Method R Estimates of Heritability for Milk, Fat, and Protein Yields of United States Dairy Cattle

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ABSTRACT

Heritabilities for milk, fat, and protein yields were estimated from first lactation data used for USDA-Dairy Herd Improvement Association (DHIA) genetic evaluations. Contemporary group assignments and standard deviations within herd-year were determined with the procedure used for national evaluations. Pedigree data were included for animals born since 1970; yield data were included for cows born since 1980. Lactation records were divided into four mutually exclusive data sets based on standard deviations. Ranges for standard deviations were chosen so that data sets were approximately equal in size. Method R was used to estimate heritability with 25 different random samples of half of the data for each data set. Because of the large number of Holstein observations, estimates of heritability for Holsteins were based on random subsets of the complete data file; each subset included approximately 5% of the data. Mean heritability estimates increased with standard deviations, and estimates ranged from 0.18 to 0.51 across breeds. Repeatability estimates for milk yield of Holsteins were approximately 0.50 and did not change with standard deviation. These heritability estimates were higher than those previously used in the USDA-DHIA genetic evaluation. Heritability used in the USDA-DHIA genetic evaluation have been increased based on these results.
(**Key words:** heritability, Method-R, genetic evaluation, milk yield)

Abbreviation key: AIPL = Animal Improvement Programs Laboratory.

INTRODUCTION

Estimates of variance components are required by the USDA Animal Improvement Programs Laboratory (**AIPL**) to calculate national genetic evaluations of dairy cattle. However, because of computational limitations, parameters have never been estimated using the complete national data set of lactation records maintained at AIPL.

Many researchers have estimated heritability greater than 0.25 for yield traits (e.g., 1, 17, 18, 20, 22), and many countries now assume heritability greater than 0.25 (6, 7). Additionally, there is abundant evidence for heterogeneous variance in dairy cattle populations with heritability increasing with phenotypic variation (2, 10, 16, 21). Because of these factors, the USDA-DHIA genetic evaluation accounts for heterogeneous variance by standardizing records to a constant genetic variance and accounts for differences in residual variance (24).

The objective of this study was to obtain estimates of parameters using data and analysis models as similar as possible to those used for genetic prediction and to obtain these estimates for different levels of herd-year variation.

MATERIALS AND METHODS

Data

Data were obtained from the AIPL database for the six major breeds of dairy cattle: Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and Milking Shorthorn. Data for Red and Whites were combined with Holstein data because Red and White cattle were less than 1% of the Holstein data and have a similar genetic background (i.e., primarily Holstein ancestors). The AIPL database includes historical yield and pedigree information for cows enrolled in DHIA programs throughout the United States. All records were extended to 305 d as needed. Further adjustments were made so that yields were on a mature equivalent and twice daily milking basis. Finally, records were adjusted with an expansion factor to stabilize phenotypic variance using procedures described by VanRaden et al. (19), but records were not adjusted with the heterogeneous variance adjustment of Wiggans and VanRaden (24).

The complete data set included records from first lactations of all cows born after 1980. This data set was reduced by removing records for single record contemporary groups. For the Holsteins only, analyses were based on random subsets of 5% of the complete data set. The data to be included in the subset were selected

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TABLE 1. Numbers of observations used in Method R heritability estimates for milk, fat, and protein yields by breed of dairy cattle.

Breed	Yield trait	Quartile set 1	2	3	4
Ayrshire	Milk and fat	12,309	12,680	11,318	12,171
	Protein	10,843	11,445	10,809	11,796
Brown Swiss	Milk and fat	18,693	16,962	17,407	19,801
	Protein	16,742	16,156	16,577	18,742
Guernsey	Milk and fat	29,210	30,446	28,165	29,300
	Protein	24,442	28,056	26,491	27,843
Holstein[1]	Milk and fat	2,028,208	2,004,257	2,028,724	2,123,314
	Protein	1,711,437	1,773,732	1,793,881	1,882,413
Holstein[2]	Milk	101,788	100,512	100,399	103,985
	Fat	102,275	101,517	98,796	105,704
	Protein	85,751	88,510	90,029	95,128
Jersey	Milk and fat	108,991	112,309	106,961	111,863
	Protein	96,417	105,510	102,491	107,912
Milking Shorthorn	Milk and fat	2799	3008	2497	2739
	Protein	2289	2593	2315	2617

[1] Complete data set.

[2] Mean of 25 random 5% subsets of the total Holstein data set.

by randomly including a herd with a probability of 5%. For all breeds, the resulting data set was divided into four mutually exclusive groups based on standard deviation within herd-year for milk yield. These data sets, formed by dividing the complete data set, were called quartile sets. Quartile set 1 had records with the lowest standard deviations; quartile set 4 had records with the highest standard deviations. Herd-year standard deviation was chosen as the criterion for dividing the data because this value has been used as an indicator of heterogeneous variance in the USDA-DHIA genetic evaluation (24). Use of four data subsets was an arbitrary choice to attempt to balance the amount of data used in each quartile with computational feasibility while allowing inference about trends. Quartiles were defined to result in four data sets with similar numbers of observations; numbers of herds or contemporary groups were not considered in determining quartile break points. Numbers of observations in each data set are given by quartile for each breed in Table 1. Means and standard deviations of observations are given by quartile for each breed in Table 2.

Pedigree data were included for animals born since 1970. Pedigree data was first reduced by eliminating all animals born before 1970. The remaining pedigree was reduced using an iterative process: parents or progeny without observations were removed from the pedigree if they did not contribute genetic ties between animals with observations.

Additional analyses of Holstein milk yield were conducted to evaluate the influence of time versus herd-year standard deviation on heritability estimates. These factors were partially confounded in the complete data set because of a trend of increasing standard deviation over time. Two subsets of data were created for this evaluation: the first included first lactations of cows born from 1970 to 1979, and the second was for first lactations of cows born from 1980 to 1989. Pedigree information for the two data sets was included for animals born since 1960 and 1970, respectively. The quartile divisions from the complete data set were used for these subsets so that the influence of time would be evaluated.

Parameter Estimation

Method R, a relatively new procedure that allows analysis of large data sets, was used for parameter estimation. Method R requires R values, which are regressions of predicted random effects that are calculated using complete data on predicted random effects that are calculated using random subsets of the same data. All R values will be 1, if the parameters are appropriate for the population.

The concept of Method R as a tool for variance component estimation originated when researchers used the regression of recent genetic evaluations on historical evaluations that were based on fewer data (14). The authors showed that if the parameters used in a genetic evaluation system were appropriate, then the regression had an expected value of 1. Reverter et al. (15) then suggested that this concept could be used to estimate parameters by calculating regressions for complete and random subsets of the data and by adjusting the appropriate parameter until the regressions = 1.

The main advantage of using Method R is that large data sets can be used for parameter estimation because the procedure is based on repeated solutions of standard

TABLE 2. Means and standard deviations in kilograms for total data sets and observations used in Method R heritability estimates for milk, fat, and protein yields by breed of dairy cattle.

Breed	Yield trait	Quartile set 1		2		3		4	
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Ayrshire	Milk	6064	1074	6323	1210	6816	1342	7367	1583
	Fat	235	43	246	48	265	52	286	62
	Protein	205	37	214	40	230	44	248	51
Brown Swiss	Milk	6670	1350	7258	1456	7666	1595	8189	1921
	Fat	269	58	291	62	308	66	327	79
	Protein	239	49	258	51	272	55	291	66
Guernsey	Milk	5352	1048	5763	1171	6191	1289	6783	1539
	Fat	243	49	260	53	280	57	305	66
	Protein	192	37	204	40	219	43	238	50
Holstein[1]	Milk	8258	1533	8989	1671	9511	1790	10,130	2001
	Fat	300	59	326	64	344	68	365	75
	Protein	261	47	284	51	301	54	321	60
Holstein[2]	Milk	8266	1524	9003	1673	9494	1791	10,104	1999
	Fat	300	59	326	64	343	68	364	75
	Protein	261	47	284	50	301	54	322	61
Jersey	Milk	5376	1100	5923	1223	6466	1311	6989	1525
	Fat	253	53	279	57	305	61	328	68
	Protein	204	40	224	44	245	47	265	54
Milking Shorthorn	Milk	5635	1138	6049	1301	6558	1411	7297	1866
	Fat	203	45	218	49	236	53	259	68
	Protein	191	36	203	42	218	45	242	59

[1] Complete data set.

[2] Mean of 25 random 5% subsets of the total Holstein data set.

mixed model equations. Additionally, standard errors and confidence intervals for heritability can be estimated using the Method R sample estimates of heritability (11). The disadvantage of this method is that extension to multiple random effects and multiple traits is difficult because constrained optimization is needed to obtain parameters that result in all regressions of 1. Estimation of parameters for data sets with as many as 4 million animals has been accomplished using Method R (12).

The model used for complete data analysis was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Zu} + \mathbf{e},$$

where $\mathbf{y}$ is an $n \times 1$ vector of observations (milk, fat, or protein yields), β is an $f \times 1$ vector of fixed effects, $\mathbf{u}$ is an $r \times 1$ vector of random effects, $\mathbf{e}$ is a vector of random residual effects, and $\mathbf{X}$ and $\mathbf{Z}$ are appropriately dimensioned incidence matrices. In this analysis, β included contemporary groups in a herd, and $\mathbf{u}$ included animal genetic effects. Standard assumptions were made about parameter means and variances:

$$\mathrm{E}\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{X}\beta\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix};\ \mathrm{Var}\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{Z'GZ} + \mathbf{R} & \mathbf{ZG} & \mathbf{R}\\ \mathbf{GZ'} & \mathbf{G} & \mathbf{0}\\ \mathbf{R} & \mathbf{0} & \mathbf{R}\end{bmatrix}.$$

For this analysis, $\mathbf{R} = \mathbf{I}\,\sigma_e^2$, $\mathbf{G} = \mathbf{A}\sigma_a^2$, and $\mathbf{A}$ = numerator relationship matrix describing genetic relationships among animals.

Solutions to the equations were obtained with mixed model equations of Henderson (5):

$$\begin{bmatrix}\mathbf{X'X} & \mathbf{X'Z}\\ \mathbf{Z'X} & \mathbf{Z'Z} + \mathbf{A}^{-1}\gamma\end{bmatrix}\begin{bmatrix}\hat{\beta}\\ \hat{\mathbf{u}}\end{bmatrix} = \begin{bmatrix}\mathbf{X'y}\\ \mathbf{Z'y}\end{bmatrix}, \qquad [1]$$

where $\gamma = \sigma_e^2/\sigma_a^2 = (1 - h^2)/h^2$.

Data subsets were chosen randomly with a chance of 0.5 that any observation would be included. Data in the subsets were adjusted for solutions of fixed effects from the complete data set prior to analysis. That is, subset data ($\mathbf{y}_s$) were randomly selected from $\mathbf{y} - \mathbf{X}\hat{\beta}$. Solutions for random effects ($\mathbf{u}_s$) for $\mathbf{y}_s$ were obtained as solutions to

$$[\mathbf{Z'}_s\mathbf{Z}_s + \mathbf{A}^{-1}\gamma]\hat{\mathbf{u}}_s = \mathbf{Z'}_s\mathbf{y}_s, \qquad [2]$$

where $\mathbf{Z}_s$ = incidence matrix relating animal effects to randomly selected observations.

Solutions to both sets of linear equations (i.e., [1] and [2]) were obtained using ITPACK (8, 9). Based on preliminary testing, the Jacobi conjugate gradient method was used. Because Method R requires fully converged solutions (I. Misztal, 1998, personal communication) a relatively stringent convergence criteria (8, 9) of 1.0×10^{-12} was used. Rounds of iteration required to achieve convergence generally ranged from 200 to 500 rounds for the full set of equations and from 100 to 400 for the equations of the data subset. Rounds of iteration that were required tended to decrease as the round of heritability update progressed.

Finally, the regression of estimates of random effects from complete data on estimates of those same effects from data subsets was calculated:

$$\text{R value} = \frac{\hat{\mathbf{u}}'\mathbf{A}^{-1}\hat{\mathbf{u}}_s}{\hat{\mathbf{u}}'_s\mathbf{A}^{-1}\hat{\mathbf{u}}_s}.$$

Based on the R value, a new proposed heritability was used to obtain new solutions for the random effects ($\mathbf{u}$ and $\mathbf{u}_s$), and the process was repeated until the R value was nearly 1.

Initial heritability was 0.25. If the resulting R value was >1, a proposed heritability of 0.5 was used; otherwise, a value of 0.125 was used. After the second round, linear prediction of proposed heritability based on the last two rounds was used to obtain the heritability where the R value would be 1. Convergence for the R value was declared with a difference of $<1.0 \times 10^{-8}$. Convergence was usually achieved in 6 to 8 rounds of iterative updating of heritability.

For Holsteins, 25 distinct, complete data sets were generated containing approximately 5% of the observations, and then the Method R algorithm was applied to these data in which a random half of the data was selected for the subset solutions. For all other breeds, the complete data file used for Method R included all data that passed edits, and the Method R algorithm was applied to these data sets 25 times. Each time a different randomly selected subset of the complete data was used.

Repeatability (i.e., the fraction of variance accounted for by genetic, herd-sire interaction, and permanent environmental effects) was estimated using MTDFREML (3). This analysis assumed cows as the only random source of variation and again fit contemporary groups as fixed effects. Cow effects were assumed to be uncorrelated. Fraction of variance explained by cows in this model provided an estimate of repeatability.

RESULTS AND DISCUSSION

Results discussed excluded parameter estimates for Milking Shorthorn because of small sample sizes; results from Holstein and Jersey were of primary interest. Estimated heritabilities ranged from 0.18 to 0.51 (0.26 to 0.48 for Holsteins and Jerseys, Table 3). In general, heritability estimates increased with herd-year standard deviation. Trait and breed combinations without strong evidence of increasing trend included Guernsey fat and protein yields and Holstein fat yield. Mean (across breeds) heritability estimates by quartile set were 0.29, 0.33, 0.39, and 0.46 for milk yield; 0.30, 0.33, 0.33, and 0.37 for fat yield; and 0.25, 0.32, 0.30, and 0.35 for protein yield. These heritability estimates were larger than those in a number of studies (2, 10, 16); however, these studies included data other than first lactation records, which could result in lower heritability estimates. These results agree with studies in which data were limited to first lactation records (17, 18, 20, 21, 22), and parameters were within the range used in most national dairy cattle evaluations (7). Additionally, heritability estimates were consistently greater from Jersey data than from Holstein data, which was consistent with results from Lofgren et al. (10). One possible reason for larger heritabilities for Jersey data compared with Holstein data could be a greater percentage of registered cattle (13), which may result in more accurate and complete animal identification.

Estimated heritability and standard errors of estimates for milk yield of Holsteins for data split by time were compared with results from the complete data set (Table 4). Because the estimates showed no evidence of time differences, heritability changes over time can be considered only as a function of herd-year standard deviation; evidence for additional time trend was not found.

Repeatability estimates were calculated only for milk yield of Holsteins. Estimates were 0.495, 0.499, 0.505, and 0.494 by quartile set. Approximate standard errors were ≤ 0.006. Thus, no evidence existed for increasing heritability to be associated with reduced residual variance. The change in heritability must be associated with other effects in the model. That is, heritability increases must correspond to decreases in fraction of variance associated with herd-sire interaction or permanent environmental effects.

Changes Made in USDA-DHIA Genetic Evaluation

The results of this study have brought about modifications to the procedure used in the USDA-DHIA genetic evaluation. Average heritability for animals was increased from 0.25 to 0.30 for all breeds with an allowable range from 0.25 to 0.35, based on herd-year standard deviation, using the procedure described by Wig-

TABLE 3. Means of heritability estimates for first lactation milk, fat, and protein yields with maximum estimated standard deviations by breed of dairy cattle from 25 Method R samples.

Breed	Yield trait	Maximum SD	Quartile set 1	2	3	4
Ayrshire	Milk	0.07	0.25	0.28	0.35	0.44
	Fat	0.07	0.27	0.30	0.30	0.38
	Protein	0.07	0.25	0.32	0.29	0.40
Brown Swiss	Milk	0.06	0.29	0.34	0.41	0.48
	Fat	0.08	0.28	0.39	0.38	0.46
	Protein	0.08	0.23	0.35	0.39	0.43
Guernsey	Milk	0.05	0.25	0.37	0.43	0.51
	Fat	0.04	0.30	0.30	0.33	0.42
	Protein	0.04	0.18	0.32	0.34	0.43
Holstein	Milk	0.03	0.32	0.34	0.36	0.40
	Fat	0.03	0.35	0.34	0.33	0.36
	Protein	0.03	0.25	0.28	0.30	0.36
Jersey	Milk	0.02	0.38	0.41	0.45	0.48
	Fat	0.02	0.31	0.36	0.35	0.37
	Protein	0.02	0.32	0.34	0.38	0.42
Milking Shorthorn	Milk	0.13	0.21	0.16	0.37	0.61
	Fat	0.12	0.18	0.23	0.37	0.63
	Protein	0.12	0.16	0.17	0.38	0.57

gans and VanRaden (24). The estimates of repeatability did not support any change from its current value of 0.55. However, repeatability is the sum of heritability, the proportion of variation due to the interaction of sire and herd (i.e., the environmental correlation between daughters of a sire in the same herd), and the proportion of variation due to permanent environment. To allow heritability to increase to 0.30 while repeatability remained at 0.55, the proportion of overall variation was reduced from 0.14 to 0.10 for herd-sire interaction and from 0.16 to 0.15 for permanent environment. The proportion of variation attributed to herd-sire interaction and permanent environmental effects were somewhat arbitrary. While little evidence exists for true herd-sire interaction, it was included to minimize the potential impact of any single herd on the genetic evaluation of a bull (23). Dimov et al. (4) found that using a herd by sire interaction effect that accounted for a larger fraction of the variance than estimated from data caused reranking of PTA, but the impact on average breeding values of selected animals and genetic improvement was quite small.

The increase in heritability for yield traits in the genetic evaluation also increased the emphasis on performance of an animal relative to information from relatives. This increased emphasis on performance was expected to cause large deviations from management group averages to have a greater impact on genetic evaluations. To limit this impact, deviations were restricted to within ±4 herd-year standard deviations from the management group average while the previous practice was continued of imposing a lower limit for deviations of half of the management group average. Such large deviations might be due to many causes including illness, data error, or preferential treatment. Deviations larger than 4 herd-year standard deviations are expected to be extremely rare if data are assumed to be distributed normally.

To determine the impact of these changes on the genetic evaluations, evaluations for May 1997 were recal-

TABLE 4. Means and estimated standard deviations of heritability estimates for first lactation milk yield for Holsteins from 25 Method R samples.

Analysis data[1]	Quartile set 1		2		3		4	
	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
Complete (1980–1997)	0.32	0.03	0.34	0.03	0.36	0.03	0.40	0.03
Early (1970–1979)	0.33	0.03	0.33	0.06	0.31	0.05	0.35	0.07
Late (1980–1989)	0.33	0.03	0.34	0.03	0.35	0.04	0.41	0.03

[1] Dates in parentheses indicate birth years for cows with first lactations included in analysis.

culated using the new heritability estimates and yield deviation limitations. Results from these evaluations indicated that the impact of these changes was not dramatic. Predicted transmitting abilities from the two evaluations were similar for most AI bulls. Correlations of PTA exceeded 0.99 for all birth years, and the correlation was 0.998 across birth years.

The effect of the system changes on bull evaluations as they progressed to include second-crop daughter data also was examined. Changes in PTA for protein were compared for the new and previous evaluation systems. Data were from May 1997 evaluations for PTA for Holstein cows that freshened before January 1, 1993. Evaluations based on first-crop daughters included data from at least 10 but not more than 500 daughters. Evaluations based on first- and second-crop daughters had to have an increase in reliability of at least 0.09 between the two evaluations. A total of 263 Holstein bulls met these criteria. Correlations between first-crop PTA and PTA that also included second-crop daughter data were larger for the new system than for the previous system.

Evaluations for Holstein AI bulls from August 1997 (after system changes) were compared with May 1997 evaluations (before system changes) for those bulls. The increase in heritability caused the average reliability to increase by 0.04. The increase in heritability also resulted in an increase in variation among evaluations. For bulls born in 1990 or later, the standard deviations of milk, fat, and protein PTA for bulls with 100 daughters or less in August were 5% larger than were the standard deviations for bulls with 100 daughters or less in May. For 543 bulls in active AI service after May 1997, the average PTA in August declined slightly from the May averages: 3.5 kg of milk, 0.28 kg of fat, and 0.23 lb of protein.

CONCLUSIONS

Parameter estimates obtained using Method R provided evidence for heritability greater than that used in the USDA-DHIA genetic evaluation system. Based on these parameter estimates, changes were implemented and tested in the USDA-DHIA genetic evaluation system. The most significant changes were to increase average heritability from 0.25 to 0.30 and to truncate extreme deviations of cows. These changes in the genetic evaluation system resulted in relatively small changes in PTA, but comparisons of evaluations with and without changes indicated that the changes improved accuracy. Increased heritability in the genetic evaluation system primarily affected young sires and resulted in these sires having more extreme PTA with the same number of daughters. In addition, reliabilities increased for the same number of daughters. One potential impact is an increased rate of genetic improvement as these high genetic merit bulls are identified and used as service sires earlier.

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