between MEM and CR, implying that continued genetic improvement for MEM would lead to an increase in LMSCS and to CR deterioration in first lactation Holstein cows. The actual genetic gain for MEM of 139 kg of milk/yr per cow (18) may be associated with an annual increase of 0.014 in LMSCS and a decrease of 0.43% in CR as expected correlated responses. Presently, besides natural selection, no selection pressure is directed toward fertility traits except indirectly via correlation through length of productive life, whereas SCS receive about one-tenth of the weight of milk production in the net merit formula. The magnitude of the negative genetic association between MEM and LMSCS and between MEM and CR suggests that appropriate economic weights for these traits should be determined, and the traits should be included in breeding programs to prevent future genetic deterioration.

The magnitude of the antagonistic genetic correlations between MEM and LMSCS and between MEM and CR changed with the environmental class and were higher in the low class than in the high environmental class. This change in the genetic correlation between traits is indicative of genotype by environment interaction and suggests that, for the pairs of traits considered, the genes with pleiotropic effect act differently in high and low environment class herds.

It is often suggested that improvement in fertility and health traits should be easier to achieve through better management than through selection. The major difference between low and high environment classes as defined in this study is very likely the level of management. Our results support this suggestion and indicate that the genetic antagonism between MEM and CR and between MEM and SCS is reduced in high environment herds likely because of superior management in these herds. Therefore, good management brings about superior phenotypic performance for all three traits and greatly reduces the correlated genetic deterioration in CR and LMSCS brought about by selection for MEM. The herds in low environment group should develop a strategic plan to improve the level of management and, therefore, move into high environment class. While taking active steps to improve the level of management, farmers may also consider including fertility and SCS traits when selecting service sires for their herds.

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