EFFECT OF HERD ENVIRONMENT ON THE GENETIC AND PHENOTYPIC RELATIONSHIPS AMONG MILK YIELD, CONCEPTION RATE AND SOMATIC CELL SCORE IN HOLSTEIN CATTLE

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Keywords: milk yield, conception rate, somatic cell score, management

Abstract:

A total of 248,230 primiparous records of Holstein cows calving from 1987 to 1994, daughters of 588 sires in 3,042 herds, were used to evaluate potential genotype by environment interactions among mature equivalent milk yield (MEM), lactation mean somatic cell score (LMSCS), and conception rate at first service (CR). Herds were classified into low and high environmental groups using three different criteria: herd MEM standard deviation, a combination of herd MEM mean and herd MEM standard deviation, and the herd mean of body weight at first calving (BWFC) divided by age at first calving (AFC). Genetic parameters were modeled using multiple trait linear mixed models and fitted using the Multiple Trait Derivative Free software (MTDFREML). Heritabilities for MEM, LMSCS and CR were 0.221, 0.106, 0.015 and 0.300, 0.093, 0.009 in low and high environment herds, respectively. Genetic (and phenotypic) correlations between MEM and LMSCS, MEM and CR, LMSCS and CR 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. Breeding programs designed to increase milk while controlling unfavorable correlated changes in LMSCS and CR must take into account the unequal genetic correlations between these traits in the two environments. Our results suggest that the relative weight of LMSCS and CR in selection indexes, should be smaller in well managed herds than in other environments.

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~~RELATIONSHIPS AMONG MILK YIELD, CONCEPTION RATE AND SCS.~~

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

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ABSTRACT

A total of 248,230 primiparous records of Holstein cows calving from 1987 to 1994, daughters of 588 sires in 3,042 herds, were used to evaluate potential genotype by environment interactions among mature equivalent milk yield (MEM), lactation mean somatic cell score (LMSCS), and conception rate at first service (CR). Herds were classified into low and high environmental groups using three different criteria: herd MEM standard deviation, a combination of herd MEM mean and herd MEM standard deviation, and the herd mean of body weight at first calving (BWFC) divided by age at first calving (AFC). Genetic parameters were modeled using multiple trait linear mixed models and fitted using the Multiple Trait Derivative Free software (MTDFREML). Heritabilities for MEM, LMSCS and CR were 0.221, 0.106, 0.015 and 0.300, 0.093, 0.009 in low and high environment herds, respectively. Genetic (and phenotypic) correlations between MEM and LMSCS, MEM and CR, LMSCS and CR 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. Breeding programs designed to increase milk while controlling unfavorable correlated changes in LMSCS and CR must take into account the unequal genetic correlations between these traits in the two environments. Our results suggest that the relative weight of LMSCS and CR in selection indexes, should be smaller in well managed herds than in other environments.

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

Abbreviation key: **MEM** = mature equivalent milk, **CR** = conception rate at first service, **LMSCS** = lactation mean somatic cell score, **FCM** = fat corrected milk.

INTRODUCTION

Milk yield, reproductive performance and health are important factors determining profitability of dairy farms. High milk yield increases susceptibility to disease (25, 30) and reduces reproductive performance of cows (1, 13, 14). Mastitis decreases milk yield and its quality and increases the risk of culling (3, 22) and its economic impact is well documented (9, 12). The logarithmic transformation of milk somatic cell count, into a somatic cell score (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), while 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, 26). It has also been shown that the phenotypic antagonistic relationship between milk yield and reproductive efficiency was inversely related to the level of management (11) and that better management reduces the genetic increase in susceptibility to mastitis expected as a correlated response to genetic change in milk yield (27). Other study (2), however, did not show differences among the genetic correlations 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. To accomplish this objective, the phenotypic and genetic correlations among milk yield, conception rate, and SCS in first lactation cows performing in alternative herd environment classifications were estimated and the correlated response for conception rate and SCS in different environments were evaluated.

DATA AND METHODS

Data and Edits

The data for this study were provided by the Animal Improvement Processing Laboratory of the USDA. Only herds with 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 (ME) and with age at first calving between 18 and 36 months were kept. Data were also restricted to sires with at least 50 first calving daughter records.

The binary variable CR was set to zero if number of services was > 1 or unity if second calving was 260 to 290 d after first breeding. Age at first calving (AFC) and age at second calving (ASC) were calculated for every record. Maturity (MAT) was calculated as the ratio of body weight at first calving divided by AFC.

Lactation mean of SCS (LMSCS) was defined as the average of up to 12 SCS test days as in (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 3,042 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 high class representing the upper quartile (MEM herd SD ≥ 1,737 kg) and low class representing the lower quartile (MEM herd SD ≤ 1,344 kg).

The second criterion (C2) was based on a combination of MEM herd mean and MEM herd standard deviation.

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 (≥ 9,864 kg) and for MEM herd standard deviation (≥ 1,621 kg) for high class, and to lower 40% for MEM herd mean (≤ 9,307 kg) and for MEM herd standard deviation (≤ 1,479 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, with the high class (MAT herd mean ≥ 0.733 kg/day) representing upper quartile and the low class (MAT herd mean ≤ 0.638 kg/day) representing 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 diagonal represent 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, while 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 were 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

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

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

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

with $\mathbf{V} = \text{var}(\mathbf{Y}) = \mathbf{ZGZ'} + \mathbf{R}$,

$\mathbf{G} = \text{var}(\mathbf{u})$, the genetic (co)variance matrix, and

$\mathbf{R} = \text{var}(\mathbf{e})$, 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 where 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.

The matrix **A** contains the relationships among sires, sires of sires, and maternal grand sires of sires. Therefore, 588 sires were present in the data but the number 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;

d) low and high environment classes together for every classification criterion.

These analyses were performed (a) to estimate the genetic (co)variance structure in the entire population, each (b) and (c) to estimate the genetic (co)variance structure within environment class, and (d) to perform the likelihood ratio test (LRT) to compare a model with 6 (co)variances versus a model with 12 (co)variances, 6 for each environment.

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

$$\text{Var}\begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix} = \begin{bmatrix} \sigma^2_{u_{11}} & \sigma_{u_{12}} & \sigma_{u_{13}} \\ & \sigma^2_{u_{22}} & \sigma_{u_{23}} \\ \text{Symm} & & \sigma^2_{u_{33}} \end{bmatrix} \otimes \mathbf{A} = \mathbf{Go} \otimes \mathbf{A} = \mathbf{G},$$

where $\mathbf{u}_j$ is the vector of sire effects for the *jth* trait, while here and elsewhere $\otimes$ stands for 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

$$\text{Var}\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{u_{11}} & \sigma_{u_{12}} \\ \text{Symm} & \sigma^2_{u_{22}} \end{bmatrix} \otimes \mathbf{A} = \mathbf{Go} \otimes \mathbf{A} = \mathbf{G}.$$

Where $\mathbf{u}_j$ represents the vector of the sire effects for the same trait in the *jth* environment class.

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

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, 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 the *i*th trait were estimated as

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

where

$\hat{\sigma}^2_{u_i}$ is the sire additive genetic variance for the *i*th trait, and

$\hat{\sigma}^2_{e_i}$ is the residual variance for the *i*th trait.

With genetic variance $\hat{\sigma}^2_{g_{ii}} = 4\hat{\sigma}^2_{u_i}$ and genetic covariance $\hat{\sigma}_{g_{ij}} = 4\hat{\sigma}_{u_{ij}}$, genetic correlations between the *i*th and *j*th traits were estimated as

$$\hat{r}_{g_{ij}} = \hat{\sigma}_{g_{ij}} / (\hat{\sigma}^2_{g_{ii}} \cdot \hat{\sigma}^2_{g_{jj}})^{1/2},$$

and coefficients of additive genetic variation were calculated as

$$\text{CAV} = 100 \cdot (2\hat{\sigma}_{u_i}) / \hat{\mu}_{p_i},$$

where $\hat{\mu}_{p_i}$ is the estimate of the phenotypic mean for the *i*th trait.

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

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

Comparing Genetic (Co)Variance Structures

Two approaches were considered to compare the genetic (co)variance structures, the heritabilities and the genetic correlations between low and high management environments for the traits studied. First, a LRT was used to compare the two **Go** 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 **Go** matrices); and (b) that there exists genotype by environment interaction. Second, approximate standard errors for heritabilities and genetic correlations were calculated (17, 29) and used to asses differences between these parameters in high and low environment classes.

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, 31). An antagonistic phenotypic and genetic association was found between MEM and CR. Similarly, genetic and phenotypic correlations showed that higher LMSCS was associated with lower CR, while 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

is not surprising given that a large proportion of the herds in the study is insensitive to classification the criteria used (Table 5). Therefore, only results using the C2 criterion are presented.

To determine if sires were differentially used within environment classes, the sires' predicted transmitting abilities (PTA) from the entire data set were weighted by the number of daughters in each environment class. 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 LRT test shows that the genetic (co)variance structure is not the same for low and high environment classes ($P < 0.001$).

A non-proportional 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 heritability for LMSCS did not differ in the high and low environment classes. Similar results were reported by Banos and Shook (2) using herd average SCS as a criterion for defining environments.

Heritability for CR was similar and small in both environments.

Based on the approximate standard errors, genetic correlations between MEM and LMSCS in the two environments were antagonistic and significantly ($P < 0.01$) larger 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 significantly ($P < 0.01$) larger 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 significantly ($P < 0.01$) 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).

Statistically different genetic correlations between MEM and LMSCS, MEM and CR, and LMSC 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.

Coefficients of Additive Genetic Variation

The coefficients of additive genetic variation (CAV) were 8.05%, 13.08%, and 11.91% for MEM, LMSCS, and CR, respectively. Higher CAV values for CR than for milk were also reported in other studies (14, 16).

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 1,000 kg genetic improvement in MEM is expected to be associated with a reduction 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, while Seykora and McDaniel (20) reported an increase of 5 to 10 days open.

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 average CR in each group. In other words, the genetic deterioration of CR is close to three times larger in the low relative to high environment class (see Low/High in Table 9). These results are in agreement with Studer's (28) findings, who reported a 25% decline in conception rates over the last 20 years, and with Weller and Ezra (31) who reported a decrease in the inverse of the number of services to conception of 2.39% over 10 years in Israeli Holsteins.

In the entire population 1,000 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, 31) 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 class, or 6.08 % and 2.39 % of the LMSCS average of each class, indicating that management may reduce the genetic increase of LMSCS, even when this trait is not 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 between MEM and CR, and between MEM and SCS, 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/year per cow reported in a review by Schutz (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.

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 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. It is very likely that the major difference between low and high environment classes as defined in this study is the level of management. Our results indicate that, through superior management in high class, the genetic antagonism between MEM and CR and between MEM and SCS is reduced but not eliminated. Therefore, good management by itself could not completely prevent genetic deterioration in these traits brought by selection for MEM.

Presently, no selection pressure is directed toward fertility traits except indirectly via correlation through length of productive life, while SCS receive about one tenth the weight of milk production in the Net Merit formula. This study suggests

that CR could also be included in Net Merit formula and also suggests that weights on CR and SCS should also vary with environment class, with higher weights for herds in low environment class.

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

Variable	Mean	SD	n
Mature Equivalent Milk (Kg)	9916	1944	248,230
Conception Rate at First Service	0.504	0.500	248,230
Age at First Calving (days)	821	100	248,230
Age at Second Calving (days)	1219	120	144,795
Lactation Mean Somatic Cell Score	2.73	1.23	248,230
Body Weight at First Calving (kg)	570.3	22.6	246,719
MAT* (kg/day)	0.704	0.109	246,719

n = Number of records.
* MAT = Body weight at first calving/Age at first calving.

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

Variable	Mean	SD
Mature Equivalent Milk Herd Mean (Kg)	9586	1159
Mature Equivalent Milk Herd Standard Deviation (Kg)	1550	294
Conception Rate at First Service Herd Mean	0.514	0.109
Conception Rate at First Service Herd Standard Deviation	0.492	0.025
Lactation Mean Somatic Cell Score Herd Mean	2.78	0.465
Lactation Mean Somatic Cell Score Herd Standard Deviation	1.14	0.189

Number of herds = 3,042.

Table 3 Descriptive statistics of the variables by herd environment *

	Low Level			High Level		
Variable	Mean	SD	n	Mean	SD	n
Mature Equivalent Milk (kg)	8450	1448	41,355	10,821	1946	87,090
Conception Rate at First Service	0.536	0.499	41,355	0.487	0.500	87,090
Age at First Calving	867	106	41,355	793	88	87,090
Age at Second Calving	1261	123	18,688	1190	109	38,670
Lactation Mean Somatic Cell Score	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 (kg/day)	0.642	0.097	40,709	0.742	0.106	86,887

* Herd environment class is criterion C2 (see text for details).
MAT = Body weight at first calving/age at first calving.
n = Number of records.

Table 4 Number of records per sire, number of herds, and number of herd-year-season of calving for complete data set and for low and high environmental class for each herd classification criteria

Classification	Environment	Records per sire		Number of		
Criteria[a]	Class	Mean	SD	Herds	HYS	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

Number of sires = 588.
HYS = Herd-year-season of calving.
[a] Herd classification criteria:
C1 = Herds classified by mature equivalent milk herd standard deviation.
C2 = Herds classified by herd mean and herd standard deviation of mature equivalent milk.
C3 = Herds classified by the ratio body weight at first calving/age at first calving.

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

	Number of herds										
		C1				C1				C2	
C2	L	M	H	C3	L	M	H	C3	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

[a] Herd 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 of mature equivalent milk.

C3 = Criterion 3: herds classified by the ratio body weight at first calving/age at first calving.

L = Low environment herd class.

M = Medium environment herd class (herds not included in low or high).

H = High environment herd class.

Table 6 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 for the complete data set*

	MEM	LMSCS	CR
MEM	**0.276** (0.0010)	0.222 (0.0025)	-0.413 (0.0027)
LMSCS	-0.075	**0.103** (0.0004)	-0.153 (0.0033)
CR	-0.173	-0.036	**0.015** (0.0001)

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

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 *

	MEM	LMSCS	CR	Class
MEM	**0.300** **(0.00110)**	0.173 (0.00282)	-0.318 (0.00473)	High
	0.221 **(0.00096)**	0.277 (0.00317)	-0.417 (0.00504)	Low
LMSCS	-0.087	**0.093** **(0.00043)**	-0.144 (0.00575)	High
	-0.049	**0.106** **(0.00058)**	-0.209 (0.00656)	Low
CR	-0.166	-0.035	**0.009** **(0.00013)**	High
	-0.180	-0.040	**0.015** **(0.00027)**	Low

* Herds classified by criterion C2 (see text for details).
Heritabilities in diagonal (bold), genetic correlations above diagonal and phenotypic correlations below diagonal.
Approximate standard errors in parentheses.

Table 8 Sire genetic and residual (co)variance components for mature equivalent milk yield (MEM), lactation mean somatic cell score (LMSCS) and conception rate at first service (CR) within low and high herd environment class *

	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	

* Herds classified by criterion C2 (see text for details).
Variances in diagonal (bold) and covariances above diagonal.

Table 9 Expected correlated responses for lactation mean somatic cell score (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 *

Class	LMSCS	Low/High	CR	Low/High
Low	0.1764		-0.0447	
		2.77		2.84
High	0.0638		-0.0157	
Complete Data Set	0.0995		-0.0311	

* For every 1,000 kg of MEM genetic gain.
Herds classified by criterion C2 (see text for details).
Low/High represents the ratio of the expected correlated responses in the low and high environment classes for the traits studied.