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Comparison of Heritability Estimates from Daughter on Dam Regression with Three Models to Account for Production Level of Dam

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ABSTRACT

Three models were used to estimate heritabilities for milk yields at different production levels and for different years as twice the regression of daughter residual effects on dam residual effects. The denominator is the residual mean square for dams. The numerator is the difference between the residual term for sum of dam's and daughter's records and sum of residual terms for records of dams and daughters. Model 1 included sire of daughter and herd-year-season of daughters only. Model 2 included sire of daughter, herd-year-season of dam, and herd-year-season of daughter. Model 3 included sire of daughter and herd-year-season of dam and herd-year-season of daughter combination. The weighted mean estimates for each method were, respectively, .35, .38, .38 for milk production and .61, .67, .67 for fat test. Yearly time trends in heritability were slightly positive for both milk production and fat test. Standard errors of heritability estimates from model 1 were 40 to 50% smaller than those from models 2 and 3 due to the smaller number of effects in the model. Estimates for model 2 from low to high production levels averaged .30, .38, .38, and .42 for milk yield and .64, .68, .67, and .71 for fat test.

INTRODUCTION

Heritability estimates from daughter on dam regression have been primarily from records expressed from a contemporary average (2). The properties of such deviations are not well understood (6). Other estimates have been from residual variances and covariances of models that assume the herd-year-season (HYS) effect on the dams' records is the same for all daughters with records in a common HYS (9, 10). The assumption is that knowledge of the HYS of the daughter adequately accounts for the HYS effect on the dam's record. The method has the computational advantage of allowing the residual covariance to be estimated from analyses of daughter and dam records and their sum.

This study compared estimates of heritability from residual variances and covariances from daughter on dam regression for milk yield and fat test that were obtained from three models. The models account for the HYS effects of daughter and dam records in different ways (1) but share the computational advantage of allowing the residual covariance to be estimated from analysis of the sum of daughter and dam records as well as of daughter records and of dam records.

MODELS

An "ideal" model would account for HYS and sire of the daughter and HYS of the dam (shown as parent in the models):

$$\text{Daughter} = \text{HYS}_D + \text{Sire}_D + \text{Residual}_D$$
$$\text{Parent} = \text{HYS}_P + \text{Residual}_P$$

The model used by Van Vleck et al. (9) (model 1) accounts for the HYS and sire of the daughter. The model for the dam, however, approximates the HYS effect and includes the sire of the daughter as a dummy effect, expected to be essentially random with respect to dam's yield, that is, included to allow analysis of the sum of daughter and dam records and dam records with the same model as daughter records.

Model 1:

$$\text{Daughter} = \text{HYS}_D + \text{Sire}_D + \text{Residual(I)}_D$$
$$\text{Parent} = \text{HYS}_D^{**} + \text{Sire}_D^{*} + \text{Residual(I)}_P$$

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** = Approximation assumes a constant time difference between dam and daughter, and * = dummy factor.

Model 2 accounts for the HYS effect of the dam directly but includes dummy HYS effects for the daughter record and for the dam record to allow using the same computing procedure for daughter, dam, and sum of daughter and dam records.

Model 2:

$$\text{Daughter} = HYS_D + HYS_P^{**} + Sire_D + Residual(II)_D$$

$$\text{Parent} = HYS_D^{**} + HYS_P + Sire_D^{*} + Residual(II)_P$$

** = Dummy HYS effect, and * = dummy factor.

Model 3 essentially incorporates, as well, a dummy interaction effect between the HYS of the daughter and dam by using the HYS of daughter by HYS of dam subclass to account for the HYS effect on the daughter's record and HYS effect on the dam's record.

Model 3:

$$\text{Daughter} = HYS_{D-P} + Sire_D + Residual(III)_D$$

$$\text{Parent} = HYS_{D-P} + Sire_D^{*} + Residual(III)_P$$

* = Dummy factor.

The goal for using models 2 and 3 as compared with model 1 is to account more completely for the HYS effect of the dam's record, thereby allowing for a cleaner estimate of residual variance for the denominator of the estimate of heritability.

For all three models, the residual variances (daughter records, dam records, daughter plus dam records) were estimated as (total sum of squares minus reduction due to full model) divided by the residual degrees of freedom, which is number of pairs minus the rank of the coefficient matrix for the least squares equations for the full model.

If the models are written in matrix form as:

$$y = X\beta + Zu + e$$

what can be noticed is that X and Z, the matrices associating records with HYS and sire effects in the model (real or dummy), are the same when y represents the vector of daughter records (y_D), or y represents the vector of dam records (y_P) or when y represents the vector of daughter plus dam records (y_{D+P}). Then the solution vectors have the following relationships: $\hat{\beta}_{D+P} = \hat{\beta}_D + \hat{\beta}_P$, $\hat{u}_{D+P} = \hat{u}_D + \hat{u}_P$, and $\hat{e}_{D+P} = \hat{e}_{D+P} = \hat{e}_D + \hat{e}_P$, so that $\hat{\sigma}^2_{e_{D+P}} = \hat{\sigma}^2_{e_D} + \hat{\sigma}^2_{e_P} + 2\hat{\sigma}_{e_De_P}$ has expectation, $\sigma^2_{e_D} + \sigma^2_{e_P} + 2\sigma_{e_De_P}$. Thus, the estimate of $\sigma_{e_De_P}$ is $\hat{\sigma}_{e_De_P} = (\hat{\sigma}^2_{e_{D+P}} - \hat{\sigma}^2_{e_D} - \hat{\sigma}^2_{e_P})/2$.

Heritability was estimated from regression of the residual for daughter records on the residual for dam records as $h^2 = 2\hat{\sigma}_{e_De_P}/\hat{\sigma}^2_{e_P}$.

DATA

Data consisted of pairs of first lactation records of dams and daughters taken from 667,913 records used by Mirande and Van Vleck (4), further edited and matched in pairs for the present study. A dam could be matched with more than one daughter, although only one match per year of daughter freshening was allowed. The records included milk, fat, and fat test (mature equivalent, 2×, 305 d) for artificially sired Holstein cows obtained from the Northeast Dairy Records Processing Laboratory. Each record was classified into one of two yearly seasons (December through April and May through November) and into one of four management categories based on the associated rolling herd average for actual milk yield for the year (3, 4). For the present study, only matches for daughters freshening from 1965 through 1982 were used. Some pairs were excluded because the daughter initiated lactation less than 3 or more than 24 seasons after the dam. The resulting data file contained 193,858 pairs. The distribution of the records is summarized in Table 1.

RESULTS AND DISCUSSION

Residual degrees of freedom are considerably reduced for models 2 and 3 compared with model 1 as expected (Figure 1). Many of the levels of HYS effects in models 2 and 3 contain only one record so that record does not contribute to the residual variance. The residual degrees of freedom for model 3 are slightly less

TABLE 1. Distribution of daughter-dam pairs of records according to year of freshening and management level of the daughters.

Year	Management category				Total
	Low	Medium low	Medium high	High	
1965	196	573	922	402	2093
1966	271	853	1273	510	2907
1967	351	969	1555	691	3566
1968	424	1346	1832	867	4469
1969	555	1834	2252	1311	5952
1970	550	2085	2765	1464	6864
1971	711	2215	3125	1652	7703
1972	750	2641	3610	1757	8758
1973	984	3037	3797	1940	9758
1974	1213	3362	4088	2375	11,038
1975	1255	3742	4887	2372	12,256
1976	1414	4560	5229	2335	13,538
1977	1601	4434	5981	2568	14,584
1978	1560	5003	5795	2952	15,310
1979	1931	5778	7174	3351	18,234
1980	1956	6414	7836	3906	20,112
1981	2243	7181	8629	4795	22,848
1982[1]	1279	3989	5718	2882	13,868

[1] Partial year.

than for model 2 because of the greater number of factors in this model. The records for 1982 were for only a part of the year and resulted in fewer records and fewer degrees of freedom than might be expected.

Figure 2 shows how successful model 2 (and model 3) was in accounting for HYS effects of records of the dams. The residual standard deviations for daughter records were similar for all three models. Models 2 and 3, however, resulted in smaller residual standard deviations for dam records than model 1. As expected, the covariances of residuals for daughters and dams were similar for all three models (Figure 3), which indicates that the different heritability estimates are due to the ability of the methods to reduce the residual variance for records of dams. The values in Figure 3 correspond to estimates of the genetic standard deviation for milk yield if there were no selection on dams. The reduction in residual variances for dam records by models 2 and 3 and similar residual covariances resulted in larger estimates of heritability than by model 1.

Heritability estimates by year obtained by pooling records from all categories are in Figure 4 for milk yield and Figure 5 for fat test. In general, estimates from models 2 and 3 exceeded estimates from model 1. Estimates over time averaged by weighting by residual degrees of freedom were .35, .38, and .38 for milk yield and .61, .67, and .69 for fat test for models 1, 2, and 3—a nearly 10% increase for models 2 and 3 compared with model 1.

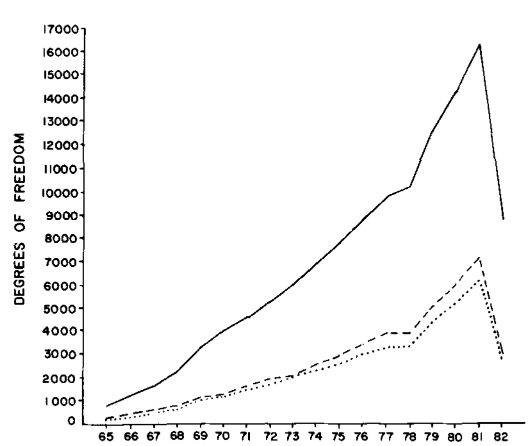

Figure 1. Degrees of freedom for residual variances overall management categories by year of freshening of daughters for models 1 (—), 2 (- - -), and 3 (. . .).

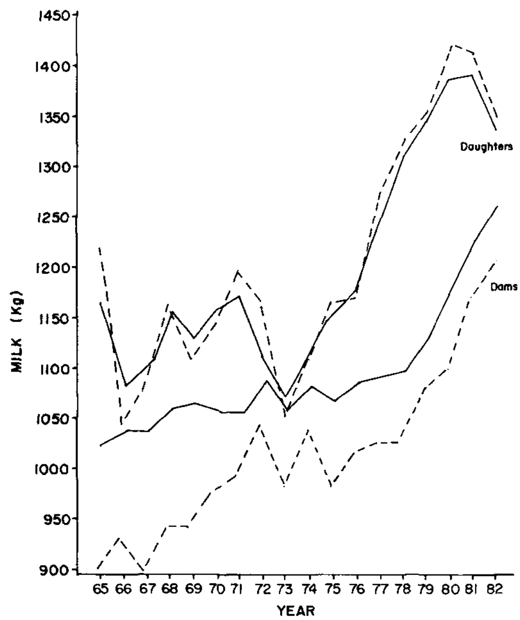

Figure 2. Estimates of residual standard deviations for records of daughters and of dams for milk yield for models 1 (—) and 2 (- - -) by year of freshening of daughters.

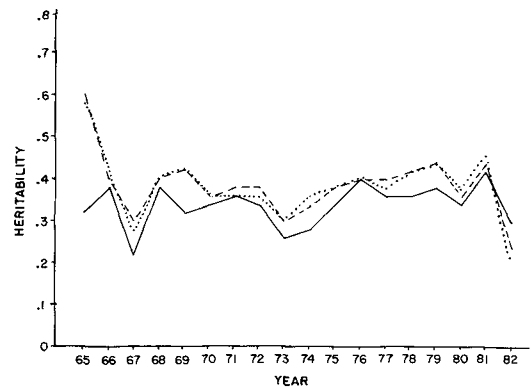

Figure 4. Estimates of heritability for milk yield for models 1 (—), 2 (- - -), and 3 (. . .) by year of freshening of daughters.

Heritability Estimates by Management Category

The heritability estimates by herd management category follow the pattern reported by Van Vleck et al. (10) and Powell and Norman (7), using daughter-dam regression, and Powell and Norman (8), using paternal half sister analyses. The smoothed estimates for milk yield for model 1 are shown in Figure 6 for model 1 and in Figure 7 for model 2. The smoothing was done by averaging the estimate for a year with those of the two preceding and the two following years. Therefore, the first 2 yr and the last 2 yr are not displayed. Heritability estimates (Table 2) average larger in higher than in lower production herds for both milk yield and fat test, although the proportional increase with higher management is greater for milk yield than for fat test. Models 2 and 3 increased heritability at all

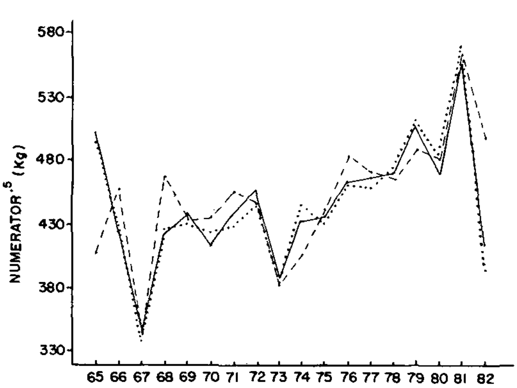

Figure 3. Estimates of the square root of twice the residual covariance of daughter and dam milk records (corresponding to estimates of the genetic standard deviation) for models 1 (—), 2 (- - -), and 3 (. . .) by year of freshening of daughters.

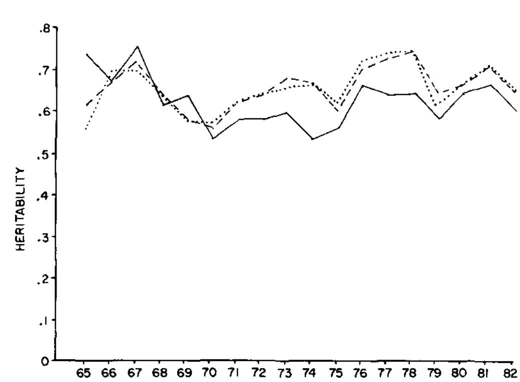

Figure 5. Estimates of heritability for fat test for models 1 (—), 2 (- - -), 3 (. . .) by year of freshening of daughters.

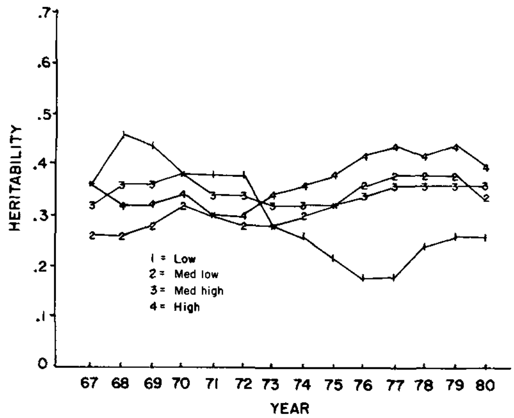

Figure 6. Estimates of heritability for milk yield for model 1 by year of freshening and management category of daughters.

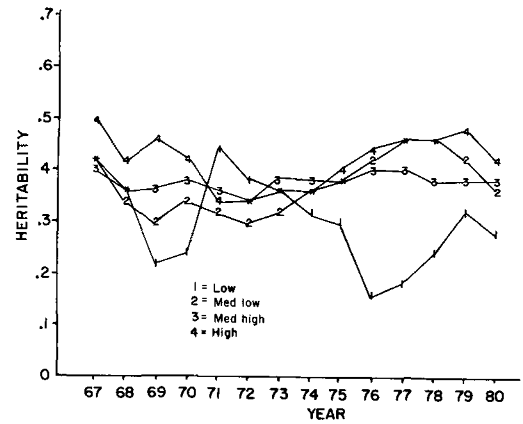

Figure 7. Estimates of heritability for milk yield for model 2 by year of freshening and management category of daughters.

production categories for both milk yield and fat test with values at the high end of reported estimates (2) for the high management: .42 for milk and .70 for fat test. Norman et al. (5) reported an estimate from a model apparently similar to models 2 and 3 of .40 for milk yield as compared with estimates of .34 from contemporary deviations in an earlier study (7).

The estimates in Figure 7 are more variable than those in Figure 6, as expected from the reduction in degrees of freedom and the corresponding increase in standard errors. The standard errors are approximately 2/(degrees of freedom)$^{.5}$. Standard errors for 1981 are shown in Table 3. The most noticeable difference in the patterns is that with model 1, heritability estimates for low management are large from 1967 through 1972 relative to the other management categories. With model 2, estimates for low management average considerably less from 1967 through 1972. However, when weighted by their degrees of freedom (Table 2), the same pattern emerges for all models except that estimates for models 2 and 3 are larger than for model 1.

Change in Heritability Estimates with Time

Regression coefficients from weighted regression of heritability estimates on year of daughter freshening are in Table 4. Weighting was by residual degrees of freedom. At higher management heritability estimates for milk yield tended to increase slowly. The increase was less for estimates for models 2 and 3 than for model 1. Slightly negative trend in heritability estimates for milk yield is seen for low management for all three models and for fat

TABLE 2. Weighted means of heritability estimates for milk and fat production.

	Milk production			Fat test		
Management category	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Low	.27	.30	.34	.59	.64	.66
Medium low	.34	.38	.39	.62	.68	.69
Medium high	.35	.38	.38	.64	.67	.68
High	.39	.42	.42	.66	.71	.70
Overall	.35	.38	.38	.61	.67	.67

TABLE 3. Standard errors for heritability estimates, 1981.

Model	Management category				Overall
	Low	Medium low	Medium high	High	
1	.06	.03	.03	.03	.02
2	.10	.05	.04	.05	.04
3	.11	.05	.04	.05	.04

TABLE 4. Coefficients for regression of heritability estimates for milk yield and fat test on year of freshening of daughters by management category and overall management categories.

Management category	Milk production			Fat test		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Low	−.0058	−.0023	−.0024	.0074	−.0038	−.0008
Medium low	.0069	.0001	.0010	.0010	−.0028	−.0034
Medium high	.0019	.0005	.0012	.0019	.0040	.0027
High	.0078	.0023	.0012	.0012	.0034	.0029
Overall	.0038	.0005	.0012	.0012	.0041	.0038

test at below average management for models 2 and 3.

CONCLUSIONS

Models 2 and 3, which more adequately account for the HYS effects on dam records, resulted in larger estimates of heritability for milk yield and fat test. Patterns over time suggest little change in heritability. Larger heritability estimates for both milk yield and fat test were found at higher management categories. Although many degrees of freedom are used in the estimation of dummy effects, models 2 and 3 seem to be better than model 1 because they more adequately account for HYS effects on the dam's record. The difference in heritability estimates, however, is of little practical importance.

A suggested model for future daughter-dam studies follows from the ideal model. For all records, calculate the residual term for a model containing HYS and sire effects. Also, calculate a residual term for a model containing only HYS effects. Then regress the first residual for daughters on the second residual for dams. Such a procedure would not account for the sampling variances of the residuals. An alternative would be to weight the regression by the inverse of the sampling variance of the residuals of the dams, which would be easy to compute. Based on the current results, heritability estimates are likely to be slightly larger but not enough larger to be practically important than those found in this study.

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