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P. R. N. Rorato
*University of Nebraska-Lincoln*

Jeffrey F. Keown
*University of Nebraska-Lincoln*, jkeown1@unl.edu

L. Dale Van Vleck
*University of Nebraska-Lincoln*, dvan-vleck1@unl.edu

# Variance Caused by Cytoplasmic Line and Sire by Herd Interaction Effects for Milk Yield Considering Estimation Bias[1]

**P.R.N. RORATO,*,[2] J. F. KEOWN,* and L. D. VAN VLECK†**
*Department of Animal Science, University of Nebraska, Lincoln 68583-0908
†Roman L. Hruska US Meat Animal Research Center, ARS, USDA, Lincoln, NE 68583-0908

## ABSTRACT

A total of 138,869 lactation milk yields (305 d, milked twice daily, mature equivalent) from the first three parities of 68,063 New York Holstein cows were used to estimate variance components that were due to additive direct genetic effects, cow permanent environmental effects (cow within sire for sire model), sire by herd interaction effects, and cytoplasmic line effects. The original data were assigned to 10 random samples, which were each analyzed using an animal model and a sire model. From each sample of original data, 20 other samples were analyzed with levels assigned randomly to cytoplasmic and interaction effects (data with randomly simulated levels). Ten of those samples were analyzed with an animal model and 10 with a sire model. The models also included fixed effects of herd-year-seasons. For the animal model and sire model, average fractions of phenotypic variance and average standard errors were, respectively, for additive direct genetic effects 0.300 (0.029) and 0.228 (0.040) for original data and 0.325 (0.025) and 0.262 (0.039) for data with randomly simulated levels. For cow permanent environmental effects the respective averages were 0.242 (0.024) and 0.444 (0.014) for original data and 0.235 (0.025) and 0.492 (0.016) for data with randomly simulated levels. The averages for sire by herd interaction effects were 0.015 (0.008) and 0.018 (0.007) for original data and 0.003 (0.007) and 0.004 (0.009) for data with randomly simulated levels. For cytoplasmic line effects, the respective averages were 0.011 (0.007) and 0.043 (0.008) for original data and 0.003 (0.006) and 0.003 (0.007) for data with randomly simulated levels. The differences between estimates of variance components for original data and data with randomly simulated levels suggest that estimates of fractions of total variance caused by sire by herd interaction and cytoplasmic effects estimated with REML may be biased upward by 0.003 to 0.004.

(**Key words**: genetic parameters, Holsteins, REML, milk yield)

**Abbreviation key**: **OD** = original data.

## INTRODUCTION

A successful breeding program depends, for a large part, on accurate evaluation of genotypes of animals utilized as parents of the next generation, and accurate genetic evaluation depends on the model utilized for analysis of the data. According to Southwood et al. (18), the genetic models underlying performance traits are not fully understood. Traits are generally assumed to be under the control of many genes, each with small additive effects. Analyses with more complex models, including effects of dominance, epistasis, and maternal genetics, have often been prohibited by computational constraints.

The current model for genetic evaluation in the United States accounts only for additive effects of nuclear genes and, therefore, considers the genetic relationships between sires and their offspring and between dams and their offspring to be equivalent. This assumption results in a statistical model that is more operational but possibly less valid than one that considers other genetic effects (6).

Van Vleck and Bradford (20) obtained higher heritability coefficients with the daughter-dam regression method than with the paternal half-sib correlation method for milk yield. They hypothesized that the larger estimate from daughter-dam regression may be due to genetic maternal effects. Milk yield, intrauterine environment, and mothering ability in mammals are common components of maternal effects, which may be both genetically and environmentally determined (17). According to Wagner (22), another possible source of maternal effects are cytoplasmic effects, especially mitochondrial DNA, which is maternally transmitted. Mitochondria contain their own DNA with inheritance almost exclu-

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[2]Permanent address: Departamento de Zootecnia, Universidade Federal de Santa Maria (UFSM) 97119-900 Santa Maria, RS, Brazil.

sively from the female parent providing a possible mechanism of cytoplasmic inheritance (13).

Bell et al. (4) reported that maternally transmitted cytoplasmic effects appeared to influence production traits of Holsteins from North Carolina. Kennedy (14), using simulated data, concluded that such estimates of relative variance due to cytoplasmic effects could be due to random genetic drift. Southwood et al. (18) and Salehi and James (16), using simulated data, showed that in the presence of cytoplasmic or maternal effects estimates of variance due to other effects were biased unless the correct model was used. Schutz et al. (17), using a least squares analyses, found significant maternal lineage effects for milk yield that explained 4.1 and 3.8% of the total variation for first and second lactations of Holstein cows, respectively. However, with an animal model, the same authors found the contribution of maternal lineage to total variance to be nearly 0 for yield traits. Albuquerque et al. (2), in a study of the three first lactations of New York Holstein cows, concluded that cytoplasmic effects were responsible for approximately 1% of the phenotypic variance in milk and fat yields. Boettcher et al. (7), with pooled data of Holstein cows from Iowa and North Carolina, concluded that differences between maternal lineages for yield traits were not significant.

Gibson et al. (12) concluded that the predicted breeding values of progeny tested sires would be only slightly affected by the presence of mitochondrial effects. However, Boettcher et al. (6) suggested that progeny testing programs could be decreased in size by up to 8% by correctly accounting for cytoplasmic effects and by not sampling sons of dams with predicted breeding values biased upward by favorable cytoplasmic effects. Gibson et al. (12) further stated that when selecting dams of commercial cows, the relevant genetic merit should be the sum of the additive and cytoplasmic genetic components. The effects on accuracy of this selection failing to allow for cytoplasmic effects in genetic evaluation does not appear to have been investigated. If maternal lineage effects are substantial, then ignoring them in a national genetic evaluation will decrease selection accuracy. Accurate estimates of the fractions of variance that are due to effects of maternal lineage are needed to assess the potential impact on genetic evaluation (12). Later Boettcher and Gibson (5) concluded from analyses of a large set of records that maternal lineage variance was less than 0.5% of the total variance for all traits studied, a fraction which would have no appreciable effect on estimates of breeding value.

The objectives of this study were 1) to estimate the importance of bias from REML on estimates of variances that were due to effects such as cytoplasmic line and sire by herd interaction for milk yield, which also tend to have relatively small effects on total variance [e.g., Dimov et al. (9)]; 2) to compare animal and sire models; and 3) to compare the standard errors of estimates of relative variance calculated from an average information matrix algorithm [Dodenhoff et al. (10)] with empirical standard errors calculated from estimates from 10 samples.

## MATERIAL AND METHODS

The data were 138,869 lactation milk yields (adjusted to 305 DIM, mature equivalent, and milked twice daily) and comprised the first three lactations of 68,063 Holstein cows in New York freshening from 1980 through 1991. The data were those used by Albuquerque et al. (2) who described how cytoplasmic line was determined and who had assigned the data randomly to 10 samples (original data = **OD**) based on the herd code. The summary of the samples is presented in Table 1.

The 10 OD samples were analyzed using an animal and a sire model, and for each OD, 20 other samples were simulated (with levels assigned randomly to certain effects): 10 to be analyzed with an animal model and 10 with a sire model. The data sets with simulated levels resulted from substituting randomly assigned levels to the records in place of the actual sire by herd combinations and cytoplasmic lines. The random levels were obtained from a uniform distribution bounded by 1 and the number of actual levels. All records of a cow were assigned the same random level for cytoplasmic line and sire by herd interaction effects. Because of the sampling procedure, the numbers of levels randomly assigned were slightly less than the actual number of levels. The number of records and animals were the same as for the OD.

The data were analyzed using a derivative-free algorithm (MTDFREML) developed by Boldman et al. (8) but with modifications developed by Dodenhoff et al. (10) to obtain standard errors of estimates of relative variance at convergence. The animal model used was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{Ps} + \mathbf{Dc} + \mathbf{Wp} + \mathbf{e}$$

were **y** = vector of observations, **b** = vector of fixed effects of herd-year-seasons, **g** = vector of additive direct genetic random effects of animal for the animal model (and is the transmitting ability or one-half additive genetic value of the sire for the sire model), **s** = vector of random sire by herd interaction effects, **c** = vector of random cytoplasmic line effects, **p** = vector of

TABLE 1. A summary of the structure of data for analyses of 10 samples of milk yield each with 10 samples with simulated levels for sire by herd (SH) combinations and cytoplasmic lines.

| Sample | Records | Animals | HYS[1] | $\bar{X}$[2] | SH-L[3] | | | DL-L[4] | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | OD | AM | SM | OD | AM | SM |
| | (no.) | | | | (no.) | | | | | |
| 1 | 13,454 | 6463 | 1419 | 8960 | 2446 | 2243 | 2227 | 1768 | 1678 | 1684 |
| 2 | 16,637 | 7704 | 1848 | 8975 | 3186 | 2785 | 2784 | 2428 | 2193 | 2203 |
| 3 | 13,465 | 6647 | 1351 | 8993 | 2537 | 2319 | 2323 | 2082 | 1918 | 1920 |
| 4 | 12,320 | 6127 | 1519 | 8985 | 2490 | 2244 | 2228 | 1925 | 1784 | 1805 |
| 5 | 14,001 | 6790 | 1454 | 9116 | 2589 | 2344 | 2344 | 1788 | 1718 | 1718 |
| 6 | 12,819 | 6578 | 1410 | 9301 | 2588 | 2317 | 2322 | 2184 | 1996 | 1999 |
| 7 | 13,548 | 6542 | 1379 | 9035 | 2539 | 2305 | 2296 | 1638 | 1540 | 1544 |
| 8 | 11,760 | 5678 | 1292 | 8844 | 2196 | 1988 | 1981 | 1692 | 1594 | 1598 |
| 9 | 16,563 | 8023 | 1908 | 8960 | 3105 | 2811 | 2811 | 2541 | 2380 | 2372 |
| 10 | 15,302 | 7501 | 1714 | 9043 | 3004 | 2709 | 2711 | 2214 | 2090 | 2091 |
| $\bar{X}$ | 13,987 | 6806 | 1529 | 9021 | . . . | 2407 | 2403 | . . . | 1889 | 1939 |
| Minimum[5] | | | | | | 1976 | 1967 | | 1517 | 1534 |
| Maximum[5] | | | | | | 2878 | 2874 | | 2400 | 2836 |

[1]Number of herd-year-seasons.

[2]Means for milk yield (kilograms).

[3]Number of levels of SH effects (SH-L) for sample using original data (OD) and mean number for 10 simulated samples for animal model (AM) and sire model (SM).

[4]Number of levels of dam lines (DL-L) for sample using OD and mean number for 10 simulated samples for AM and SM.

[5]Minimum and maximum levels from 100 simulated samples for AM and SM.

random permanent environmental effects associated with cows for the animal model (and is the cow within sire effect for the sire model), **e** = vector of residual random effects, and **X**, **Z**, **P**, **D**, and **W** = incidence matrices that associate the appropriate effects to **y**. For this model, the expectation of **y** is **Xb**, and the expectations of **g**, **s**, **c**, **p**, and **e** are null vectors. The variances are, respectively, $\mathbf{A}\sigma_g^2$, $I_S\sigma_s^2$, $I_C\sigma_c^2$, $I_P\sigma_p^2$, and $I_N\sigma_e^2$, where S, C, P, and N are the number of sire by herd combinations, maternal lines, cows with records, and records, respectively, and **A** is the matrix of relationships for the animal model. For the sire model, the sires were assumed to be uncorrelated, which is common with sire models even though a slight increase in estimates of heritability is likely when relationships among sires are considered [e.g., (11, 21)].

The convergence criterion chosen for stopping the search procedure of the simplex algorithm of MTDFREML was when the variance of –2 log likelihoods in the simplex was less than $10^{-6}$. At apparent convergence, the program was restarted to guard against local rather than global minimization.

The standard errors of the parameter estimates were calculated at convergence from the average information matrix [Dodenhoff et al. (10)] for all analyses. For comparison, empirical standard errors were calculated from the 10 sample estimates of the original data.

## RESULTS AND DISCUSSION

Averages of variance components expressed as ratios to phenotypic variance for both the animal and sire models are presented in Tables 2 and 3; the estimates for data with randomly simulated levels analyses from OD are for the same sample. The averages (Table 4) for estimates of proportion of variance due to additive direct genetic effects (and standard errors) for the observed data were 0.300 (0.029) and 0.233 (0.040) and for the simulated data were 0.325 (0.025) and 0.259 (0.039) for animal and sire models, respectively. The sire components of variance were multiplied by four and divided by the sum of variance components to obtain heritability estimates. The average estimates of heritability obtained with the animal model were greater than those obtained with the sire model (Table 4) for both the original and simulated data, which is probably because of selection effects on sires. For the observed data, the estimates of heritability by sample ranged from 0.240 (0.027) to 0.340 (0.031) for the animal model (Table 2) and 0.168 (0.036) to 0.288 (0.040) for the sire model (Table 3). For the averages of 10 analyses of simulated data of each OD set, the range was from 0.292 (0.023) to 0.351 (0.026) for the animal model

TABLE 2. Estimates of phenotypic variance and fractional components of variance[1] and their standard errors for milk yield using an animal model for 10 samples of the original data (OD) and for the corresponding means from 10 sets of simulated levels (SL).

| Sample | Data | $g^2$ | | $pe^2$ | | $sh^2$ | | $c^2$ | | $e^2$ | | $\sigma^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | |
| 1 | OD | 0.310 | 0.028 | 0.220 | 0.023 | 0.012 | 0.009 | 0.015 | 0.008 | 0.450 | 0.010 | 1743 |
| | SL | 0.340 | 0.025 | 0.209 | 0.025 | 0.002 | 0.008 | 0.002 | 0.007 | 0.442 | 0.010 | 1748 |
| 2 | OD | 0.320 | 0.027 | 0.250 | 0.023 | 0.024 | 0.009 | 0.007 | 0.007 | 0.400 | 0.009 | 1723 |
| | SL | 0.324 | 0.024 | 0.246 | 0.024 | 0.004 | 0.008 | 0.004 | 0.007 | 0.400 | 0.009 | 1722 |
| 3 | OD | 0.290 | 0.029 | 0.270 | 0.024 | 0.016 | 0.009 | 0.006 | 0.009 | 0.420 | 0.010 | 1636 |
| | SL | 0.310 | 0.025 | 0.265 | 0.025 | 0.003 | 0.008 | 0.000 | 0.000 | 0.420 | 0.009 | 1635 |
| 4 | OD | 0.290 | 0.031 | 0.240 | 0.025 | 0.008 | 0.009 | 0.017 | 0.010 | 0.440 | 0.010 | 1769 |
| | SL | 0.325 | 0.026 | 0.229 | 0.027 | 0.005 | 0.009 | 0.002 | 0.008 | 0.440 | 0.010 | 1774 |
| 5 | OD | 0.270 | 0.028 | 0.250 | 0.023 | 0.019 | 0.009 | 0.032 | 0.010 | 0.430 | 0.010 | 1643 |
| | SL | 0.330 | 0.025 | 0.229 | 0.025 | 0.007 | 0.008 | 0.005 | 0.006 | 0.430 | 0.010 | 1649 |
| 6 | OD | 0.340 | 0.031 | 0.220 | 0.025 | 0.005 | 0.009 | 0.006 | 0.010 | 0.430 | 0.010 | 1909 |
| | SL | 0.351 | 0.026 | 0.207 | 0.026 | 0.003 | 0.008 | 0.004 | 0.008 | 0.430 | 0.010 | 1912 |
| 7 | OD | 0.330 | 0.028 | 0.230 | 0.023 | 0.018 | 0.009 | 0.000 | 0.000 | 0.430 | 0.010 | 1724 |
| | SL | 0.331 | 0.024 | 0.236 | 0.024 | 0.003 | 0.008 | 0.000 | 0.000 | 0.430 | 0.010 | 1722 |
| 8 | OD | 0.330 | 0.030 | 0.210 | 0.025 | 0.011 | 0.009 | 0.000 | 0.000 | 0.440 | 0.011 | 1671 |
| | SL | 0.340 | 0.026 | 0.211 | 0.027 | 0.003 | 0.009 | 0.003 | 0.008 | 0.440 | 0.011 | 1671 |
| 9 | OD | 0.280 | 0.026 | 0.280 | 0.022 | 0.007 | 0.007 | 0.006 | 0.008 | 0.420 | 0.009 | 1663 |
| | SL | 0.292 | 0.023 | 0.278 | 0.023 | 0.000 | 0.000 | 0.004 | 0.007 | 0.423 | 0.009 | 1667 |
| 10 | OD | 0.240 | 0.027 | 0.250 | 0.022 | 0.025 | 0.009 | 0.022 | 0.009 | 0.460 | 0.010 | 1777 |
| | SL | 0.292 | 0.023 | 0.243 | 0.024 | 0.003 | 0.008 | 0.008 | 0.007 | 0.460 | 0.010 | 1779 |
| Minimum[2] | | 0.280 | 0.022 | 0.200 | 0.024 | 0.000 | 0.000 | 0.000 | 0.000 | 0.400 | 0.009 | |
| Maximum[3] | | 0.360 | 0.026 | 0.290 | 0.023 | 0.023 | 0.008 | 0.016 | 0.009 | 0.460 | 0.010 | |

[1]$g^2$ = Genetic effects, $pe^2$ = permanent environmental effects, $sh^2$ = sire by herd interaction, $c^2$ = cytoplasmic line, $e^2$ = temporary environmental effects, and $\sigma^2$ = phenotypic variance ($kg^2/1000$).

[2]Minimum and maximum from 100 analyses of simulated data.

(Table 2) and 0.204 (0.036) to 0.340 (0.040) for the sire model (Table 3). These estimates are similar to those reported previously [e.g., (1, 9, 15, 19, 20, 22)]. Albuquerque et al. (2), from analyses of the same 10 OD sets used in this study, obtained estimates from 0.278 to 0.326 with an average of 0.298 using different animal models.

The averages (Table 4) for estimates of the proportions of phenotypic variance that were due to random permanent environmental effects of cows and due to cow within-sire effects were 0.242 and 0.444 for OD and 0.235 and 0.492 for the simulated data of the animal and sire models, respectively. The estimates ranged from 0.210 to 0.280 and from 0.400 to 0.490 for OD and from 0.207 to 0.278 and from 0.474 to 0.509 for the averages of samples of simulated data for the animal and sire models, respectively.

The averages for estimates of the variance of sire by herd interaction effects as a fraction of total phenotypic variance were 0.015 (0.008) for the animal model and 0.018 (0.007) for the sire model for OD and 0.003 for the animal model and 0.004 for the sire model for the simulated data (Tables 2 and 3), which were five to six times greater for OD than for the simulated data, respectively. For the observed data, the fractional estimates ranged from 0.005 to 0.025 for the animal model and from 0.011 to 0.068 for the sire model and for the simulated data ranged from 0 to 0.004 for the animal model and 0.002 to 0.004 for the sire model (Tables 2 and 3). These results are similar to those of Dimov et al. (9), who from analysis of data from California, New York, and Pennsylvania, reported relative estimates of 1.5% for the first lactation and 1.9% when considering all lactations, and of Albuquerque et al. (2), who reported estimates ranging from 1.6 to 1.8%. With a sire model, Banos and Shook (3) reported estimates of 1.84, 2.11, and 3.0%, respectively, for the first, second, and third lactations, which are greater than the estimates obtained for the current study.

The averages for variance due to cytoplasmic line effects as a fraction of phenotypic variance for the observed data were 0.011 (0.007) for the animal model and 0.043 (0.008) for the sire model and for the simulated data were 0.003 (0.006) for the animal model and 0.003 (0.007) for the sire model (Table 4). The average estimate was three times greater for the sire model than for the animal model for the observed

TABLE 3. Estimates of phenotypic variance and fractional components of variance[1] and their standard errors for milk yield using a sire model for 10 samples of the original data (OD) and for the means from 10 sets of simulated levels (SL).

| Sample | Data | $s^2$ | | $(c/s)^2$ | | $sh^2$ | | $c^2$ | | $e^2$ | | $\sigma^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | $\overline{X}$ | SE | |
| 1 | OD | 0.056 | 0.011 | 0.420 | 0.014 | 0.024 | 0.011 | 0.050 | 0.009 | 0.450 | 0.010 | 1731 |
| | SL | 0.067 | 0.010 | 0.474 | 0.016 | 0.005 | 0.009 | 0.004 | 0.007 | 0.450 | 0.010 | 1730 |
| 2 | OD | 0.072 | 0.010 | 0.450 | 0.014 | 0.028 | 0.010 | 0.050 | 0.009 | 0.400 | 0.009 | 1712 |
| | SL | 0.085 | 0.010 | 0.509 | 0.015 | 0.004 | 0.009 | 0.002 | 0.007 | 0.400 | 0.009 | 1712 |
| 3 | OD | 0.060 | 0.011 | 0.440 | 0.015 | 0.017 | 0.010 | 0.063 | 0.010 | 0.420 | 0.009 | 1633 |
| | SL | 0.073 | 0.011 | 0.504 | 0.016 | 0.001 | 0.009 | 0.002 | 0.008 | 0.420 | 0.009 | 1630 |
| 4 | OD | 0.061 | 0.010 | 0.420 | 0.016 | 0.011 | 0.010 | 0.068 | 0.010 | 0.440 | 0.010 | 1759 |
| | SL | 0.065 | 0.010 | 0.488 | 0.017 | 0.004 | 0.010 | 0.002 | 0.008 | 0.441 | 0.010 | 1752 |
| 5 | OD | 0.063 | 0.009 | 0.480 | 0.013 | 0.000 | 0.000 | 0.017 | 0.005 | 0.440 | 0.009 | 1601 |
| | SL | 0.058 | 0.009 | 0.494 | 0.015 | 0.004 | 0.008 | 0.004 | 0.007 | 0.440 | 0.009 | 1618 |
| 6 | OD | 0.059 | 0.010 | 0.480 | 0.015 | 0.000 | 0.000 | 0.011 | 0.006 | 0.450 | 0.010 | 1854 |
| | SL | 0.061 | 0.010 | 0.492 | 0.017 | 0.004 | 0.009 | 0.003 | 0.008 | 0.440 | 0.010 | 1883 |
| 7 | OD | 0.042 | 0.009 | 0.430 | 0.014 | 0.051 | 0.012 | 0.047 | 0.009 | 0.430 | 0.010 | 1704 |
| | SL | 0.051 | 0.009 | 0.504 | 0.015 | 0.004 | 0.009 | 0.002 | 0.006 | 0.439 | 0.010 | 1691 |
| 8 | OD | 0.053 | 0.011 | 0.430 | 0.015 | 0.020 | 0.011 | 0.047 | 0.009 | 0.450 | 0.011 | 1649 |
| | SL | 0.060 | 0.010 | 0.483 | 0.017 | 0.003 | 0.009 | 0.004 | 0.008 | 0.450 | 0.011 | 1645 |
| 9 | OD | 0.069 | 0.009 | 0.490 | 0.012 | 0.000 | 0.000 | 0.011 | 0.005 | 0.430 | 0.009 | 1641 |
| | SL | 0.070 | 0.009 | 0.496 | 0.015 | 0.004 | 0.008 | 0.002 | 0.007 | 0.428 | 0.009 | 1657 |
| 10 | OD | 0.047 | 0.009 | 0.400 | 0.014 | 0.029 | 0.009 | 0.064 | 0.009 | 0.460 | 0.010 | 1771 |
| | SL | 0.058 | 0.009 | 0.477 | 0.015 | 0.002 | 0.008 | 0.003 | 0.007 | 0.460 | 0.010 | 1759 |
| Minimum[2] | | 0.050 | 0.009 | 0.460 | 0.016 | 0.000 | 0.000 | 0.000 | 0.000 | 0.400 | 0.009 | |
| Maximum[3] | | 0.080 | 0.010 | 0.520 | 0.016 | 0.019 | 0.009 | 0.068 | 0.010 | 0.460 | 0.010 | |

[1]$s^2$ = Sire transmitting ability, $(c/s)^2$ = cow within sire for sire model, $sh^2$ = sire by herd interaction, $c^2$ = cytoplasmic line, $e^2$ = temporary environmental effects, and $\sigma^2$ = phenotypic variance ($kg^2/1000$).

[2]Minimum and maximum from 100 analyses of simulated data.

data but was the same for the simulated data. For 7 of 10 OD sets, the fraction of variance that was due to cytoplasmic line effects was from 5 to 6% for the sire model (Table 3). The reason for the higher estimate with a sire model may be due to not considering relationships among cows. Estimates ranged from 0.000 to 0.032 for the animal model and from 0.011 to 0.068 for the sire model for the observed data. For the simulated data, estimates were from 0.000 to 0.004 for the animal model and 0.002 to 0.004 for the sire model (Tables 2 and 3). The average estimate for the observed data with the animal model is the same as the average obtained by Albuquerque et al. (2) for the same data set, using six different animal models. This result is similar to other reports (14, 18) but does not agree with the report of Schutz et al. (17), who reported variance of cytoplasmic line effects equal to 0 for milk yield. The estimate (4.3%) from the observed data with the sire model is almost four times greater than that obtained with the animal model and more than three times greater than the highest estimate reported for milk yield based on the animal model. The estimates of 0.3% for the simulated data using both animal and sire models appear to agree with Gibson et al. (12) that the limit for the cytoplasmic line effect contribution for total variance is about 0.5%. However, standard errors that are higher than the estimate for the parameter suggest that estimates will not be consistently near 0.5%.

The estimates of the proportion of variance due to residual effects relative to the phenotypic variance were similar for observed and simulated data and for animal and sire models as were estimates of phenotypic variance (Tables 2, 3, and 4).

The average standard errors obtained from the average information matrix (Table 4) were, for practical purposes, generally similar to the empirical standard errors calculated from the 10 samples for the original data analyses. The average standard errors obtained from the average information matrix were similar for the original and simulated data.

## CONCLUSIONS

The difference between estimates from analyses with original data and with simulated assignment of levels of cytoplasmic and interaction effects suggests for effects with relatively small variance that the upward bias that was due to REML estimates being

TABLE 4. Mean fractions[1] of phenotypic variance with mean asymptotic standard errors of average information matrix and mean empirical standard errors (ESE) from 10 samples of original data for both animal (AM) and sire (SM) models.

| | | Original data | | | Data with simulated levels | |
|---|---|---|---|---|---|---|
| Fraction | Model | Average | SE | ESE | Average[2] | SE[2] |
| $g^2$ | AM | 0.300 | 0.029 | 0.032 | 0.325 | 0.025 |
| $4s^2$ | SM | 0.233 | 0.040 | 0.028 | 0.259 | 0.039 |
| $pe^2$ | AM | 0.242 | 0.024 | 0.023 | 0.235 | 0.025 |
| $(c/s)^2$ | SM | 0.444 | 0.014 | 0.030 | 0.492 | 0.016 |
| $sh^2$ | AM | 0.015 | 0.008 | 0.007 | 0.003 | 0.007 |
| | SM | 0.018 | 0.007 | 0.016 | 0.004 | 0.009 |
| $c^2$ | AM | 0.011 | 0.007 | 0.010 | 0.003 | 0.006 |
| | SM | 0.043 | 0.008 | 0.022 | 0.003 | 0.007 |
| $e^2$ | AM | 0.432 | 0.010 | 0.017 | 0.432 | 0.010 |
| | SM | 0.437 | 0.010 | 0.018 | 0.447 | 0.010 |
| $\sigma^2$ | AM | 1726 | | | 1728 | |
| | SM | 1706 | | | 1708 | |

[1]$g^2$ = Genetic effects, $s^2$ = sire transmitting ability, $pe^2$ = permanent environmental effects, $(c/s)^2$ = cow within sire, $sh^2$ = sire by herd interaction, $c^2$ = cytoplasmic line, $e^2$ = temporary environmental effects, and $\sigma^2$ = phenotypic variance ($kg^2/1000$).

[2]Average of 100 samples with simulated levels.

forced to be positive may be 0.3 to 0.4% of total variance.

The fractional estimate for variance of cytoplasmic effects with a sire model was almost four times greater than with an animal model, which may indicate an inadequacy of the sire model to separate cytoplasmic from other effects. The estimate of either the fraction of variance due to cytoplasmic effects (1.1%) or the fractional variance adjusted for a bias of 0.3% suggests that cytoplasmic effects with an animal model are not an important source of variation for milk yield. The random assignment of levels to cytoplasmic and interaction effects, however, increased the estimate of additive genetic variance with no reduction in variance caused by temporary environmental effects. This increase indicates that variance caused by cytoplasmic or sire by herd interaction effects is partitioned to the component associated with additive genetic effects.

The technique of sampling the data seems to give standard errors of fractional variance that are of similar magnitude to standard errors obtained from the average information matrix.

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