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T. H. Short
Cornell University

R. W. Blake
Cornell University

R. L. Quaas
Cornell University

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

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Short, T. H.; Blake, R. W.; Quaas, R. L.; and Van Vleck, L. Dale, "Heterogeneous Within-Herd Variance. 1. Genetic Parameters for First and Second Lactation Milk Yields of Grade Holstein Cows" (1990). *Faculty Papers and Publications in Animal Science*. 137.

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Heterogeneous Within-Herd Variance. 1. Genetic Parameters for First and Second Lactation Milk Yields of Grade Holstein Cows¹

T. H. SHORT,² R. W. BLAKE, R. L. QUAAS, and L. D. VAN VLECK³
Department of Animal Science
Cornell University
Ithaca, NY 14853

ABSTRACT

Genetic and environmental (co)variance components for 4% FCM yield were simultaneously estimated by REML for grade cows from herds stratified by within-herd SD for 305-d mature equivalent milk and time period. Data were lactation records from 299,441 daughters of 2489 AI bulls that calved for the first time from 1970 to 1985 in California, New York, or Texas.

Sire and residual variance components for FCM increased with SD in all time periods and were slightly larger for second than for first lactations. Residual components were of uniform size across time periods within each SD class, but sire components were as much as 21% less for first lactations and 27% less for second lactations in the latter periods than in the earliest one. Heritabilities of first lactation FCM were largest (.154, .263, and .226 for low, medium, and high SD classes) in the earliest time period. Variance components for log-transformed records in each time period differed less than on the original scale, but both sire and residual components remained largest in the most variable herds. Genetic correlation coefficients between yields in first and second lactation were greater (.75 to .99) in all SD classes and time periods

than phenotypic correlations (.40 to .61). Heterogeneous phenotypic variation for milk yield was attributed to genetic and environmental components. However, genetic variation only increased with environmental opportunity (variation). (Key words: heterogeneous variance, milk yield, variance components)

INTRODUCTION

Heterogeneity of genetic and residual variances for yield traits of dairy cattle is widely documented (1, 5, 6, 8, 12, 15, 29). Most studies reported increasingly larger genetic and environmental variances as herd average milk yield increased (1, 5, 6, 12, 19). Trends were similar in herds differing by within-herd variability of yield (12, 15). With few exceptions (14, 15), the heritability of milk yield increased with the mean and variance of yield in different herd environments (1, 5, 6, 12, 19).

Most studies of heterogeneous variance were with herds classified by average milk yield. Famula (8) reported that stratifying herds by mean yield was analogous to selecting on herd means, which could result in biased estimates of genetic and residual variances. Estimates of the correlation between herd mean and variance have been less than .5 according to Brotherstone and Hill (2) indicating that variation within a herd is poorly predicted by average milk yield. Meinert et al. (17) regressed daughter Modified Contemporary Deviation (MCD) for milk on sire Predicted Difference in herds classified by mean yield and by SD. Regression coefficients increased with increasing herd SD within each yield classification. Examined conversely, coefficients did not differ by mean yield within the SD classifications. Conclusions were that response to selection was affected by factors described by herd variance but not by average milk.

Received December 11, 1989.

Accepted June 6, 1990.

¹Project 414, a contributing project to Southern Regional Project S49, Genetic Methods of Improving Dairy Cattle for the South.

²Present address: Holstein Association, Brattleboro, VT 05302.

³Present address: Department of Animal Science, University of Nebraska, Lincoln 68583.

A logarithmic transformation has been applied to lactation records to adjust for the relationship between mean and variance (7). Genetic variances were stabilized from the logarithmic transformation (5, 7), but the resulting residual variances were greatest for herds with smallest residual variances on the untransformed scale (1, 5, 19). Hill et al. (12) reported a similar finding in British Friesian herds classified by average milk yield. However, when the same data were classified by within-herd variance instead of yield (12), genetic and environmental variances were greatest for the most variable herds on both the normal and transformed scales.

Other methods to adjust for heterogeneous variances have been to scale observations so that all herds either have the same variance (12) or the same coefficient of variation (2). Lofgren et al. (16) concluded that the best method to calculate cow indices was to standardize MCD to the same variance and a constant heritability. Gianola (10) suggested a multiple-trait analysis in which records from herds with different variances would be considered different traits. However, this method requires estimates of variance components for each herd environment.

Lofgren et al. (15) estimated the heritability of Modified Contemporary Average (MCA) milk in herds grouped by SD of MCA. Heritability increased with increasing SD of MCA for Holsteins (.178 to .206), but it increased more for Jerseys (.246 to .331). The sire and environmental components of variance were not reported. Dong and Mao (6) reported estimates of sire and residual variances, and heritability increased with increasing intraherd-year phenotypic SD for cows in the Northeastern US (6). Heritability estimates were as much as 1.4 times greater in high than low variance herds (6).

Records from nonregistered (grade) animals comprise about 65% of records in the Northeast (R. W. Everett, personal communication) and USDA genetic evaluation (20). In herds with registered and grade cows, management practices (e.g., preferential treatment) may favor registered animals, thus causing different within-herd variances for these groups of cows. Dentine et al. (4) documented different culling strategies for grade and registered cows.

Objectives of this study were 1) to estimate genetic and environmental parameters of milk

yield for grade Holsteins by various classifications of within-herd variance for milk yield and 2) to investigate changes in these parameters with time.

MATERIALS AND METHODS

Data

Mature equivalent 305-d lactation records from 1,450,420 AI-sired grade Holstein cows that calved in California, New York, and Texas from 1970 to 1985 were used to estimate within-herd-year phenotypic SD for milk yield. Herd-years were required to have at least 25 cows to restrict the sampling variance associated with estimating the SD. The effect of season of calving was considered by calculating the variances within each of three seasons and pooling them for each herd-year to estimate the within-herd-year variance. Seasons were January through April, May through August, and September through December.

Final data were 299,441 first lactation and 207,013 second lactation milk records corrected to a 4% fat composition basis (FCM) from daughters of 2489 AI sires. Records from California and Texas were those passing edits required for the USDA genetic evaluation, and those from New York passed edits for the Northeast genetic evaluation. These data were stratified into within-herd-year SD classes and time periods to create nine data sets. Break points for SD classes were chosen to ensure no overlap in the within-herd SD classifications (e.g., to account for sampling variance associated with estimating the within-herd SD). Standard deviation classes were low (less than 1018 kg), medium (1131 to 1357 kg), and high (greater than 1471 kg). Time periods for first calving were chosen to balance the number of sires represented in each SD class, and were 1970 to 1975, 1977 to 1981, and 1982 to 1985. First and second lactation milk yields of cows were stratified into SD classifications based on their corresponding within-herd SD for first lactation ME milk yield. Numbers of observations, sires, and herd-year-seasons for each data set are in Table 1.

Ideally, daughters of sampling sires rather than proven bulls should be used to estimate genetic variance (22). Even then, selection of parents of young bulls can reduce sire variance.

TABLE 1. Numbers of herd-year-seasons (HYS), sires, cows with records, and average phenotypic herd standard deviation (APSD, kg) for each time period and herd standard deviation class.¹

Period	Parameter	Within-herd SD class		
		Low	Medium	High
1970 to 1975	HYS	2632	4097	1283
	Sires	398	493	509
	Lactation 1	14,671	32,920	13,927
	Lactation 2	11,144	22,941	8850
	APSD	904	1245	1597
1977 to 1981	HYS	1475	8417	10,198
	Sires	397	872	985
	Lactation 1	8049	43,019	72,223
	Lactation 2	6291	31,837	50,185
	APSD	916	1260	1626
1982 to 1985	HYS	1285	6376	10,015
	Sires	386	1071	968
	Lactation 1	6857	30,715	77,060
	Lactation 2	3361	21,277	51,127
	APSD	920	1264	1634

¹Standard deviation of 305-d mature equivalent milk yield: low, 0 to 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

Also, the number of sire comparisons within contemporary groups would be reduced drastically by this requirement. Therefore, records from daughters of proven and sampling sires were utilized. Each sire was required to have at least 25 daughters in a given time period, but all daughters were not required to be in one SD class. Each data set was restricted to 500 bulls or less. Because relatively more data were available for the middle and high SD classes in the later time periods, analyses for those periods were replicated using records from daughters of a second set of sires. Replicates were formed by sorting by sire all data in a time period and SD class and by choosing records from every other sire. Results for the medium and high SD classes in the later time periods are averages of replicates.

Statistical Model

A multiple-trait sire model was used to analyze FCM yield and calving interval records in first and second lactations. The mixed linear model included random effects of sire and residual and a fixed contemporary group effect.

Contemporary groups were defined as cows calving in the same herd, year, and season.

Cows were required to have a sequential data pattern to be included in the analysis to allow for simplification of the computational methods used to estimate (co)variance components (9). Consider the four traits in the current study: first parity fat-corrected yield (FCM1), first calving interval (CI1), second parity fat-corrected yield (FCM2), and second calving interval (CI2). Cows with trait *i* also have observations on all preceding traits 1, . . ., *i*-1, where *i* = 1, . . ., 4. Only records from cows that had this systematic pattern were included, which means that no cow with FCM2 was included unless she also had records for FCM1 and CI1.

Genetic (co)variance components were estimated using an expectation-maximization algorithm described by Garrick (9) for sequentially missing data. Residual (co)variance components were estimated by an algorithm of successive approximations (9). All estimates of (co)variance components were from 25 rounds of iteration, although most solutions did not change after round 10. Standard errors of genetic correlations were approximated using the method by Robertson (21). Standard errors of heritability estimates were approximated by the method of Swiger et al. (26).

RESULTS AND DISCUSSION

Measured Scale

Mean FCM yields in first and second lactations for each data set are in Table 2. Mean

TABLE 2. Average 4% FCM (kg) in first and second lactations for each time period and herd standard deviation class.

Period	Lactation	Within-herd SD class ¹		
		Low	Medium	High
1970 to 1975	1	6080	6981	7467
	2	6397	7347	7906
1977 to 1981	1	6648	7430	8104
	2	7017	7711	8239
1982 to 1985	1	6711	7610	8326
	2	7031	8005	8654

¹Standard deviation of 305-d ME milk yield: low, 0 to 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

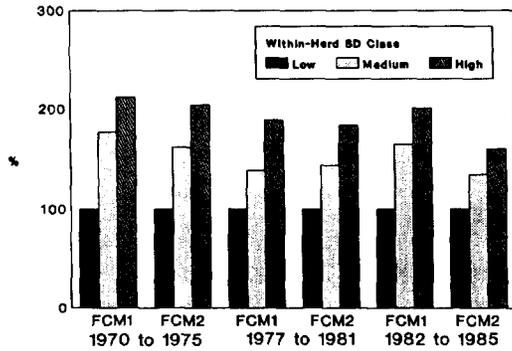


Figure 1. Sire standard deviations for FCM yields in first (FCM1) and second (FCM2) lactations as a percentage of the value for the low SD class in each time period.

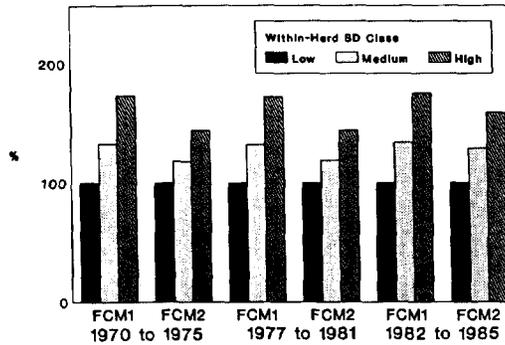


Figure 2. Residual standard deviations for FCM yields in first (FCM1) and second (FCM2) lactations as a percent of the value for the low SD class in each time period.

yields increased with SD classification in first and second lactations, and they increased with time in each SD class. Within each herd SD classification, average phenotypic herd SD also increased with time (Table 1).

Estimates of sire and residual SD for FCM yields are in Table 3. Both components increased with SD classification in each time period, but the sire components increased more. Sire SD were greater for second than for first lactation FCM yield. Sire SD were greatest in the earliest time period in all SD classes, but

residual components remained uniform in time. Sire components changed least with time in the smallest SD class.

Figure 1 shows the sire SD by time period, expressed as percentages of the components for the smallest SD class. Sire SD for both lactations increased up to 212% from smallest to largest SD class with greatest increases occurring in the earliest time period. Residual SD also expressed in percentage of the smallest SD in each time period, are in Figure 2. Increases in residual SD with phenotypic SD classifica-

TABLE 3. Estimates of sire ($\hat{\sigma}_s$) and residual ($\hat{\sigma}_e$) standard deviations for measured and log FCM yields in first and second parity.

Period and estimates	Parity	Within-herd SD class ¹			Within-herd SD class		
		Low	Medium	High	Low	Medium	High
		— Measured scale (kg) —			— Log scale (1000 × ln kg) —		
1970 to 1975							
$\hat{\sigma}_s$	1	154	273	326	25	40	44
	2	178	289	363	28	39	48
$\hat{\sigma}_e$	1	771	1029	1334	132	158	194
	2	1013	1192	1457	165	173	198
1977 to 1981							
$\hat{\sigma}_s$	1	144	200	272	26	26	36
	2	158	228	291	29	29	37
$\hat{\sigma}_e$	1	800	1057	1379	125	152	187
	2	1051	1247	1511	156	174	200
1982 to 1985							
$\hat{\sigma}_s$	1	129	213	259	22	29	32
	2	168	226	268	29	30	33
$\hat{\sigma}_e$	1	789	1058	1379	124	148	184
	2	949	1220	1507	142	165	191

¹Standard deviation of 305-d ME milk yield: low, 0 to 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

tion were similar for each time period, increasing more for FCM1 than for FCM2. In the low SD class, the residual SD of FCM1 was about 75% as large as for FCM2, for the medium class it was 86% as large, and for the high class it was 91% as large (see Table 3). Apparently, yields of younger cows were restricted more than yields of older cows in herds with the least environmental variation. Residual SD were virtually the same across time in all SD classifications. However, Mirande and Van Vleck (19) reported that the residual variance in milk yield increased in time, especially after 1976, when first lactation records were stratified by rolling herd average yield.

Heritabilities of FCM1 and FCM2 by SD classification are in Table 4. Heritability was least in the low SD classification for all time periods. Heritability showed a linear increase with SD from 1977 to 1981, but no trend was detected in the other periods. In the earliest and latest time periods, heritability was greatest in the medium SD class, except for FCM2 in the earliest period. Heritability estimates in the later periods were less than in the first and less than most findings for milk yield. However, our estimates were similar to those reported by Janson and Andreasson (13) for 4% FCM yields in two breeds of Swedish dairy cattle and by Carabaffo et al. (3) for milk yield in grade Holsteins in the US.

Some of the decrease in estimated heritability can be attributed to more intense selection

of parents of AI sires during the latter time periods. Mirande and Van Vleck (19) reported a similar decrease in heritability of milk yield with time using paternal half-sister analysis of sampling daughters. However, heritabilities were uniform in time (~.34) when the same data were analyzed by regressing daughters on dams (27).

Estimates of heritability for the latter time periods were smaller than in recent studies of records from the Northeast (6, 23, 25). Robinson (23) obtained heritability estimates of .32 and .29 for milk yields in first and second lactations using a sire model and only considering records of first daughters of all sires sampled by the Eastern AI Cooperative. The difference between estimates in this study and those of Robinson (23) may be partially due to using daughters of proven sires as well as young sires. The influence of large numbers of sires from highly selected bulls can dramatically reduce heritability (22). Also, Robinson (23) used records from both grade and registered cows, whereas only grade cows were considered in the present study. Swalve and Van Vleck (25) used an animal model to obtain heritabilities of milk yield of .33 in first and second parities for cows calving in New York from 1977 to 1984. Differences between estimates from animal and sire models may be partially attributed to effectiveness of accounting for selection. The reduction in variance in parents can be more completely represented in an animal model. Esti-

TABLE 4. Heritability of FCM yields in first and second parity on the measured and log scales.¹

Period	Parity	Within-herd SD class ²					
		Low		Medium		High	
		h ²	SE	h ²	SE	h ²	SE
1970 to 1975	1	.154	.018	.263	.019	.226	.022
	2	.136	.018	.244	.019	.194	.020
1977 to 1981	1	.119	.018	.223	.018	.237	.028
	2	.109	.017	.188	.018	.220	.027
1982 to 1985	1	.126	.023	.138	.010	.150	.009
	2	.163	.024	.113	.009	.140	.008
	1	.088	.024	.129	.011	.143	.010
	2	.136	.027	.105	.010	.134	.009
	1	.104	.023	.156	.012	.136	.008
	2	.118	.024	.148	.012	.119	.007
		.122	.042	.133	.014	.123	.009
		.165	.044	.128	.014	.116	.009

¹Top values are on the measured scale and bottom values are on log scale. Approximate SE from Swiger et al. (26).

²Standard deviation of 305-d ME milk yield: low, 0 to 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

mates of sire variance from paternal half-sib correlation theoretically represents one-quarter of additive genetic variance. Selection on sires reduces the estimate of sire variance, and hence, reduces the estimate of heritability.

Logarithmic Transformation

Analyses were repeated using log-transformed FCM records. Estimates of variance components from the log scale are in Table 3. Sire and residual variances also increased with SD classification in all time periods for transformed records. Sire variances on the transformed scale were largest in the earliest time period except for the low SD class, but residuals did not differ appreciably across time periods. Both sire and residual components were greatest in second lactations except for the medium class in the earliest period. The log transformation reduced differences in sire variances in each SD class, especially in the later time periods.

Residual variances for transformed records were less heterogeneous than for untransformed records, especially in second lactation. Estimates of residual variances of transformed records were largest in the most variable herds. This is different from studies where herds were classified by average yield instead of variance (1, 5), where residual variances were largest in lowest yielding herds. Correlation coefficients between the phenotypic mean and variance for

untransformed milk yield all were less than .5 and tended to decrease with increasing herd size (from .48 for herd-years with more than 25 cows to .27 for herd-years with more than 1000 cows). Heritabilities of log-transformed yields for each SD class (Table 4) tended to be smaller than for untransformed records, but they still varied in the same way with within-herd variance. Hill et al. (12) obtained slightly larger heritabilities for log-transformed than for untransformed records from British Friesians.

Correlations Between Lactation Yields

Genetic and phenotypic correlations between FCM yields in first and second lactations are in Table 5. All genetic correlations were .75 or larger and were smallest in the low SD class. Correlations increased with SD in the earliest time period but were largest in the medium SD class (.88 and .93) after 1977. Phenotypic correlations were moderate (.61 or less) and increased slightly (from .40 to .61) across SD classes in every time period.

Genetic and phenotypic correlations for log-transformed FCM yields are in Table 5. Genetic correlation coefficients were slightly smaller than for untransformed records, were also smallest in the low herd SD, and increased with SD classification except in the last period. Phenotypic correlations also increased with SD class but differed little from those calculated on the untransformed scale.

TABLE 5. Genetic (r_g) and phenotypic (r_p) correlations between FCM yields in first and second lactations.¹

Period	Correlations	Within-herd SD class ²		
		Low	Medium	High
1970 to 1975	r_g	.88 (.02)	.97 (.00)	.99 (.00)
	r_p	.85 (.03)	.90 (.01)	.95 (.01)
1977 to 1981	r_g	.42	.55	.61
	r_p	.42	.52	.60
1972 to 1985	r_g	.86 (.04)	.88 (.01)	.86 (.01)
	r_p	.74 (.05)	.75 (.03)	.85 (.01)
1972 to 1985	r_g	.40	.51	.57
	r_p	.39	.50	.57
1972 to 1985	r_g	.75 (.09)	.93 (.01)	.84 (.01)
	r_p	.67 (.09)	.85 (.02)	.83 (.01)
		.42	.52	.59
		.41	.52	.58

¹Top values are on the measured scale and bottom values are on the log scale. Approximate SE in parentheses (21).

²Standard deviation of 305-d ME milk yield: low, 0 to 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

All genetic correlations between first and second FCM yields were large (.84 to .99, except one value of .75). This result suggested no important interaction between growth and first lactation performance in the range of herd environments in this study in spite of greater environmental restriction on yield of primiparous cows compared to pluriparous cows in herds with least environmental variation (Table 3). Cows with greatest genetic potential in first lactation were essentially the same cows with most genetic ability in second lactation yield in all SD classes.

CONCLUSIONS

Genetic and environmental variances for milk yield of grade Holsteins differed by two-fold among herds classified by variance in mature equivalent milk yield. Sire variances were relatively more heterogeneous than environmental variances. Heritabilities of FCM yields were smallest in the low SD classification and were similar for medium and high SD classes. Both sire and residual variances were made more uniform across SD classifications by a log transformation. However, sire and residual variances of log-transformed records remained largest in herds with the most variability in milk yield, which is probably expected, because when a random variable x is normally distributed, the $\text{var}(\log x)$ is approximately equal to $\text{var}(x)/[E(x)]^2$.

Hammond (11) stated that genetic variance for a trait may be expressed only when environmental variation (opportunity) is sufficient to permit differential genetic expression. Within an environmental setting, animals with greatest genetic merit would always outrank those with lowest merit, but differences between animals would vary by herd environmental opportunity. Consequently, unequal responses could arise from differential activation of the genes for yield in various environments, which could truncate genetic variation 1) if some gene effects are nil in poor environments or 2) if average gene effects are reduced in herd environments with less opportunity.

Vinson (28) suggested that differences in environmental variation are likely associated with management differences between farms (e.g., nutrition, housing, climate). Nutritional management of the milking herd probably has a

large impact on genetic and environmental variances among herds. Other factors being equal, lactation potentials are expressed when cows maximize nutrient intake relative to requirements in each stage of lactation. However, herd managers differ in knowledge, skill, or resources to ensure that all cows perform to their potential.

Consider two herd situations in which feeding management could differ for any of these reasons. Cows in the first trimester of lactation are grouped by daily yield of FCM in one, and by daily FCM and days in milk in the other. Cows with same yields in ascending and descending stages of lactation receive the same ration in the first herd, but different rations are fed in the herd in which cows also are grouped by stage of lactation. Consequently, less genetic variation is expected to be expressed in the first herd than in the second, if other factors are equal, because opportunity for nutrient intake relative to requirements was restricted. The number of rations (i.e., feeding groups) and the differential nutrition management among groups also may help explain heterogeneous variation in milk yield among herds.

If increases in genetic variance are simply scalar increases from increased environmental opportunity, the problem facing animal breeders is to determine the value(s) of the scalar(s), which is not straightforward unless variances due to differential management are known. Statistical models closely accounting for management and other nongenetic factors affecting milk yield likely would reduce the heterogeneous variation between herds. Meyer et al. (18) proposed a model for genetic evaluation of individual test-day yields instead of lactation milk yield. Effects that are accountable on test days that are likely associated with heterogeneous within-herd variances are age of cow, month of calving, days in milk, fresh date, days carried calf, and management interventions of varying duration (e.g., nutritional group, pharmaceutical treatments like bovine somatotropin).

Estimates of heritability of FCM in first and second parities were considerably lower for the latter two time periods. Sorenson and Kennedy (24) indicated that this might be expected under directional selection, assuming an additive genetic model with large number of loci, due to inbreeding and gametic disequilibrium. As a

result of selection, analysis of variance estimators such as Henderson's method 3 are biased, whereas minimum variance, quadratic, unbiased estimators using an animal model with complete relationships provide unbiased estimates of genetic variance in the base population (24). However, in this study, data from previous time periods (on which selection was based) were not considered in analysis of later time periods. Estimates of heritability would likely have been higher in the last two periods had records from the earliest time period been considered.

Lower estimates of heritability of yield in this study may be partially attributed to only grade records being used, although this is difficult to document. Another study (3) reported similar estimates of heritability for grade cows using records from two of the same states, and data from Wisconsin instead of Texas. Analysis of records from herds in which both registered and grade paternal half-sibs are present might help determine if variance components and heritability differ between the two populations. When data were combined across SD classes within each time period, heritabilities were .28, .18, and .18 for first parity FCM for the three time periods, respectively. Corresponding heritabilities of second parity yields were .24, .16, and .16. This finding supports Famula's (8) caution on interpretation of estimates of heritability when data have been stratified into groups according to production.

ACKNOWLEDGMENTS

The authors thank Shayle R. Searle for many helpful suggestions. Eastern Artificial Insemination Cooperative, Inc. is gratefully acknowledged for partial funding of this project. Computing support was provided by the Cornell National Supercomputer Facility, which is partly funded by the National Science Foundation, New York State, and the IBM Corporation.

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