Genetic Correlations Among Production, Body Size, Udder, and Productive Life Traits Over Time in Holsteins

S. Tsuruta,¹ I. Misztal,¹ and T. J. Lawlor²

¹Animal and Dairy Science Department,
University of Georgia, Athens 30602

²Holstein Association USA Inc.,
Brattleboro, VT 05301

ABSTRACT

Genetic correlations among milk, fat, and protein yields; body size composite (BSC); udder composite (UDC); and productive life (PL) in Holsteins were investigated over time. The data set contained 25,280 records of cows born in Wisconsin between 1979 and 1993. The multiple trait random regression (MT-RR) animal model included registration status, herd-year, age group, and stage of lactation as fixed effects; additive genetic effects with random regressions (RR) on year of birth using the first-order Legendre polynomial; and residual effects. Heterogeneous residual variances were considered in the model. Estimates of variance components and genetic correlations among traits from MT-RR were compared with those estimated with a multiple trait interval (MT-I) model, which assumed that every 3-yr interval was a separate trait and included the same effects as in the MT-RR model except for the RR. Genetic correlations estimated with MT-RR and MT-I models over time among all traits were compared with correlations among breeding values predicted with the single trait (ST) model without RR. Correlations among breeding values predicted with MT-RR, ST, and MT models were also calculated.

Additive genetic and residual variances for all traits except PL increased over time; those for PL were constant. As a result, heritability estimates had no significant changes during the 15 yr. Genetic correlations of PL with milk, fat, protein, and BSC declined to zero or negative; those with UDC remained positive. Correlations among breeding values predicted with ST, MT, and MT-RR models were relatively high for all traits except PL.

Genetic correlations between PL and other traits varied over time, with some correlations changing sign. For accurate indirect prediction of PL from other traits,

the genetic correlations among the traits need to be re-estimated periodically.

(Key words: genetic correlation, random regression, Holstein)

Abbreviation key: BSC = body size composite, HPD = highest posterior density interval, MT = multiple trait, MT-I = MT interval, PL = productive life, RR = random regression, ST = single trait, UDC = udder composite.

INTRODUCTION

The genetic evaluation of type traits in Holsteins has been conducted with a multiple trait (MT) model by Holstein Association USA, Inc. (Brattleboro, VT). The MT model assumes that additive genetic and environmental variances and genetic and environmental correlations among traits are constant over time. Indirect prediction of productive life (PL) from type traits (Weigel et al., 1998; VanRaden, 2001) also uses the same assumption. However, this assumption may not be valid. Additive genetic variance could be changed not only by selection but also by other factors such as migration, segregation, mutation, inbreeding, and redefinition of the recording system. Dairy producers' decisions on culling cows are based on various reasons, such as milk, reproduction problems, mastitis, and labor costs. All of these factors can change over time. Environmental or residual variances could change because of economic and management reasons. Selection on one trait may impede the genetic improvement of other traits because of linkage disequilibrium. Weigel et al. (1998) showed weights and maximum reliability for direct and indirect PL. If genetic parameters change over time, those weights for PL may also vary over time. Some linear type traits may have an intermediate optimum. Selection on a linear index assumes that the extremes are best.

Lawlor et al. (2002) presented changes in genetic parameters of production traits, linear type traits, and PL over time using a random regression (RR) model. Tsuruta et al. (2003) also investigated changes in genetic parameters of final score by RR models with re-

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Corresponding author: S. Tsuruta; E-mail: shogo@uga.edu.

Table 1. Data description for milk, fat, and protein yields; productive life (PL); body size composite (BSC); and udder composite (UDC).

Year of birth	Records ¹	Mean (SD)					
		Milk	Fat	Protein	PL	BSC	UDC
	(no.)		(kg)		(mo)		
1979	112 (53)	8882 (1365)	340 (57)	271 (34)	30.8 (9.9)	29.0 (6.5)	25.7 (6.9)
1980	952 (510)	8786 (1487)	329 (53)	269 (44)	30.2 (12.1)	26.7 (7.2)	23.3 (6.4)
1981	1337 (1082)	8829 (1500)	333 (55)	269 (44)	29.9 (12.2)	25.7 (7.4)	22.0 (5.8)
1982	1518 (1411)	8951 (1549)	332 (56)	273 (45)	28.4 (12.1)	25.8 (7.3)	21.9 (6.0)
1983	1482 (1428)	9150 (1606)	340 (59)	278 (46)	28.3 (12.6)	27.7 (7.2)	23.4 (6.4)
1984	1638	9405 (1567)	347 (58)	281 (44)	27.5 (12.5)	26.6 (7.1)	22.7 (6.1)
1985	1645	9593 (1515)	353 (55)	278 (42)	27.6 (12.5)	26.6 (7.2)	23.0 (6.4)
1986	1879	9794 (1673)	363 (64)	284 (46)	27.1 (12.5)	26.8 (7.5)	24.0 (6.5)
1987	1923	9957 (1694)	373 (66)	290 (48)	26.4 (12.1)	27.0 (7.4)	23.9 (6.8)
1988	2254	10,201 (1746)	380 (69)	298 (49)	26.4 (12.1)	27.4 (7.7)	23.6 (6.8)
1989	2236	10,387 (1709)	385 (68)	304 (48)	26.1 (11.8)	28.0 (7.6)	24.2 (7.0)
1990	2202	10,758 (1738)	398 (68)	317 (49)	26.7 (11.7)	28.2 (7.8)	23.9 (6.9)
1991	2187	10,962 (1738)	405 (71)	324 (50)	26.1 (11.9)	27.5 (7.6)	22.8 (7.0)
1992	2047	11,102 (1856)	407 (72)	328 (53)	25.9 (12.1)	27.4 (7.5)	22.7 (6.9)
1993	1868	11,249 (1860)	410 (72)	334 (55)	26.2 (12.1)	27.1 (7.4)	22.8 (7.1)
Total or average	25,280 (24,363)	10,074 (1861)	373 (70)	299 (53)	27.1 (12.2)	27.1 (7.5)	23.2 (6.7)

¹Number of protein records in parentheses.

gression on year of birth. As verified by simulation, such estimation can be successful; however, changes in genetic parameters must be gradual over time, and residual variances need to be modeled as heterogeneous.

The objective of this study was to estimate changes in genetic parameters for PL, production, and selected type traits over time.

MATERIALS AND METHODS

Data

Production data (305-d milk, fat, and protein yields) and PL were provided by USDA-AIPL, and linear type data were obtained from Holstein Association USA, Inc. The final data set included 25,280 records of Wisconsin Holstein cows born over 15 yr between 1979 and 1993, with a total of 40,838 in the pedigree that included 3 generations preceding the recorded animals. The numbers of records; means; standard deviations for milk, fat, and protein yields; PL; body size composite (**BSC**); and udder composite (**UDC**) are shown in Table 1. Milk, fat, and protein yields for 305 d were pre-adjusted by age at calving to mature equivalent records. Productive life was defined as months in milk at age 84 mo as described by VanRaden and Klaaskate (1993) but was not adjusted for milk yield. According to formulas in Sire Summaries (2003), BSC and UDC were defined with weighted linear type traits as follows:

$$\text{BSC} = (\text{stature} \times 0.50) + (\text{strength} \times 0.25) + (\text{body depth} \times 0.15) + (\text{thurl width} \times 0.10);$$

$$\text{UDC} = (\text{udder depth} \times 0.30) + (\text{fore udder attachment} \times 0.16) + (\text{front teat placement} \times 0.16) + (\text{rear udder height} \times 0.16) + (\text{rear udder width} \times 0.12) + (\text{udder cleft} \times 0.10).$$

Multiple-Trait Animal Model with RR

Multiple trait RR (MT-RR) models were defined as follows.

For milk, fat, and protein yields:

$$y_{ijklmn} = \text{reg}_i + hy_j + ag_k + moc_l + \sum_{p=0}^1 a_{np}Z_{np} + e_{ijklmn};$$

for BSC and UDC,

$$y_{ijklmn} = \text{reg}_i + hy_j + ag_k + sl_m + \sum_{p=0}^1 a_{np}Z_{np} + e_{ijklmn}; \text{ and}$$

for PL,

$$y_{ijklmn} = \text{reg}_i + hy_j + ag_k + \sum_{p=0}^1 a_{np}Z_{np} + e_{ijklmn};$$

where y_{ijklmn} = observations for registration status i , management group j , age group k , month of calving l , stage of lactation m , and cow n ; reg_i = effects of registration status i (registered or grade); hy_j = effects of herd-year j ; ag_k = effects of age group k ; moc_l = month of

Table 2. Minimum and maximum additive genetic and residual variances and heritability ($1.96 \times \text{SD}$) for milk, fat, and protein yields; productive life (PL); body size composite (BSC); and udder composite (UDC) in 15 yr estimated with a multiple trait random regression model.

Trait	Additive genetic variance	Residual variance	Heritability
	Minimum – maximum ($1.96 \times \text{SD}$)		
Milk, $\text{kg}^2 (\times 10^4)$	78.5 – 126.2 (7.9 – 18.4)	79.1 – 116.0 (7.8 – 12.3)	0.43 – 0.52 (0.04 – 0.08)
Fat, $\text{kg}^2 (\times 10^2)$	10.5 – 16.1 (1.1 – 2.6)	11.1 – 19.3 (1.1 – 1.8)	0.42 – 0.50 (0.04 – 0.09)
Protein, $\text{kg}^2 (\times 10^2)$	5.4 – 8.1 (0.6 – 1.3)	6.5 – 9.2 (0.6 – 1.0)	0.40 – 0.49 (0.04 – 0.08)
PL, mo^2	12.1 – 26.5 (3.7 – 12.4)	117.9 – 133.3 (5.6 – 10.8)	0.09 – 0.18 (0.02 – 0.08)
BSC	11.3 – 17.3 (1.1 – 3.0)	13.8 – 19.1 (1.3 – 2.1)	0.40 – 0.49 (0.04 – 0.09)
UDC	5.5 – 8.4 (0.7 – 1.6)	10.5 – 15.9 (0.9 – 1.3)	0.26 – 0.38 (0.03 – 0.08)

calving l , sl_m = effects of stage of lactation $\times$ year at classification m ; a_{np} = RR coefficient p on year of birth for additive genetic effect on animal n ; z_{np} = Legendre polynomials; and e_{ijklmn} = residual effects. The first-order Legendre polynomial standardized to the range of -1 to $+1$ for the years from 1979 to 1993 was applied to the MT-RR model. In matrix notation, the model is

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e}$$

where $\mathbf{y}$ = a vector of final scores, $\boldsymbol{\beta}$ = a vector of fixed effects, $\mathbf{a}$ = a vector of intercepts and linear RR coefficients for additive genetic effects, $\mathbf{e}$ = a vector of residual effects, $\mathbf{X}$ = an incidence matrix for fixed effects, and $\mathbf{Z}$ = a matrix of covariates of Legendre polynomials for additive genetic effects. The variances are defined as

$$\mathbf{V} = \text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A}_p & 0 \\ 0 & \mathbf{R} \otimes \mathbf{I}_i \end{bmatrix}$$

where $\mathbf{G}$ = an additive genetic covariance matrix with size 12 [6 traits $\times$ (intercept + linear RR) for linear RR], $\otimes$ = the direct matrix product, $\mathbf{A}_p$ = the additive genetic relationship matrix for p animals, $\mathbf{R}$ = a residual variance matrix for 6 traits with σ_{ei}^2 for interval i , and $\mathbf{I}_i$ = an identity matrix for interval i . Heterogeneous residual variances were estimated in 5 intervals of 3 yr.

MT Interval Animal Model

A multiple trait interval (**MT-I**) model was used to compare the genetic parameters with those from the MT-RR model. The MT-I model treated 3-yr intervals as separate traits for a total of 30 traits (5 intervals $\times$

6 original traits). Effects included in this model were the same as those in the MT-RR model except additive genetic effects did not include RR. Therefore, the additive genetic covariance matrix consisted of 30×30 parameters including covariances among the intervals, and the residual variance was the same size without the covariances.

Single-Trait Animal Model Without RR

A single trait (**ST**) model without RR was used to predict breeding values. Effects in the model were the same as those in the MT-RR model without RR. In the ST model, breeding values were predicted ignoring correlations among 6 traits. Afterward, correlations among all traits were calculated using predicted breeding values on all animals to compare with genetic correlations estimated with the MT-RR model.

MT Animal Model Without RR

A MT model without RR was also used to predict breeding values. The MT model assumes constant correlations among traits over time. Effects in the model were the same as those in the MT-RR model without RR. Correlations of these predicted breeding values with those from the ST model and from the MT-RR model were calculated for bulls with ≥ 10 daughters.

Computer Programs

Variance components were estimated with GIBBS3F90 (Misztal, 2003), which is the Gibbs sampling program with heterogeneous residual variances. After 20,000 Gibbs samples were discarded as burn-in,

Figure 1. Posterior means and highest posterior density intervals at 95% (upper and lower) for additive genetic variances using multiple trait random regression and posterior means using multiple trait interval (MT-I) models: A) milk, B) fat, C) protein, D) productive life, E) body size composite, and F) udder composite. Legend: mean (—), lower limit (---), upper limit (---), and MT-I results (■).

80,000 samples were used to calculate posterior means and standard deviations for variance components, heritability, and genetic correlations. Breeding values were calculated with BLUP90IOD (Tsuruta et al., 2001), which uses the pre-conditioned conjugate gradient algorithm with iteration on data.

RESULTS AND DISCUSSION

Data description

Means and standard deviations for 305-d milk, fat, and protein yields; PL; BSC; and UDC are presented in Table 1. Means and standard deviations for milk,

Figure 2. Posterior means and highest posterior density intervals at 95% (upper and lower) for residual variances using multiple trait random regression and posterior means using multiple trait interval (MT-I) models: A) milk, B) fat, C) protein, D) productive life, E) body size composite, and F) udder composite. Legend: mean (—), lower limit (—), upper limit (---), and MT-I results (■).

fat, and protein increased gradually over the years. Means for PL decreased by 4.6 mo in 15 yr, but the standard deviations were relatively stable; means and standard deviations for BSC and UDC fluctuated over the years.

Variance Components and Heritability

Minimum and maximum additive genetic variances and residual variances in 15 yr for milk, fat, and protein yields; PL; BSC; and UDC estimated with the MT-RR

Figure 3. Posterior means and highest posterior density intervals at 95% (upper and lower) for heritability using multiple trait random regression and posterior means using multiple trait interval (MT-I) models: A) milk, B) fat, C) protein, D) productive life, E) body size composite, and F) udder composite. Legend: mean (—), lower limit (—), upper limit (---), and MT-I results (■).

model are presented in Table 2. That table also shows minimum and maximum $1.96 \times$ posterior standard deviations (at 95%) in 15 yr for all traits. The ranges for those variances were large, indicating heterogeneity over the years. However, the ranges for heritability estimates were relatively small except for PL. Figure

1 (a–f) demonstrates posterior means and highest posterior density intervals (HPD) at 95% for additive genetic variances for milk (a), fat (b), protein (c), PL (d), BSC (e), and UDC (f) with the MT-RR model and with the MT-I model. Those means for all traits from the MT-I model were approximately analogous to those from the

Table 3. Minimum and maximum genetic correlations ($1.96 \times \text{SD}$) among milk, fat and protein yields, productive life (PL), body size composite (BSC) and udder composite (UDC) in 15 years estimated with multiple trait random regression model.

Trait	Fat	Protein	PL	BSC	UDC
	Minimum – maximum ($1.96 \times \text{SD}$)				
Milk	0.48 – 0.69 (0.04 – 0.07)	0.82 – 0.87 (0.02 – 0.03)	–0.03 – 0.26 (0.13 – 0.20)	0.11 – 0.16 (0.07 – 0.14)	–0.20 – –0.09 (0.17 – 0.14)
Fat	—	0.58 – 0.82 (0.03 – 0.07)	–0.17 – 0.32 (0.13 – 0.23)	0.08 – 0.17 (0.07 – 0.15)	–0.18 – 0.03 (0.08 – 0.14)
Protein	—	—	0.00 – 0.22 (0.13 – 0.19)	0.14 – 0.17 (0.07 – 0.14)	–0.23 – –0.01 (0.08 – 0.14)
PL	—	—	—	–0.19 – 0.12 (0.12 – 0.21)	0.29 – 0.44 (0.13 – 0.29)
BSC	—	—	—	—	–0.15 – 0.04 (0.08 – 0.15)

MT-RR model, although some of the additive genetic variances were out of the HPD.

Additive genetic variances for all traits except for PL tended to increase over time; those for PL were nearly constant with larger HPD, indicating that increases in additive genetic variances could be due to scaling effects. As means of production traits increased, those variances increased, but mean and variances of PL did not change. Posterior means and HPD for residual variances for all traits are presented in Figure 2 (a–f). Residual variances increased dramatically for milk and fat and increased slightly for protein and BSC. Residual and additive genetic variances for PL were constant. The rise in UDC from 1983 to 1986 might have been due to definition changes for udder traits.

Increases in additive genetic and residual variance for milk, fat, and protein yields were consistent with increases in phenotypic standard deviations shown in Table 1. The MT-I model clearly showed heterogeneity of the residual variance, suggesting that it was essential to consider heterogeneous residual variances in the MT-RR model. Posterior means for heritability for all traits from the MT-I model and the MT-RR model are presented in Figure 3 (a–f). Because changes in additive genetic and residual variances were similar in direction, heritability estimates from the MT-I model for all traits were relatively constant over time and within HPD from the MT-RR model. However, those from the MT-RR model for type traits were underestimated in comparison with those from the MT-I model.

Genetic Correlations

Minimum and maximum genetic correlations with $1.96 \times$ standard deviations in 15 yr among all traits are presented in Table 3. Genetic correlations among milk, fat, and protein yields were highly or moderately positive. Genetic correlations of production traits with BSC

were low and positive over the years; those with UDC were low and negative. Genetic correlations of PL with production traits and BSC were low with large standard deviations, ranging from negative to positive. However, those with UDC were moderately positive.

Genetic correlations and their HPD at 95% among milk, fat, protein, PL, BSC, and UDC for 15 yr using MT-RR and MT-I models are presented in Figure 4 (a–o). Genetic correlations between milk and fat were positive and slightly decreased from 0.7 to 0.5 over time (Figure 4a). Genetic correlations of milk with protein were around 0.8 and constant (Figure 4b). Miller et al. (1967) estimated high genetic correlations (from 0.54 to 0.77) between herd life and milk production. Genetic correlations of milk with PL decreased from positive to zero over the years with large HPD, demonstrating dramatic changes over time and implying that higher producing cows used to live longer (Figure 4c).

Genetic correlations of milk with BSC were positive but low as shown in Table 3, indicating that larger cows might produce more milk, although the trend was not strong (Figure 4d). Low negative genetic correlations of milk with UDC imply that higher UDC does not reflect more milk production (Figure 4e). Genetic correlations of fat with protein were high and decreased over the years (Figure 4f). Genetic correlations of fat with PL also declined and approached zero or turned negative, but those with type traits were low and increased (Figure 4g–i). Genetic correlations of protein with PL decreased, and those with type traits were low and slightly increased or remained constant (Figure 4j–l). Genetic correlations of PL with BSC were low and decreased from positive to negative as did those between fat and PL (Figure 4m). Hansen et al. (1999) reported that larger cows had shorter PL in selected lines for large vs. small body size. Our results in the latter years showed negative genetic correlations.

Figure 4. (a-f) Posterior means and highest posterior density intervals at 95% (upper and lower) for genetic correlations between traits using multiple trait random regression and posterior means using multiple trait interval (MT-I) models and correlations between predicted breeding values for those traits with a single-trait (ST) model: A) milk:fat, B) milk:protein, C) milk:productive life, D) milk:body size composite, E) milk:udder composite, F) fat:protein, G) fat:productive life, H) fat:body size composite, I) fat:udder composite, J) protein:productive life, K) protein:body size composite, L) protein:udder composite, M) productive life:body size composite, N) productive life:udder composite, and O) body size composite:udder composite. Legend: mean (—), lower limit (---), upper limit (- - -), MT-I results (■), and ST results (▲).

Figure 4. (g-l) Posterior means and highest posterior density intervals at 95% (upper and lower) for genetic correlations between traits using multiple trait random regression and posterior means using multiple trait interval (MT-I) models and correlations between predicted breeding values for those traits with a single-trait (ST) model: A) milk:fat, B) milk:protein, C) milk:productive life, D) milk:body size composite, E) milk:udder composite, F) fat:protein, G) fat:productive life, H) fat:body size composite, I) fat:udder composite, J) protein:productive life, K) protein:body size composite, L) protein:udder composite, M) productive life:body size composite, N) productive life:udder composite, and O) body size composite:udder composite. Legend: mean (—), lower limit (—), upper limit (---), MT-I results (■), and ST results (▲).

Figure 4. (m–o) Posterior means and highest posterior density intervals at 95% (upper and lower) for genetic correlations between traits using multiple trait random regression and posterior means using multiple trait interval (MT-I) models and correlations between predicted breeding values for those traits with a single-trait (ST) model: A) milk:fat, B) milk:protein, C) milk:productive life, D) milk:body size composite, E) milk:udder composite, F) fat:protein, G) fat:productive life, H) fat:body size composite, I) fat:udder composite, J) protein:productive life, K) protein:body size composite, L) protein:udder composite, M) productive life:body size composite, N) productive life:udder composite, and O) body size composite:udder composite. Legend: mean (—), lower limit (---), upper limit (---), MT-I results (■), and ST results (▲).

Genetic correlations between PL and UDC were low but positive (Figure 4n), suggesting that better udder quality may be required to keep producing milk longer. However, because of low negative correlations between milk and UDC, cows may not be able to produce more milk in their lifetime. A producer's main reasons to cull cows are changing over time. In the past, milk yield was influential, but now reproduction and mastitis are more important. These changes in trait definition for PL must have occurred gradually over the years. Vollema and Groen (1997) concluded that genetic correlations between conformation and longevity traits differed among years of birth and that genetic correlation between herd life and udder depth was positive. As they indicated, genetic relationship between 2 traits could be nonlinear. In addition, Larroque and Ducrocq (2001) and Pérez-Cabal and Alenda (2002) reported nonlinearity of relationships between type traits and PL or longevity in Holsteins; Fuerst-Waltl et al. (1998) found nonlinear genetic relationships between milk and type traits. Productive life is a trait that strongly deviates from the normal distribution, and some of the nonlinearity could be due to the use of linear methodology, which assumes a normal distribution. Pasman and Reinhardt (1999) also presented similar genetic correlations when functional (milk-adjusted) PL was obtained by survival analysis. Their correlations of PL with body size and udder traits were -0.17 and 0.33 , respectively.

Correlation between breeding values for 2 traits may be a good indicator of the genetic correlation estimated directly from additive genetic (co)variances and, thus, may be used for validation. Figure 4 also shows correlations between breeding values predicted with the ST model for the 6 traits over the years. These correlations were in agreement with those from the MT-RR model.

Correlation Among Predicted Breeding Values

Correlations among predicted breeding values of milk, fat, protein, PL, BSC, and UDC for 435 bulls with ≥ 10 daughters using ST and MT models and the MT-RR model in 1992, 1986, and 1980 are presented in Table 4. Breeding values predicted with the MT-RR model were compared with those with the ST model, which ignores genetic correlations among traits, and the MT model, which assumes that genetic correlations were constant over time. Overall, correlations among breeding values for all traits with different models were high (>0.9) except correlations for PL (0.4 to 0.9). Those low correlations might have been due to large standard deviations of those genetic parameters estimated with the MT-RR model and changes of genetic correlations with other traits. Table 4 also presents correlations between additive genetic effects in 1992, 1986, and 1980

Table 4. Correlation among predicted breeding values for 435 bulls with ≥ 10 daughters using single-trait (ST), multiple-trait (MT), and multiple trait random-regression (MT-RR) models for milk, fat, and protein yields; productive life (PL); body size composite (BSC); and udder composite (UDC) and estimated genetic correlation between additive genetic effects in 1992 and 1986 and in 1992 and 1980 using the MT-RR model.

Model (year in MT-RR model)	Milk	Fat	Protein	PL	BSC	UDC
Correlation between predicted breeding values with different models						
ST:MT	0.99	0.99	0.99	0.98	0.99	0.99
ST:MT-RR (1992)	0.97	0.97	0.95	0.74	0.96	0.95
ST:MT-RR (1986)	0.99	0.98	0.95	0.88	0.99	0.98
ST:MT-RR (1980)	0.93	0.92	0.86	0.74	0.94	0.88
MT:MT-RR (1992)	0.98	0.97	0.95	0.78	0.96	0.95
MT:MT-RR (1986)	0.99	0.99	0.95	0.91	0.99	0.99
MT:MT-RR (1980)	0.94	0.92	0.86	0.76	0.94	0.89
MT-RR (1992):MT-RR (1986)	0.98	0.97	0.96	0.83	0.97	0.95
MT-RR (1992):MT-RR (1980)	0.88	0.85	0.84	0.42	0.86	0.76
Estimated genetic correlation between additive genetic effects with MT-RR model						
MT-RR (1992):MT-RR (1986)	0.94	0.94	0.92	0.74	0.93	0.91
MT-RR (1992):MT-RR (1980)	0.72	0.72	0.64	0.22	0.67	0.62

derived from estimates of variance components. Those genetic correlations for PL were relatively low (0.22 between in 1992 and 1980 and 0.74 between in 1992 and 1986, respectively), but those for other traits were from 0.62 to 0.72 between 1992 and 1980 and >0.9 between 1992 and 1986, respectively, which suggests that although other traits changed moderately between 1980 and 1992, PL became a different trait. Estimates from RR models may be inflated particularly at the extremes, and it is possible that the actual correlations are somewhat higher.

Comparison of Models

One of the most important questions in this study is whether the MT-RR can provide reliable estimates. Shapes of correlations in this study, where RR were limited to linear, were constrained to approximately linear changes in correlations and quadratic changes in additive variances. Constraints in the MT-I model were smaller, but at higher computing costs. The estimates by MT-RR and MT-I models were mostly similar, although some differences were outside the 95% HPD interval. Also, the comparison of breeding values under MT-RR, MI, and ST models were in agreement. Thus, the MT-RR model with linear regression can be a reasonable tool for looking at genetic changes over time if such changes are gradual. Modeling of changes over time with higher flexibility can be accomplished by the use of nonlinear RR. With higher order polynomials, computing becomes more expensive, and modeling artifacts may be stronger (Tsuruta et al., 2003).

CONCLUSIONS

Genetic correlations among traits can increase or decrease over time and even change sign. A RR model can estimate such changes if they are gradual. A producer's culling decisions may be the primary reason for the change of genetic correlations between PL and some linear type traits. Periodical re-estimation of genetic parameters would be required for more accurate indirect prediction of PL.

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REFERENCES

- Fuerst-Waltl, B., J. Sölkner, A. Essl, I. Hoeschele, and C. Fuerst. 1998. Non-linearity in the genetic relationship between milk yield and type traits in Holstein cattle. *Livest. Prod. Sci.* 57:41–47.
- Hansen, L. B., J. B. Cole, G. D. Marx, and A. J. Seykora. 1999. Productive life and reasons for disposal of Holstein cows selected for large versus small body size. *J. Dairy Sci.* 82:795–801.
- Larroque, H., and V. Ducrocq. 2001. Relationships between type and longevity in the Holstein breed. *Genet. Sel. Evol.* 33:39–59.
- Lawlor, T. J., S. Tsuruta, L. Klei, and I. Misztal. 2002. Use of a random regression model to investigate changes in genetic parameters over time. *Proc. 7th WCGALP, Montpellier, France. CD-ROM Communication* 17:06.
- Miller, P., L. D. Van Vleck, and C. R. Henderson. 1967. Relationships among herd life, milk production, and calving interval. *J. Dairy Sci.* 50:1283–1287.

- Misztal, I. 2003. BLUPF90 Manual. [Online]. Available at <http://nce.ads.uga.edu/~ignacy/newprograms.html>. Accessed Nov. 17, 2003.
- Pasman, E., and F. Reinhardt. 1999. Genetic relationship between type composites and length of productive life of Black-and White Holstein cattle in Germany. *Interbull Bull.* 21:117–121.
- Pérez-Cabal, M. A., and R. Alenda. 2002. Genetic relationships between lifetime profit and type traits in Spanish Holstein cows. *J. Dairy Sci.* 85:3480–3491.
- Sire Summaries. 2003. Linear Type Evaluations. Holstein Association USA. Brattleboro, VT.
- Tsuruta, S., I. Misztal, and I. Strandén. 2001. Use of the preconditioned conjugate gradient algorithm as a generic solver for mixed model-equations in animal breeding applications. *J. Anim. Sci.* 79:1166–1172.
- Tsuruta, S., I. Misztal, T. J. Lawlor, and L. Klei. Modeling final scores in US Holsteins as a function of year of classification using a random regression model. *Livest. Prod. Sci.* (accepted)
- VanRaden, P. M. 2001. Methods to combine estimated breeding values obtained from separate sources. *J. Dairy Sci.* 34(E. Suppl.):E47–E55.
- VanRaden, P. M., and E. J. H. Klaaskate. 1993. Genetic evaluation of length of productive life including predicted longevity of life cows. *J. Dairy Sci.* 76:2758–2764.
- Vollema, A. R., and A. F. Groen. 1997. Genetic correlations between longevity and conformation traits in an upgrading dairy cattle population. *J. Dairy Sci.* 80:3006–3014.
- Weigel, K. A., T. J. Lawlor, Jr., P. M. VanRaden, and G. R. Wiggans. 1998. Use of linear type and production data to supplement early predicted transmitting abilities for productive life. *J. Dairy Sci.* 81:2040–2044.