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Variance of Interaction Effects of Sire and Herd for Yield Traits of Holsteins in California, New York, and Pennsylvania with an Animal Model¹

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ABSTRACT

An animal model with a REML algorithm was used to estimate variances of additive genetic effects and interaction effects of sire and herd. Milk and fat yields were analyzed for first, second, and third lactations of Holsteins from California, New York, and Pennsylvania. Twenty samples of data were used in the study: 10 from California, 4 from New York, and 6 from Pennsylvania. Mean number of lactations per sample was 36,820 from 18,189 cows in 156 herds. Mean fractions of phenotypic variance of interaction effects of sire and herd for milk and fat yields were .015 and .019 for first lactation and .019 and .021 for all (up to three) lactations rather than the .14 used for national genetic evaluations in the US. Mean heritability estimates for milk and fat yields were .26 and .24 for first lactation and .21 and .21 for all

lactations in California and .34 and .35 for first lactations and .28 and .29 for all lactations in New York. Sums of variances of permanent environmental and interaction effects of sire and herd were similar to those used for national genetic evaluations in the US.

Analysis of another 10 samples from California and 10 samples from New York showed only slightly different fractions of phenotypic variance for milk yield for interaction effects of sire by herd, sire by herd by year, and sire by herd by year by season: .023, .027, and .037 for California and .023, .017, and .023 for New York, respectively.

(Key words: lactation yields, interaction of genotype and environment, restricted maximum likelihood)

Abbreviation key: c^2 = fraction of variance that was due to sire and herd interaction effects, CA = California records, NYP = New York and Pennsylvania records.

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INTRODUCTION

Interaction of sire and herd occurs when the differences among progeny groups are not the same in different environments. Similarity among progeny in the same environment may be due to management (22, 28). Then, the genetic correlations among expressions of the same genotype in different environments (11,

15, 35, 47) are less than unity. Interaction variance also may be a consequence of heterogeneous variances within environmental groups (e.g., herds) and has been termed a pseudo interaction effect (11, 41). Meyer (19) concluded that interaction variance is mostly due to common environmental effects rather than to interaction of genotype and environment.

Ignoring interaction of sire and herd would inflate estimates of additive genetic variance (18, 19, 38, 41) and lead to an overestimation of accuracy of EBV (2, 19). The effect is more important for evaluation of cows and natural service bulls than for bulls used in AI service (3, 18, 19, 42). Dong and Mao (13) and Meyer (19) found that interaction effects were relatively higher for models with effects of herd-year-season than for models with effects of herd-year.

Variances due to interaction of sires and herds have been estimated by intraclass correlation (1, 37), Henderson's method 1 (18, 38, 44), Henderson's method 3 (3, 4, 8, 26, 27, 36), and single-trait REML with a sire model (19, 23, 25). Multiple-trait REML (9, 33) has been used to estimate genetic correlation between regions. For yield traits, REML estimates of variance of interaction of sire and herd with a sire model were between 1 and 4% of phenotypic variance (2, 19). A preliminary study of first lactation records with an animal model reported mean estimates of 1% of phenotypic variance (12).

The objective of this project was to estimate the component of variance for effects of interaction of sire and herd with an animal model similar to that used for the national genetic evaluation in the US. An objective added after completion of these analyses was to compare three models with interaction effects of sire and management assigned to 1) sire and herd, 2) sire and herd-year, and 3) sire and herd-year-season of freshening.

MATERIALS AND METHODS

Records for first, second, and third lactations of Holstein cows for yields of 305-d, twice daily milking, mature equivalent milk and fat in California, New York, and Pennsylvania were from the Animal Improvement Programs Laboratory of the USDA. Years of calving were 1965 through 1991.

Twenty data sets were sampled randomly by herd code. Data sets 1 through 10 were from California (CA), 11 through 14 were from New York, and 15 through 20 were from Pennsylvania. Data from New York and Pennsylvania are designated as NYP.

Two edits were applied after the 20 data sets were selected. All lactations must have been more than 240 d, and a sire had to have progeny in at least two herds. Maximum size of a deleted sire progeny group was 70. These later edits decreased the data by about 22%. Corresponding numbers of lactations were 23,344 and 56,071. Table 1 summarizes the data structure for samples that were analyzed.

TABLE 1. Summary of data structure for 10 samples for California and 10 samples for New York and Pennsylvania.

Number	California			New York and Pennsylvania		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Cows with records	18,485	12,960	27,838	17,893	16,477	19,338
Animals in relationship matrix	25,070	16,407	37,510	26,978	25,283	28,685
Lactations	35,585	23,344	56,071	38,055	34,546	41,029
Herds	82	30	166	231	209	244
Sires	1266	846	1715	1264	1172	1369
Sire-herds	5083	2636	8323	7915	7414	8408
Herd-years						
First lactation	662	204	1161	2489	2126	2833
All lactations	704	209	1248	2722	2306	3131
Mixed model equations						
First lactation	30,813	19,248	46,988	37,382	34,885	39,800
All lactations	50,344	32,212	74,919	55,508	51,542	59,396

TABLE 2. Mean 305-d mature equivalent milk and fat yields and ranges in sample means for first and all lactations for 10 samples for California and 10 samples for New York and Pennsylvania.

	Milk yield		Fat yield	
	First	All	First	All
	(kg)			
California				
All cows				
Mean	9225	9478	332	339
Minimum	2063	2063	77	77
Maximum	21,783	21,783	770	770
Sample Mean				
Minimum	8894	9098	320	322
Maximum	9761	10,033	344	352
New York and Pennsylvania				
All cows				
Mean	7936	8060	289	294
Minimum	1731	1731	68	68
Maximum	18,438	18,622	726	870
Sample mean				
Minimum	7828	7939	286	290
Maximum	8135	8290	294	299

For the 10 data sets from CA, mean milk and fat yields were 9225 and 332 kg for first lactation and 9478 and 339 kg for all lactations. Corresponding means for NYP were 7936 and 289 kg for first lactation and 8060 and 294 kg for all lactations. The means were similar for all samples (Table 2).

Model [1] was used for first lactation records only, and Model [2] was used for up to three lactations:

$$Y_{ijklm} = h_{ij} + a_{kl} + c_{ik} + e_{ijklm} \quad [1]$$

$$Y_{ijklm} = h_{ij} + a_{kl} + c_{ik} + p_{kl} + e_{ijklm}, \quad [2]$$

where

- Y_{ijklm} = milk or fat yield;
- h_{ij} = fixed effect of year j in herd i ;
- a_{kl} = random effect of cow l , daughter of sire k ;
- c_{ik} = random environmental effect of sire k , associated with daughters in herd i ;
- p_{kl} = random permanent environmental effect of cow kl ; and
- e_{ijklm} = random environmental effect appropriate to the model.

For both models, variances of vectors of random effects were

$$V(\mathbf{a}) = \mathbf{A}\sigma_a^2$$

and

$$V(\mathbf{e}) = \mathbf{I}_N\sigma_e^2;$$

for Model [1],

$$V(\mathbf{c}) = \mathbf{I}_c\sigma_c^2,$$

and for Model [2]

$$V \begin{pmatrix} \mathbf{c} \\ \mathbf{p} \end{pmatrix} = \begin{pmatrix} \mathbf{I}_c\sigma_c^2 & 0 \\ 0 & \mathbf{I}_p\sigma_p^2 \end{pmatrix},$$

where \mathbf{A} is the additive genetic relationship matrix with its inverse computed by the method of Quaas (29), and \mathbf{I}_c , \mathbf{I}_p , and \mathbf{I}_N are identity matrices of order number of sire by herd levels, cows with records, and number of records.

Variance components were estimated by a derivative-free algorithm to obtain REML estimates (17, 32) using a Choleski decomposition algorithm (7). The minimization search was based on the Downhill simplex algorithm (6). The function minimized was -2 times the logarithm of the likelihood. The convergence criterion was the variance of the $n + 1$ func-

tions in the simplex less than 10^{-9} where n is the number of variance components in the model. Convergence was achieved, on average, after 51 rounds for Model [1] and 82 rounds for Model [2]. At apparent convergence, analyses were restarted to check for possible local maxima. None were found.

Empirical standard errors of estimates of variance components and fractions of total variance were calculated from estimates from the 10 samples from CA and from the 10 samples from NYP.

RESULTS AND DISCUSSION

Summaries of estimates of variance components and their empirical standard errors are represented in relative proportions of the total variance (Table 3) and in units of the traits (Table 4).

The mean ratios of variance of interaction of sire and herd to total variance (c^2) for milk yield were $.015 \pm .002$ for first lactation and $.019 \pm .002$ for all lactations for CA and $.015 \pm .002$ and $.018 \pm .002$ for NYP (Table 3). For fat yield, the corresponding ratios for CA and NYP were similar and averaged $.019 \pm .002$ and $.021 \pm .002$. Estimates from this study were smaller than for milk yield from first lactation of British Friesians, where c^2 estimated with a sire model was .031 for interaction effects of sire and herd and .036 for interaction effects of sire and herd-year-season

(19). For REML analyses of milk yield, estimates of c^2 with a sire model increased from .018 for first lactation to .030 for third lactation (2). The same tendency was reported earlier from analyses with Henderson's method 1 of milk and fat yields (44). For both models, estimates of c^2 for fat exceeded those for milk yield, although, for an earlier study with Henderson's method 1 (38), the interaction component for milk was four times greater (.04 vs. .01) than that for fat yield.

All estimates of c^2 in this study were smaller than the .14 assumed in previous and current methods used by the USDA for evaluation of sires and dams (22, 23, 28, 39, 46). After a study of changes in evaluations of natural service sampled bulls brought into AI, Norman et al. (23, 24) indicated that the c^2 value of .14 currently used by the USDA may be too high. Misztal (20) also found that the variance of interaction effects of sire and herd was not significant for final type score. A value for c^2 that is too large may lead to underestimation of genetic merit of superior sires and dams. Research is in progress to study the effect of different values of c^2 on estimation of genetic merit.

The mean estimate of heritability (Table 3) for first lactation milk yield in CA ($.26 \pm .05$) was similar to that from sire models (2, 10, 13, 30). The higher mean estimate for NYP ($.34 \pm .01$) corresponds to results for a simple animal model in which estimates ranged from .18 to

TABLE 3. Estimates of fractions of total variance and standard errors for milk and fat yields for first and all lactation analyses for 10 samples from California and 10 samples from New York and Pennsylvania.

Sample	Heritability				Sire by herd interaction				Permanent environmental effect	
	Milk		Fat		Milk		Fat		Milk	Fat
	First	All	First	All	First	All	First	All		
California										
Minimum	.198	.160	.218	.167	.008	.012	.010	.012	.259	.242
Maximum	.302	.256	.272	.242	.030	.028	.030	.033	.365	.357
Mean	.258	.208	.239	.206	.015	.019	.019	.021	.314	.297
SE	.012	.009	.007	.008	.002	.002	.002	.002	.011	.011
New York and Pennsylvania										
Minimum	.299	.248	.293	.259	.003	.013	.000	.010	.196	.188
Maximum	.393	.324	.382	.327	.026	.026	.040	.035	.273	.248
Mean	.344	.281	.348	.290	.015	.018	.018	.022	.238	.220
SE	.010	.009	.009	.007	.002	.002	.004	.003	.008	.006

.44 (5, 14, 21, 34, 43). The estimates for first lactation exceeded those for Model [2]: $.21 \pm .01$ for CA and $.28 \pm .01$ for NYP. These results agree with previous REML studies with sire (2, 10, 13, 30) and animal (45) models. The pattern was the same for estimates from regressions of daughters on dams (42). Larger estimates of heritabilities for New York data than for CA have been partially attributed (43) to a less complete identification in California herds.

Heritability estimates for fat yield (Table 3) were similar to those for milk yield. Differences between estimates for milk and fat yield in other studies (20, 28, 29, 31, 43) were only about .02, as in this study.

Variation in heritability estimates across the data sets was greater for milk yield from first lactation than from all records and was generally greater for milk than for fat yields (Table 3).

The proportions of permanent environmental variances for milk and fat yields were $.31 \pm$

$.01$ and $.30 \pm .01$ for CA and $.24 \pm .01$ and $.22 \pm .01$ for NYP (Table 3). These estimates were somewhat smaller than those for British Friesians (45). For nearly all data sets, the estimates for milk yield exceeded those for fat yield. The estimates suggest that the variance of permanent environmental effects is larger than the 14% assumed for national evaluation of bulls and cows (23, 46). The sums of the proportions of total variance from permanent environmental effects and interaction effects of sire and herd from this study, however, are similar to that sum used in the national evaluation.

Estimates of phenotypic variances were larger for CA than for NYP and were smaller for first lactation than for all lactations.

Comparison of Three Models for Interaction Effects of Sire and Management

At the suggestion of a reviewer, 10 additional data sets were analyzed from California and New York for milk yield with three differ-

TABLE 4. Estimates of variances¹ and standard errors for milk and fat yield for first lactation and all lactation analyses for 10 samples from California and 10 samples from New York and Pennsylvania.

	First lactation				All lactations				
	A ¹	SH	E	Total	A	SH	PE	E	Total
Milk yield (kg ² /100)									
California									
Minimum	3335	132	11,567	16,811	2900	243	4945	8348	18,071
Maximum	5285	524	14,224	18,760	4885	563	7206	9706	20,962
Mean	4561	265	12,837	17,663	4113	382	6193	9019	19,707
SE	236	34	279		207	34	215	140	
New York and Pennsylvania									
Minimum	4058	38	7894	12,812	3555	176	2838	6497	14,124
Maximum	5191	355	9322	13,605	4695	382	3992	6942	15,068
Mean	4587	193	8556	13,336	4088	266	3469	6733	14,556
SE	127	31	164		133	23	122	47	
Fat yield (kg ²)									
California									
Minimum	481	22	1454	2031	407	28	594	1119	2434
Maximum	617	67	1767	2381	629	80	921	1305	2792
Mean	513	40	1600	2153	524	56	765	1219	2564
SE	18	3	31		22	5	32	23	
New York and Pennsylvania									
Minimum	503	0	1035	1636	504	19	369	895	1936
Maximum	663	69	1178	1769	660	71	493	960	2029
Mean	596	32	1087	1715	569	44	438	930	1981
SE	16	6	16		15	6	12	7	

¹A = Additive genetic variance, SH = variance from interaction of sire by herd, PE = variance from permanent environmental effects, and E = variance from residual effects.

TABLE 5. Summary of the data structure for 10 California and 10 New York samples used to compare models with interaction effects of sire by herd ($S \times H$), sire by herd by year ($S \times H \times Y$), and sire by herd by year by season ($S \times H \times Y \times Se$) for milk yield.

Number	California			New York		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Cows with records	11,922	11,063	12,826	10,788	10,531	11,034
Animals in relationship matrix	18,944	16,390	21,306	17,332	16,746	18,098
Lactations	20,029	18,431	21,749	21,372	21,202	21,595
Herd-year-seasons	327	282	317	1962	1752	2127
Model						
$S \times H$	3211	2853	3742	4654	4534	4861
$S \times H \times Y$	6818	6088	7925	11,830	11,389	12,252
$S \times H \times Y \times Se$	9948	9069	11,426	15,392	14,914	15,754
Mixed model equations						
$S \times H$	34,405	30,940	38,268	34,736	33,960	36,040
$S \times H \times Y$	38,011	34,340	42,434	42,912	41,175	43,304
$S \times H \times Y \times Se$	41,141	37,147	45,880	45,474	44,824	46,702

ent models. The basic model is described in Model [2]. The three models included the interaction effects of sire by herd, or sire by herd by year, or sire by herd by year by season of freshening. Data included in the additional analyses are summarized in Table 5.

Estimates of fractions of total variance and empirical standard errors for milk yield for the 10 New York and 10 California samples for the three models are in Table 6. The mean fraction of variance from interaction effects of

sire and herd is the same for both states, .023. The corresponding fraction of variance from interaction effects of sire by herd by year is larger for California, .027, than for New York, .017. The same trend is evident in the fraction of variance due to interaction effects of sire by herd by year by season: .037 for California and .023 for New York. Regardless of the model used, no important interaction is evident among effects for sire, herd, year, or season for milk yield in either California or New York. If

TABLE 6. Mean estimates for fractions of total variance and empirical standard errors for milk yield for 10 samples from California and 10 from New York for three models for sire by management interaction.

Effect	California				New York			
	Mean	SE	Minimum	Maximum	Mean	SE	Minimum	Maximum
Model [1], sire by herd								
Genetic	.227	.009	.178	.282	.274	.005	.237	.295
Sire by herd	.023	.003	.011	.041	.023	.002	.015	.033
Permanent environmental	.298	.009	.253	.336	.258	.007	.230	.301
Residual	.453	.005	.428	.475	.445	.004	.424	.464
Model [2], sire by herd by year								
Genetic	.239	.008	.200	.283	.283	.006	.243	.302
Sire by herd by year	.027	.001	.022	.033	.017	.002	.009	.025
Permanent environmental	.304	.009	.264	.342	.269	.007	.239	.312
Residual	.430	.005	.409	.454	.432	.004	.411	.452
Model [3], sire by herd by year by season								
Genetic	.246	.007	.211	.287	.284	.006	.243	.303
Sire by herd by year by season	.037	.002	.029	.045	.023	.004	.009	.041
Permanent environmental	.298	.009	.262	.337	.269	.007	.238	.312
Residual	.419	.006	.395	.444	.425	.005	.395	.451

the interaction of sire and herd represents true interaction of genotype and environment, these estimates are probably slightly smaller than if relationships among sires had been considered in estimating the component of variance for interaction of sire and herd (16, 40).

CONCLUSIONS

The mean estimates of variance of interaction effects of sire and herd relative to phenotypic variance for yield traits of Holsteins from CA and NYP were .015 to .022. These estimates are markedly smaller than the .14 currently used for national genetic evaluations in the US. The effects on ranking of bulls and cows caused by use of a value of .14 rather than .01 to .02 should be considered. Estimates of heritabilities for first lactation were somewhat larger than for all lactations. For yield traits, these heritabilities were smaller than for most similar studies with animal models but were similar to those used for the national evaluation program. The estimates of repeatability in the data are similar to those used nationally.

The effect on selection response of using the smaller fractions of interaction variance of sire and herd found here or of using interaction variance of sire and herd equivalent to .14 of phenotypic variance is being studied on the original data sets from CA and NYP.

A more definitive study would be to use the national sire and cow evaluations updated over a number of years. The question of whether to use .14 or some smaller value for the fraction of variance for interaction of sire and herd is a policy as well as a scientific issue. One factor to consider is whether to incorporate different fractions for the three classes of sires (multiple herd sampling, standard sampling, or other sampling) identified by USDA in genetic evaluations. Such a modification of national genetic evaluation would not be difficult. Further research to estimate interaction variance of sire and herd for those three classes of sires would seem warranted to aid in making a decision on how to account for possibility of preferential treatment.

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