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Genetic and Maternal Influence on the First Three Lactations of Holstein Cows

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Abstract

Milk records of up to the first three lactations of artificially sired Holstein daughters and their dams were used to estimate heritability from both daughter-dam regression and paternal half-sib correlation. The within-herd estimates from records expressed as deviations from herd-mate averages were .37, .30, and .24 from daughter-dam regression for the first three lactations; and the corresponding estimates from half-sib correlation were .24, .21, and .23. These results suggest a large maternal effect in the first lactation, a small amount in the second, and little in the third lactation. Analysis of the records not as deviations gave the same pattern for the daughter-dam regressions, but confounding of sires with year-seasons apparently biased the half-sib correlations upward. The consequences of considering unequal heritability for different lactations if the apparent difference is due to maternal effects is illustrated for selection for first-lactation breeding value from up to three records on the cow herself and on her dam.

Some recent reports (2, 7) have suggested that the first-lactation record of a dairy cow is more important than any later records for evaluating her breeding value. Little will be added to the accuracy of prediction by using more than the first record. Evidence from other reports [see, for example, Rendel et al. (8)] which have found apparently higher heritability estimates from first-lactation records than for later records would confirm this opinion.

A question of major importance in determining the relative value of various lactation records is concerned with selecting cows which will be mated to selected bulls to produce the next generation of young bulls to be sampled in artificial insemination (A.I.). If the common opinion that one must know at least three or four records of a cow before making her

eligible to produce a son for A.I. is really folklore, then this must be proved, so that the generation interval can be shortened through use of cows with only one known record. The same reasoning will also be true for within-herd culling, but the effects of selection on the whole population will be determined much more through A.I. than through herd culling.

This study was made to determine estimates of heritability for the first three lactations and the genetic correlations among these records, so that the importance of later lactations for genetic selection can be evaluated.

Data

Milk records of up to the first three lactations of Holstein daughter and dam pairs were taken from the files of the New York Dairy Records Processing Laboratory. Both daughter and dam had to have had a record begun before 35 months of age (considered a first-lactation record) to qualify for analysis. These records were made between 1950 and 1963. A further criterion was that either the cow or her dam must have been sired by a bull used in artificial insemination.

The records were expressed in two ways: (1) as 305 day, 2×, M.E. deviations from the adjusted herd-mate averages, and (2) as 305 day, 2×, M.E. records. All were recorded to the nearest 10 lb and converted to the nearest 10 kg.

The statistical model for estimation of variance components included random effects due to sires or grandsires, herds, sire or grandsire by herd interaction, and random residual effects. This procedure probably was not appropriate for the mature equivalent records since years and seasons were not considered. Year and season effects would be minimized for the records expressed as deviations from herd-mate averages. Since most of the filled subclasses had only a few observations and most subclasses were empty, the interaction component was dropped from the model after inspection of the interaction components which were all small. Daughter-dam regressions, estimates of genetic correlations from daughter-dam covariances, and estimates of repeatability were obtained from the residual components of variance and covariance.

Analyses of variance and covariance were made for pairs where both the daughter and dam had at least a first record, for pairs where the daughter and dam each had at least two records, and for pairs where the daughter and dam each had at least three records.

The numbers of records, mean deviations from herd-mate averages, and mean milk records for the various analyses appear in Table 1.

Results and Discussion

The mean deviations in Table 1 show that animals surviving more lactations have larger deviations from herd-mate averages than those lasting only one or two lactations.

There is also considerable evidence that dams which have daughters which reach production are a selected and not a random group. The difference between daughter and dam deviations for all first-lactation records is about 160 kg from the sire analysis and nearly 270 kg from the grandsire analysis. Most of this differential between daughter and dam means disappears when both daughters and dams have two or more, or three or more records.

The percentages of total variation due to sire and herd effects are shown in Table 2, together with the total variation and heritability estimates obtained from the within herd intra-sire correlation coefficient and from the regression of daughter records on dam records.

The decrease in total variance for first records of cows having two or three records also suggests that groups having more than one record are a selected group. This is in agree-

ment with the difference in mean deviations for the different groups.

The percentages of the total variation accounted for by sire and by herd effects for deviations are relatively constant for all analyses. The herd effects (not taken out by the use of deviations from herd-mate averages) account for about 5% of the variation and the sire effects about the same proportion. The within herd estimates of heritability from the sire components do not suggest any major differences in heritability for the three lactations. From the analyses with the maximum number of records for each lactation set, the estimates were .24 for first records, .21 for second records, and .23 for third records. The corresponding estimates from grandsire components were: first records, .26; second records, .27; and third records, .23. These estimates are similar to those reported by Barr and Van Vleck (1) based on among and within sire analyses of deviations.

Heritability estimates from daughter-dam regression for deviations follow the pattern reported by others (3, 7, 8), in that the estimates for later lactations are lower than for first lactations. The estimates from the within herd-sire regression in this study were first records, .37; second records, .30; and third records, .24. The corresponding regression estimates from the grandsire by herd analyses were first records, .38; second records, .28; and third records, .26.

The paternal half-sib estimates of heritability from the analyses involving the records not

TABLE 1

Mean milk records (kg ÷ 10) and numbers of records, sire (grandsire), herd and sire (grandsire) by herd subclasses included in variance component and regression analyses

Analysis	No.					Means			
	Lacta-tion	Rec-ords	Sub-classes	Herds	Males	Deviations		Mature equiv.	
						Dau.	Dam	Dau.	Dam
All first records									
Sires	1	20,850	14,861	2,429	317	.1	16.5	610.8	591.0
Grandsires	1	15,530	9,487	2,148	269	−7.1	19.6	607.0	597.8
All pairs with at least two records									
Sires	1	11,582	8,935	1,847	279	12.8	18.8	612.8	589.5
	2	....	....	....	......	17.7	24.1	633.2	600.9
Grandsires	1	8,376	5,464	1,564	213	5.9	23.1	608.9	597.1
	2	....	....	....	......	10.5	25.9	628.1	608.0
All pairs with at least three records									
Sires	1	5,609	4,685	1,299	249	21.2	23.3	612.8	590.2
	2	....	....	....	......	30.1	30.8	633.4	603.1
	3	....	....	....	......	23.8	24.2	642.3	602.7
Grandsires	1	3,945	2.767	1,061	162	14.9	28.9	609.1	598.7
	2	....	....	....	......	24.3	34.6	628.9	611.2
	3	....	....	....	......	17.2	28.5	636.6	611.4

TABLE 2

Fraction of total variance accounted for by herd and sire (grandsire) effects and estimates of heritability from intraherd paternal (grandpaternal) intraclass correlation or within subclass daughter-dam regression for records expressed as deviations from herd-mate averages and for mature equivalent records

Analysis	Lacta-tion	Deviations from herd-mate averages					Mature equivalent records				
		Component		Total vari-ance	Heritability		Component		Total vari-ance	Heritability	
		Herd	Male		Intra-class	dau. dam	Herd	Male		Intra-class	dau. dam
		Fraction					Fraction				
All first records											
Sire	1	.048	.060	11,846	.24	.37	.266	.108	16,144	.59	.32
Grandsire	1	.053	.016	12,080	.26	.38	.278	.054	16,669	1.20	.34
All pairs with at least two records											
Sire	1	.070	.057	9,482	.24	.33	.322	.091	13,376	.53	.28
Sire	2	.009	.052	13,797	.21	.30	.231	.101	18,962	.52	.25
Grandsire	1	.057	.014	9,647	.24	.33	.323	.030	13,586	.72	.32
Grandsire	2	.005	.016	13,422	.27	.28	.240	.038	18,675	.81	.28
All pairs with at least three records											
Sire	1	.104	.051	8,807	.23	.31	.372	.080	12,379	.51	.26
Sire	2	.030	.049	11,816	.20	.22	.287	.081	16,361	.45	.21
Sire	3	.036	.056	12,551	.23	.24	.261	.109	17,345	.59	.21
Grandsire	1	.065	.004	8,858	.08	.29	.355	.009	12,528	.23	.32
Grandsire	2	.049	.010	11,246	.17	.20	.327	.012	16,107	.28	.22
Grandsire	3	.008	.014	12,063	.23	.26	.258	.032	13,232	.69	.26

expressed as deviations are obviously out of line with previous studies. The herd compo-nents, however, are in good agreement with the reports of Legates et al. (6) and Van Vleck et al. (12). The sire and grandsire components are larger than expected. The increased size of both the sire and grandsire components over the corresponding components from deviations is about the same. Multiplying by four makes the estimates of heritability from grandsire components fall outside the upper limit of one.

Probably some effects such as seasons or years not included in the model for this study, which may be partially confounded with the male components, are biasing the sire and grandsire components upward. Whether some such effects are also biasing the sire and grandsire com-ponents downward when the records are ex-pressed as deviations is open to speculation.

The daughter-dam regressions give estimates of heritability slightly lower for the records not expressed as deviations than for records ex-

TABLE 3

Estimates of genetic correlations from grandpaternal and paternal components of variance, from intraherd and sire (grandsire) daughter-dam regression, and intraherd and sire (grandsire) repeatabilities for records expressed as deviations from herd-mate averages and for mature equivalent records

Analysis:	Lacta-tion	Deviations from herd-mate averages				Mature equivalent records			
		Genetic correlation		Repeatability		Genetic correlation		Repeatability	
		Male	Dau.-Dam	Dau.	Dam	Male	Dau.-Dam	Dau.	Dam
All pairs with at least two records									
Sire	1,2	.77	.85	.58	.51	.91	.82	.59	.53
Grandsire	1,2	.58	.86	.58	.53	.89	.77	.62	.53
All pairs with at least three records									
Sire	1,2	.78	.93	.51	.48	.89	.87	.52	.48
	1,3	.68	.82	.48	.45	.84	.82	.46	.45
	2,3	1.01	1.02	.48	.51	.97	1.01	.47	.52
Grandsire	1,2	.06	.97	.54	.50	.74	.86	.58	.47
	1,3	.83	.90	.47	.47	1.10	.91	.51	.47
	2,3	1.05	.96	.52	.48	1.06	.99	.56	.50

pressed as deviations. For the sire analyses, these estimates were all first records, .32; all second records, .25; and third records, .21. The corresponding estimates from the grandsire analyses were .34, .28, and .26. The pattern is the same as for deviations.

The apparent pattern from the heritability estimates for deviations is that the paternal half-sib correlations are about the same for all lactations but that the daughter-dam estimates are higher for first lactation records, with a gradual drop in the second and third lactations to the level of the estimates derived from the paternal half-sib analyses. This result suggests a sizeable genetic maternal effect in the first lactation which drops with second lactations and disappears by the third lactation.

On the other hand, if there really is no maternal effect, the genetic correlations (shown in Table 3) among the first three lactation records support the view that although the genetic basis for the third lactation is more different from the first than the second record, the second and third lactations have a closer genetic basis than first and second lactations. The results shown in Table 3 illustrate such a point. In general, the estimates of genetic correlations were higher from the daughter-dam analyses than those from sire components of variance and covariance. These correlations are all higher than reported by Freeman (3) from daughter-dam analyses, but are similar to those found by Van Vleck (10) between first and later records from analyses of sire groups. One must also remember that selection may bias these estimates and that cows having three or more records are more highly selected than cows having fewer records. A true genetic maternal effect would be likely to reduce the genetic correlation estimates from daughter-dam covariances, because the maternal effects apparently are not of the same magnitude for each lactation.

Estimates of repeatability from regression of a later record on an earlier record on an intrasire-herd basis are also given Table 3. They follow the pattern reported by Barr and Van Vleck (1), in that adjacent records are more alike than nonadjacent records.

The practical implication of these results can now be discussed. If it can be assumed that the high first-lactation heritability is not due to maternal effects, what effect does different heritabilities for different lactations and genetic correlations less than one have on estimates of breeding value? First-record deviations are defined as the unit of measurement for breeding value for this study. Deaton and McGilliard

(2) used the same standard, and have discussed the extrapolation of results based on this definition to subsequent performance.

A similar procedure was followed in this study. Three ways of setting up the selection index equations to predict a cow's first lactation breeding value were used for sets of daughters and dams having at least two lactations and for pairs having at least three lactations.

The first two procedures gave very similar results; therefore, both are presented side by side in Table 4. The first procedure was to use standardized variables and the correlation matrix as the left-hand sides of the equations. The correlation matrix was computed from the variance-covariance matrix, with the cow's first three records corresponding to the first three variables and the dam's first three records as the fourth, fifth, and sixth variables. Note that standardizing the variables really assumes that the different variances for different lactations are due to the lactation and not to selection, certainly not a completely true assumption. The right-hand sides, for example, when a cow's three records and three records of her dam were used, are the covariances between the genetic value for first-lactation deviation of the cow and (1) her first-lactation deviation, (2) her second-lactation deviation, (3) her third-lactation deviation, (4) her dam's first-lactation deviation, (5) her dam's second-lactation deviation, and (6) her dam's third-lactation deviation. When standardized variables are used these covariances become: h_1, $g_{12}(h_1 h_2)^{1/2}$, $g_{13}(h_1 h_2)^{1/2}$, $.5 \ h_1$, $.5 \ g_{12}(h_1 h_2)^{1/2}$, and $.5 \ g_{13}(h_1 h_3)^{1/2}$ where the h's are heritabilities estimated from daughter-dam regression and the g's are genetic correlations estimated from daughter-dam covariances. What effect selection has on these estimates is not known. If there had been no selection on both daughter and dam records, the genetic correlations should not be biased; whereas, selection is not likely to affect the heritability estimates if the daughter records are not selected.

The second procedure used the right-hand sides described above and standardized variables but, instead of actual correlations, the off-diagonal elements of the coefficient matrix were determined from repeatability estimates obtained from regression and from appropriate heritabilities and genetic correlations described above. For example, the first row of coefficients on the left-hand side of the equation for three records on the cow and three on her dam were 1, r_{12}, r_{13}, $.5 \ h_1$, $.5 \ g_{12}(h_1 h_2)^{1/2}$ and $.5 \ g_{13}(h_1 h_3)^{1/2}$ where r_{12} and r_{13} are regressions of second and third records on first, respectively.

TABLE 4

Weighting factors for predicting a cow's breeding value from her own and her dam's records, assuming no material effects and unequal heritabilities for different lactations

| | Weighting factors | | | | | | |
| Records used: | Cow's records | | | Dam's records | | | R |
	1st	2nd	3rd	1st	2nd	3rd	
Using standardized variables							
Cows and dams with two or more records							
Cow's	(.333)[a] .334[b]						(.577) .578
Cow's	(.267) .271	(.142) .109					(.617) .598
Dam's				(.167) .167			(.289) .289
Dam's				(.134) .135	(.071) .055		(.308) .299
Cow's and dam's	(.315) .315			(.116) .114			(.611) .610
Cow's and dam's	(.252) .256	(.133) .101		(.090) .093	(.044) .030		(.649) .628
Cows and dams with three or more records							
Cow's	(.314) .314						(.561) .560
Cow's	(.258) .258	(.133) .110					(.600) .585
Cow's	(.238) .234	(.010) .086	(.089) .074				(.616) .600
Dam's				(.157) .157			(.280) .280
Dam's				(.129) .129	(.063) .055		(.298) .293
Dam's				(.119) .118	(.047) .042	(.043) .036	(.305) .297
Cow's and dam's	(.297) .297			(.111) .110			(.594) .593
Cow's and dam's	(.223) .222	(.095) .081	(.083) .068	(.083) .083	(.029) .026	(.022) .018	(.646) .626
Using actual variances and covariances							
Cows and dams with two or more records							
Dam's				.167			.160
Dam's				.138	.055		.168
Cows and dams with three or more records							
Dam's				.157			.155
Dam's				.129	.058		.164
Dam's				.117	.038	.049	.170

[a] The weighting factors in the brackets were obtained with the coefficient matrix described for Procedure 1 in the text.
[b] The weighting factors were obtained with the coefficient matrix described for Procedure 2 in the text.

TABLE 5

Weighting factors for predicting a cow's breeding value from her own and her dam's records, assuming equal heritabilities for all lactations

Records used:	Weighting factors						R
	Cow's records			Dam's records			
	1st	2nd	3rd	1st	2nd	3rd	
Cows and dams with two or more records							
Cow's	(.250)ᵃ .250ᵇ	………	………	………	………	………	(.500) .500
Cow's	(.171) .158	(.171) .158	………	………	………	………	(.584) .562
Dam's	………	………	………	(.125) .125	………	………	(.250) .250
Dam's	………	………	………	(.085) .079	(.085) .079	………	(.292) .281
Cow's and dam's	(.236) .236	………	………	(.087) .086	………	………	(.529) .523
Cow's and dam's	(.159) .148	(.162) .150	………	(.051) .048	(.062) .055	………	(.615) .591
Cows and dams with three or more records							
Cow's	(.250) .250	………	………	………	………	………	(.500) .500
Cow's	(.180) .171	(.167) .155	………	………	………	………	(.584) .567
Cow's	(.155) .138	(.126) .122	(.108) .102	………	………	………	(.613) .592
Dam's	………	………	………	(.125) .125	………	………	(.250) .250
Dam's	………	………	………	(.088) .085	(.082) .078	………	(.289) .283
Dam's	………	………	………	(.076) .071	(.061) .060	(.053) .049	(.303) .295
Cow's and dam's	(.236) .236	………	………	(.088) .088	(.061) .060	………	(.530) .529
Cow's and dam's	(.142) .129	(.122) .117	(.102) .096	(.047) .042	(.044) .044	(.034) .031	(.643) .621

ᵃ The weighting factors in the brackets were obtained with the coefficient matrix described for Procedure 1 in the text.
ᵇ The weighting factors were obtained with the coefficient matrix described for Procedure 2 in the text.

Slightly lower correlations with breeding value were obtained for this procedure than for the first procedure (2% maximum difference in their values).

The third procedure was to estimate a daughter's first record from the known records of her dam, using the actual estimated variances and covariances among the records. Deaton and McGilliard (2) used this method of comparison.

Results in Table 4 partially agree with the tentative conclusions of Deaton and McGilliard (2), that the second and third records of dams have little value in predicting first-lactation performance of daughters, except that in this study a little more importance is shown for second and third lactations, but not much more. The third procedure, however, is not the selection index procedure. The first two methods are more nearly optimum in the maximum likelihood sense.

Another possibility, which seems more attractive, based on the comparison of half-sib correlations and regressions, is that heritability is the same for all three lactations. Therefore, to predict the breeding value for first-lactation production, a different set of equations is needed which takes maternal effects into account. Two methods were tried: 1) The coefficient matrix was the same as in the first procedure and (2) the coefficient matrix was the same as in the second procedure, both of which ignored the possibility of a genetic maternal effect. The right-hand sides were the same for both sets of equations. Heritability was assumed to be .25. Genetic correlations between first and second, and first and third records were manufactured by reducing or increasing the covariance between daughter and dam by the ratio of .125 to the actual regression. This manipulation yielded a genetic correlation from daughter-dam covariances between first and second records for those having at least two records of over 1.00. This was set to 1.00 so that the right-hand sides for the equations based on pairs having at least two records were: .25, .25, .125, and .125. Similar operations with the covariances of pairs having at least three records gave genetic correlations of .97 and .91 between first and second, and first and third, respectively. The right-hand sides were then .2500, .2425, .2275, .1250, .1212, and .1138.

Results from solving various sets of these equations are shown in Table 5. As expected, this procedure weights all lactation records more equally, although the first-lactation record generally receives slightly more weight than second or third records. The r values are also reduced

as a consequence of the lower heritability value. This reduction is most noticeable when only the first record is used for predicting breeding value. Consequently, later records appear to add more to the accuracy of prediction when using equal heritabilities than when using estimates which may be inflated by genetic maternal variance. The use of equal heritabilities and genetic correlations only slightly less than 1.00 gives results very similar to the classic formula for estimating breeding value where each record receives the equal weight, $h/[1 + (n - 1) \ r]$.

Conclusions

The following inferences are made under the assumption that deviations from herd-mate averages are appropriate for estimating genetic variances and covariances.

The results suggest that there is little difference in heritability of milk production expressed as deviations for the first, second, and third lactations. The estimate from intra-herd paternal half-sib correlations is about .24. Heritability estimates from daughter-dam regression are higher for first (.37) than for second (.30) and third (.24) lactation records. It is hypothesized that the higher daughter-dam estimate for the first lactation is due to genetic maternal effects which have smaller effects in succeeding lactations until, at the third lactation, the estimates from both methods are the same and are both derived from direct, additive genetic effects.

If maternal effects are not considered to be the cause of the difference in heritability estimates, the conclusion is that a second or a third record when the first record is known adds very little to the prediction of a first-record breeding value. If later records are used for predicting breeding value, their weights are less than half the weight given the first record.

The high genetic correlations between first and later records also suggest that if selection is for first-lactation performance progress for later lactation performance will be nearly as great as if selection were directly for later lactation performance. Some early studies stated the same conclusions [Hickman and Henderson (5) and Robertson and Khishin (9)]. Later, Gaalaas and Plowman (4) and Van Vleck (11) and White and Nichols (13) found that cows with high first-lactation performance were likely to remain in the herd longer and produce at a higher rate in later lactations than lower producers in the first lactation.

If, on the other hand, maternal effects are considered to be the cause of the difference in apparent heritability for different lactations,

adding a second or third record when the first record is known adds to the accuracy of predicting first-record breeding value. The added accuracy is very much the same as found from the classic formula $\{h/[1 + (n-1)\ r]\}^{1/2}$, which gives equal weight to each lactation.

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