

Genetic and phenotypic relationships among milk production and composition traits in primiparous Holstein cows in two different herd environments

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Abstract

Genotype by environment interactions for mature equivalent milk yield (MEM), mature equivalent protein yield (MEP), mature equivalent fat yield (MEF), protein percentage (P%), fat percentage (F%), and lactation mean somatic cell score (LMSCS) were studied using 248 230 first parity records of Holstein cows calving from 1987 to 1994, daughters of 588 sires in 3042 herds. Herds were classified into low and high yield environment classes. Genetic parameters were estimated with bivariate linear mixed models using the multiple trait derivative free software (MTDFREML). For low yield environment herds, heritabilities for MEM, MEP, MEF, P%, F% and LMSCS were 0.22, 0.20, 0.23, 0.51, 0.58 and 0.11, while for high yield environment herds they were 0.30, 0.27, 0.27, 0.56, 0.56 and 0.09. All genetic correlations, except between MEM and P% and F%, were different in low and high yield environment herd classes. These results indicate that differences in management between the two herd environment classes modify the genetic expression of the traits studied and their genetic association. This suggests that, when these traits are considered in a selection index, appropriate weights for these traits depend on the herd environment class. These results also indicate that different correlated responses for MEP, MEF and LMSCS are expected in high relative to low yield environment herds when selection is based on MEM only.
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1. Introduction

Protein and fat yields and SCS are important factors determining the farmers return from milk. A

growing proportion of milk markets use component pricing. Higher standards for milk quality and programs to increase resistance to mastitis generate pressure toward reducing SCS (Shook and Schutz, 1994). Some of the most commonly used selection indexes, like the USDA Net Merit and Cheese Merit Indexes, are functions of milk constituents and SCS. Heritabilities for protein and fat yields are similar

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to that for milk yield (0.13–0.43) and their genetic (0.40–0.87) and phenotypic (0.66–0.91) correlations with milk yield are positive and very high (Cue et al., 1987; Van Vleck and Dong, 1988; Van Vleck et al., 1988; Schutz et al., 1990; Campos et al., 1994). The genetic relationships between these production traits and SCS in first calving cows are antagonistic (0.08–0.54) (Kennedy et al., 1982; Monardes and Hayes, 1985; Cue et al., 1987; Banos and Shook, 1990). Heritabilities for protein and fat percentages are higher than that for milk yield (0.35–0.78) and their genetic (–0.20 to –0.67) and phenotypic (–0.26 to –0.44) correlations with milk yield are negative and medium to moderately high (Cue et al., 1987; Schutz et al., 1990; Campos et al., 1994).

Estimates of heritability of fat yield have been found to increase with herd production level (from 0.23 in low and 0.36 in high), while the genetic and phenotypic association between milk yield and fat yield did not change (Danell, 1982; Van Vleck et al., 1988).

SCS has been shown to have a heritability of around 0.10 (Banos and Shook, 1990, Schutz, 1994; Shook and Schutz, 1994; Weller and Ezra, 1997) and a moderately high genetic (0.37–0.80) and moderately low to medium phenotypic (0.05–0.30) correlation with mastitis (Lund et al., 1999; Pösö and Mäntysaari, 1996; Weller et al., 1992) hence it is regarded as an indicator of the mammary health status (Kehrli and Shuster, 1994).

Strandberg and Shook (1989) showed that breeding for increased production, without regard for mastitis, will genetically increase clinical mastitis incidence as a correlated selection response. Using two environmental classes Castillo-Juarez et al. (2000) found significant genotype by environment interaction translated into lower genetic correlation between milk yield and SCS and a more favorable phenotypic association between these traits in the high yield environment class, indicating that better management associated with high yield environment herds reduces the antagonistic genetic association between these traits.

The objective of this study was to evaluate the effect of herd environment on the genetic and phenotypic relationships among milk, protein and fat yields, milk composition traits (%) and SCS in primiparous Holstein cows. A secondary objective

was to determine whether genotype by environment interaction exists for protein and fat yields and, if it exists, to quantify the expected changes in component yields across different environments as a correlated response to selection for milk yield. Accurate information regarding the interrelationships among these traits and their dependence on herd environment should prove useful for the design of effective breeding programs. To accomplish these objectives, the phenotypic and genetic correlations among milk protein and fat yields, composition traits and SCS in first lactation cows performing in alternative herd environment classifications were estimated and the correlated responses for protein and fat yields and SCS in different environments resulting from selection for milk yield were evaluated.

2. Material and methods

2.1. 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. First lactation records with recorded date of calving, age at first calving between 18 and 36 months, SCS, mature equivalent milk production (MEM), protein percentage and fat percentage were kept. As a result, a slightly minor subset of these records also provided mature equivalent protein (MEP) and mature equivalent fat (MEF) yields. A mature equivalent record is defined as the 305-day record standardized to 2 × milking, 6 years of age and average season of calving (DHIA Reports, 1994). Data were also restricted to sires with at least 50 first calving daughter records.

Lactation mean of SCS (LMSCS) was defined as the average of up to 12 SCS test days, as in Schutz et al., 1994. Similarly, lactation mean protein percentage (P%) and lactation mean fat percentage (F%) were defined as the average of up to 12 protein and fat percentage test days, respectively.

A total of 248 230 Northeast DHI Holstein records from cows calving from January 1987 to December 1994 remained after edits, representing 588 Holstein

sires in 3042 herds. Means and standard deviations of variables considered in this study are presented in Table 1.

2.2. Herd classification

Herds were classified into either of two classes based on a combination of MEM herd mean and MEM herd standard deviation. To generate two extreme environment classes with approximately 25% of the herds per class, cut-off values were set to

upper and lower 40% for MEM herd mean (≥ 9864 and ≤ 9307 kg) and MEM herd standard deviation (≥ 1621 and ≤ 1479 kg) for high and low yield environment, respectively. The means and the standard deviations for each trait for high and low environment classes as defined by the classification criterion are shown in Table 2.

The mean number of records per sire, the number of herds and herd–year–season of calving classes for the complete dataset and for the two datasets including high and low environment are shown in Table 3.

Table 1
Means, standard deviations (S.D.) and number of records (*n*) for variables in the complete dataset

Variable	Mean	S.D.	<i>n</i>
Mature equivalent milk (kg)	9916	1944	248 230
Mature equivalent protein (kg)	322.28	62.30	247 926
Mature equivalent fat (kg)	366.86	73.63	248 230
Lactation mean somatic cell score	2.73	1.23	248 230
Lactation mean protein percentage	3.26	0.22	247 926
Lactation mean fat percentage	3.72	0.44	248 230

Table 2
Mean, standard deviation (S.D.) and number of records (*n*) for milk production and composition variables in low and high herd levels, with herds classified based on herd mean and herd standard deviation of mature equivalent milk

Variable	Low level herds			High level herds		
	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>
Mature equivalent milk (kg)	8450	1448	41 355	10 821	1946	87 090
Mature equivalent protein (kg)	273.6	47.4	41 355	351.6	62.2	87 090
Mature equivalent fat (kg)	314.1	57.5	41 355	399.2	73.8	87 090
Protein (%)	3.24	0.21	41 349	3.26	0.22	87 029
Fat (%)	3.73	0.42	41 355	3.71	0.45	87 090
Lactation mean somatic cell score	2.90	1.24	41 355	2.67	1.22	87 090

Table 3
Mean number of records per sire, and number of herds and herd–year–season (HYS) of calving classes for the complete data set and for the datasets with low and high level environment herds, with herds classified based on herd mean and herd standard deviation of mature equivalent milk^a

Dataset	Records per sire		Number of		
	Mean	S.D.	Herds	HYS	Records
Complete	422.2	722.4	3042	63 416	248 230
Low environment	70.3	125.0	766	14 158	41 355
High environment	148.1	253.5	759	17 793	87 090

^a Number of sires = 588.

2.3. Model and analysis

The model used to estimate (co)variance components was a bivariate linear mixed sire model. Subsets of two traits at a time were analyzed. Traits studied were MEM, MEP, MEF, P%, F% and LMSCS. In matrix notation the model can be written as

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

where X is a known incidence 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 incidence 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

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

with $V = \text{var}(Y) = ZGZ' + R$, $G = \text{var}(u)$, the genetic (co)variance matrix, and $R = \text{var}(e)$, the residual (co)variance matrix.

If we define G_0 as the symmetric matrix containing variances of ($\sigma^2_{u_i}$) and covariances ($\sigma_{u_{ij}}$) among the sire effects for the two traits, then

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{u_{11}} & \sigma_{u_{12}} \\ \text{Symm} & \sigma^2_{u_{22}} \end{bmatrix} \otimes A = G_0 \otimes A = G$$

where u_j is the vector of sire effects for the j th trait, while \otimes stands for the Kronecker product.

The same bivariate linear sire model and was used to estimate the genetic correlations between the same trait in the two herd environment classes, but now u_j represents the vector of the sire effects for the same trait in the j th environment class.

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

This sire model was used for analyses of the following datasets: (a) complete data set; (b) low yield environment class; (c) high yield environment

class; (d) low and high yield environment classes together.

Dataset (a) were used to estimate the genetic (co)variance structure in the entire population, datasets (b) and (c) were used to estimate the genetic (co)variance structure within environment class, and estimating the genetic (co)variance structure from dataset (d) was required to perform the likelihood ratio test (LRT) to compare a model with four (co)variances versus a model with eight (co)variances, four for each environment class.

The analyses were performed by obtaining univariate estimates for genetic and residual (co)variances using the multiple trait derivative-free REML algorithm implemented by Boldman et al., 1995 in MTDFREML software and use them as starting values in the bivariate 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 (Boldman et al., 1995).

Heritability for the i th trait was estimated as

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

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

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 correlation between the i th and j th traits was estimated as

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

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

$$CR = \hat{\beta}_{\text{bv}_i, \text{bv}_j} = \hat{r}_{g_{ij}} \left(\frac{\hat{\sigma}_{g_{ii}}}{\hat{\sigma}_{g_{jj}}} \right)$$

2.4. 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 yield

environment classes for the traits studied. First, a LRT was used to compare the two *Go* matrices from low and high environment classes (Shaw, 1991). This test is an approximation because the two yield classes are environmentally independent but they share genes in common (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 (Robertson, 1959; Swiger et al., 1964) and used to assess differences between these parameters in high and low yield environment classes.

3. Results and discussion

3.1. General results

The heritabilities and the genetic and phenotypic correlations for the traits in the complete data set are presented in Table 4. These results are similar to other estimates (Monardes and Hayes, 1985; Schutz et al., 1990; Banos and Shook, 1990; Weller and Ezra, 1997).

Table 4
Heritabilities of mature equivalent milk yield (MEM), mature equivalent protein (MEP), mature equivalent fat (MEF), protein percentage (P%), fat percentage (F%), lactation mean somatic cell score (LMSCS) in the diagonal, and their genetic and phenotypic correlations above and below the diagonal, respectively, estimated with the complete dataset^a

	MEM	MEP	MEF	P%	F%	LMSCS
MEM	0.28 (0.01)	0.83 (0.01)	0.49 (0.02)	-0.43 (0.02)	-0.50 (0.02)	0.22 (0.03)
MEP	0.92	0.26 (0.01)	0.66 (0.01)	0.15 (0.02)	-0.16 (0.02)	0.22 (0.03)
MEF	0.74	0.81	0.27 (0.01)	0.20 (0.02)	0.51 (0.02)	0.07 (0.03)
P%	-0.31	0.10	0.08	0.56 (0.02)	0.63 (0.01)	-0.10 (0.02)
F%	-0.33	-0.12	0.37	0.54	0.56 (0.02)	-0.16 (0.02)
LMSCS	-0.08	-0.05	-0.09	0.07	-0.02	0.10 (0.004)

^a Approximate standard errors are given in parentheses.

Antagonistic genetic associations were found between LMSCS and all the yield traits (MEM, MEP and MEF) while their phenotypic associations were small but favorable.

The genetic and phenotypic association between MEP and MEF was high and positive, while that between MEP and F% was antagonistic, although rather low.

Whereas the phenotypic and genetic associations between MEM and MEP and MEF were high and positive, those between MEM and P% and F% were negative and moderately high, meaning that, in the long term, genetic selection based only on MEM would lead to a correlated change in milk composition.

3.2. Herd classes and the genetic (co)variance structure

No differential use of sires in the two herd environment classes was detected. The heritabilities and genetic and phenotypic correlations for low and high yield environment classes are presented in Tables 5 and 6, respectively. For every subset of traits analyzed, except for the association between MEM with P% and F%, the LRT showed that the genetic (co)variance structure was significantly different for low and high yield environment classes ($P < 0.001$), indicating presence of genotype by environment interaction.

A nonproportional change in genetic and residual variances for MEM, MEP, MEF and P% was observed in the low versus high yield environment class, leading to higher heritability in the high yield environment class, with one exception, heritability of F%, which was slightly higher for the low yield environment class.

Using approximate standard errors for testing, genetic correlations between MEP and LMSCS in the two environments were antagonistic and significantly ($P < 0.01$) larger in low (0.27) versus high (0.21) herd environment, while the genetic correlation between MEF and LMSCS did not change across yield environments. On the other hand, the genetic association between P% and LMSCS was small but antagonistic in the low yield environment class (-0.08) and positive and small in the high yield environment class (0.02). The antagonistic

Table 5

Heritabilities of mature equivalent milk yield (MEM), mature equivalent protein (MEP), mature equivalent fat (MEF), protein percentage (P%), fat percentage (F%), and lactation mean somatic cell score (LMSCS) in the diagonal, and their genetic and phenotypic correlations above and below the diagonal, respectively, estimated with the low environment herd class dataset, with herds classified based on herd mean and herd standard deviation of mature equivalent milk^a

	MEM	MEP	MEF	P%	F%	LMSCS
MEM	0.22 (0.01)	0.77 (0.01)	0.37 (0.03)	-0.44 (0.02)	-0.50 (0.02)	0.28 (0.04)
MEP	0.91	0.20 (0.01)	0.56 (0.02)	0.24 (0.03)	-0.13 (0.03)	0.27 (0.04)
MEF	0.75	0.82	0.23 (0.01)	0.21 (0.03)	0.62 (0.02)	0.07 (0.03)
P%	-0.28	0.15	0.11	0.51 (0.02)	0.58 (0.02)	-0.08 (0.03)
F%	-0.30	-0.07	0.40	0.56	0.58 (0.02)	-0.21 (0.03)
LMSCS	-0.05	-0.02	-0.07	0.07	-0.03	0.11 (0.005)

^a Approximate standard errors are given in parentheses.

Table 6

Heritabilities of mature equivalent milk yield (MEM), mature equivalent protein (MEP), mature equivalent fat (MEF), protein percentage (P%), fat percentage (F%), lactation mean somatic cell score (LMSCS) in the diagonal, and their genetic and phenotypic correlations above and below the diagonal, respectively, estimated with the high environment herd class dataset, with herds classified based on herd mean and herd standard deviation of mature equivalent milk^a

	MEM	MEP	MEF	P%	F%	LMSCS
MEM	0.30 (0.01)	0.85 (0.01)	0.52 (0.02)	-0.45 (0.02)	-0.52 (0.02)	0.17 (0.02)
MEP	0.92	0.27 (0.01)	0.68 (0.01)	0.10 (0.03)	-0.20 (0.02)	0.21 (0.03)
MEF	0.74	0.80	0.27 (0.01)	0.17 (0.02)	0.46 (0.02)	0.05 (0.03)
P%	-0.32	0.07	0.06	0.56 (0.02)	0.63 (0.01)	0.02 (0.02)
F%	-0.34	-0.15	0.37	0.54	0.56 (0.02)	-0.14 (0.03)
LMSCS	-0.09	-0.06	-0.10	0.07	-0.02	0.09 (0.004)

^a Approximate standard errors are given in parentheses.

genetic association between F% and LMSCS was larger in the low yield (-0.21) versus high yield (-0.14) herd environment class.

The antagonistic genetic association between MEP and F% was larger in the high (-0.20) versus low (-0.13) yield environment. On the other hand, the

genetic correlation between MEP and P%, between MEF and F%, and between MEF and P% were positive but larger in the low (0.24, 0.62 and 0.21) versus high (0.10, 0.46 and 0.17) yield environment class.

Genetic correlations between MEP and MEF in

the two yield environments were larger in high (0.68) versus low (0.56) yield environment ($P < 0.001$), and the phenotypic correlations were high and positive but not different across yield environment classes. Unfortunately, to our knowledge, there are not published studies related to herd environment effect on the genetic association among milk composition traits.

Genetic correlations between MEM and MEP and between MEM and MEF were positive and smaller in low (0.77 and 0.37) versus high (0.85 and 0.52) yield environment class. This result is in disagreement with Danell (1982) and Van Vleck et al., 1988 who found no changes in this genetic association across environments. On the other hand, genetic correlations between MEM and P% and F% did not change across yield environments, suggesting that milk composition is rather constant across yield environments.

3.3. Genetic correlations for the same trait between yield environments

The genetic correlations between the low and high yield environment classes for the traits studied were all >0.97 , indicating that the breeding value and ranking of the sires for each of these traits would, under single trait selection, be the same in the two yield environment classes.

3.4. Correlated responses to selection for milk yield

The expected correlated response in MEP, MEF and LMSCS for the entire population, and for low

and high yield environment classes given single trait selection on MEM are shown in Table 7. Since genetic correlation between MEM and P% and F% did not change across yield environments, the correlated responses for P% and F% were not calculated.

The correlated responses were calculated as a result of 1000 kg of genetic improvement in MEM. The expected change in MEP and MEF in entire population is an increase of 15.35 and 9.95%, respectively, relative to the mean MEP and MEF in the complete dataset. The difference in mean MEP and MEF between the two yield environment classes were 78 and 85 kg, respectively (Table 2). As a result of the correlated response associated with a genetic gain of 1000 kg MEM, these differences are expected to increase by 3.83 and 6.99 kg, respectively. The expected change in LMSCS average is an increase of 3.64% relative to the mean LMSC in the complete dataset. In the two yield environmental classes, the actual LMSCS difference is 0.23 (Table 2), and for every 1000 kg of MEM genetic gain this difference is expected to increase by 0.11. Due to different genetic correlations will the correlated response in LMSC be 2.77 times higher in the low environment herd class (Table 7).

4. Conclusions

The genetic antagonistic relationship found between MEM with P% and F%, and between MEP with F% and LMSCS indicates that, with increased selection pressure on milk and protein yield, there would be an associated decrease in F% and P% and an increase in LMSCS in first lactation Holstein

Table 7

Expected correlated responses for mature equivalent protein (MEP), mature equivalent fat (MEF) and lactation mean somatic cell score (LMSCS) as a result of 1000 kg genetic gain for mature equivalent milk yield (MEM) for complete dataset and the two datasets including low and high level environment herds, with herds classified based on herd mean and herd standard deviation of mature equivalent milk

Class	MEP	Low/high ^a	MEF	Low/high	LMSCS	Low/high
Low	46.09		30.16		0.1764	
High	49.92	0.92	37.15	0.81	0.0638	2.77
Complete data set	49.47		36.49		0.0995	

^a Low/high represents the ratio of the expected correlated responses in the low and high herd classes.

cows. The genetic association found in this study indicates that the actual genetic gain for MEM of 139 kg of milk per cow per year reported in a review by Schutz (1994) may under single trait selection result in an annual genetic increase of 6.87 kg of MEP, 5.07 kg of MEF and 0.014 in LMSCS as correlated responses.

Genetic correlations between yield environment classes for the same traits were near unity indicating that MEM, MEP, MEF, protein and fat percentages and LMSCS are genetically equivalent traits across yield environment classes. Consequently, breeding values and ranking of sires are expected to be the same in the two yield environment classes for each trait studied.

It is very likely that the major difference between low and high yield environment classes as defined in this study is the level of management. Hence, these results indicate that, through superior management in the high yield environment class, the genetic antagonism between LMSCS and the yield traits, MEM, MEP and MEF is reduced but not eliminated. Therefore, good management by itself could not completely prevent genetic deterioration in LMSCS brought about by selection for MEM, MEP, MEF or any combination of these traits. Our results also indicate that, if selection is for MEM, the correlated responses for MEP and MEF depend on yield environment class (level), but those for composition traits do not.

To achieve the same genetic goal across yield environments, this study suggests that weights on SCS, MEP and MEF in selection indexes should vary with yield environmental class, with higher weights for herds in the low yield environment class. With a milk pricing system based on protein and fat yields and SCS, our results suggest that in the future low yield environment herds would be economically affected not only because of their lower milk yield, but also because of a lower milk price as a result of lower milk quality.

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