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### COMPARISON OF HERITABILITY ESTIMATES FROM DAUGHTER-DAM REGRESSION AND PATERNAL HALF-SIB CORRELATION

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#### ABSTRACT

Analysis of 60,000 pairs of daughter and dam first-lactation records expressed as deviations from herd-mate averages for five breeds yielded markedly different heritability estimates from daughter-dam regression than from paternal half-sib correlation. These results suggest that 18% of the within-herd variation is due to genetic maternal effects. The same records analyzed as mature equivalent records and not as deviations but by a sire by herd model did not show this difference. Confounding between year and sire effects probably biased the intraclass correlation estimates upward in the latter analysis, since year effects were not included in the statistical model.

Heritability estimates of milk production are numerous. Lasley (3) lists an average based on 30 such reports. Comparisons of estimates from daughter-dam regression and paternal half-sib correlation, however, are not frequent. Bradford and Van Vleck (1) reported a value of .44 from regression for 2,580 pairs and .25 from the intrasire correlation for first lactation deviations from herd-mate averages for the same artificially sired Holstein cows. Rendel et al. (4) and Gravert (2) both reported better agreement between the two methods of estimation used on the same data. Van Vleck and Bradford (5) later found almost identical estimates of heritability from daughter-dam (.448) and granddaughter-granddam (.444) regression on 10,419 first-lactation trios. The corresponding paternal half-sib estimate was .23. The estimated variance components from a sire by herd model for mature equivalent records and deviations gave heritability estimates of about .40 for mature equivalent records from intraherd daughter-dam and granddaughter-granddam regression and also from paternal half-sib correlations.

The analyses reported here are for larger numbers of daughter-dam pairs for the major dairy breeds. The purposes of the analyses were to determine whether the discrepancy between estimates was true for all breeds and to confirm that analyses of deviations and mature equivalent records give different results.

#### DATA

Paired first-lactation (305-day, 2×, M. E.)

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records where the daughter and dam were in the same herd were taken from the files of the New York Dairy Records Processing Laboratory. The records were made between 1950 and 1963. Daughter-dam regressions were computed for first-lactation records expressed as deviations from herd-mate averages for each breed. For cows sired artificially, daughter-dam regressions and the paternal half-sib correlation were computed. Grand paternal intraclass correlations were computed for records where the dam was artificially sired. In addition, variance components for mature equivalent records and deviations from herd-mate records of artificially sired Holstein cows were estimated for a random effects model composed of sire, herd, sire by herd, and residual effects. The same was done for records classified by grandsire and herd.

#### RESULTS AND DISCUSSION

Mean deviations from herd-mate averages and numbers of records and sires are given in Table 1. The mature equivalent means are shown for the artificially sired Holstein cows. The dams averaged considerably higher than the daughters, indicating an average selection differential for all breeds of about 500 lb of milk.

Heritability estimates for records expressed as deviations are presented in Table 2. There is remarkable agreement among the estimates for the five breeds for all pairs of daughters and dams. Not as much consistency appears in the estimates obtained from artificially sired cows. The difference between the estimates from regression and from intra-sire correlation was tested statistically by a  $5\times 2$  weighted squares of means analysis. The weights were the inverses of the estimated variances of the esti-

TABLE 1

Means, variances, and numbers of records, sires, herds, and sire by herd subclasses included in daughter-dam regressions and variance component analyses

|                        | Means                                   |           | Varian        | ices       | No.    |            |
|------------------------|---|-----------|---------------|------------|--------|------------|
| $\mathbf{Breed}$       | Daughters                               | Dams      | Daughters     | Dams       | Pairs  | Sires      |
|                        | Milk deviat                             | ion (10   | lb)           |            |        |            |
| Ayrshire—all pairs     | -30.9                                   | 18.7      | 31,798        | 27,153     | 2,500  |            |
| A.I. daughter in pai   | r -14.3                                 | 26.5      | 34,362        | 26,137     | 845    | 29         |
| Guernsey-all pairs     | -26.4                                   | 17.1      | 26,946        | 22,779     | 5,770  |            |
| A.I. daughter in pa    | ir -24.4                                | 23.3      | 28,119        | 23,050     | 2,215  | 82         |
| Holstein—all pairs     | -25.6                                   | 27.3      | 57,117        | 43,570     | 47,409 |            |
| A.I. daughter in par   |   | 36.3      | 57,570        | 43,598     | 20,850 | 317        |
| Grandsires*            |   |           |               | ,          |        |            |
| A.I. dam in pair       | -15.6                                   | 43.2      | *******       |            | 15,530 | 269        |
| Jersey—all pairs       | -7.3                                    | 29.1      | 25,335        | $22,\!104$ | 3,380  |            |
| A.I. daughter in pai   | r -1.2                                  | 39.1      | 25,632        | 21,545     | 1,263  | 58         |
| Brown Swiss-all pair   |   | 31.5      | 62,609        | 44,645     | 1,010  |            |
| A.I. daughter in pair  | 8.8                                     | 57.7      | 69,834        | 42,381     | 394    | 26         |
|                        | Mat                                     | ure equiv | alent means ( | (10 lb)    |        | No.        |
|                        | ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,, | Daught    |               |            | Herds  | Subclasses |
| Holstein A.I. daughter | in pair                                 | 1,346.    |               |            | 2,429  | 14,861     |
| Holstein A.I. dam in p |   | 1,338.    | ,             |            | 2,148  | 9,467      |

<sup>&</sup>lt;sup>a</sup> Number of grandsires in the analysis where dams were sired artificially.

mates. The analysis of variance appears in Table 3. The difference between the methods of estimation is statistically significant at any reasonable probability level. The F value to test differences in heritability among breeds is less than one, suggesting that there are no major differences in heritability among breeds. Note that the two estimates for a breed are not independent but were considered so for the analysis of variance.

The weighted estimate over all breeds of the difference between the daughter-dam estimate and the paternal half-sib estimate is 0.183. This estimates  $2.5 \ A_o A_m + A_m^s$  in the notation of Willham (8) where  $A_m^s$  is the additive maternal genetic variance and  $A_o A_m$  is the covariance between the additive genetic effects of the individual and the additive maternal genetic effects coming from its mother. This procedure assumes that none of the discrepancy between estimates is due to environmental correlation

TABLE 3

Analysis of variance of heritability estimates from daughter-dam regression and intra-sire correlation for artificially sired cows

| Source                    | d.f. | F-ratio |
|---------------------------|------|---------|
| Breeds                    | 4    | 0.8     |
| Method                    | 1    | 46.0    |
| Interaction (mean square) | 4    | (1.23)  |

between daughter and dam records or additive by additive genetic effects. Van Vleck and Bradford (5) have shown from daughter-dam and granddaughter-granddam regressions that additive by additive effects are unlikely to be important in accounting for the difference between methods of estimation. Van Vleck and Hart (6) concluded from daughter-dam regressions where the records were made in different herds that environmental correlations are probably not causing the discrepancy.

TABLE 2
Heritability estimated from the regression of daughter's deviation on dam's deviation from herd-mate average and paternal half-sib correlations of deviations from herd-mate averages

| Breed Ayrshire | All pairs    |         | A.I. sired cows |          |                      |        |  |
|----------------|--------------|---------|-----------------|----------|----------------------|--------|--|
|                | Daughter-dam |         | Daug            | hter-dam | Paternal<br>half-sib |        |  |
|                | .37          | (.042)a | .29             | (.078)   | .40                  | (.129) |  |
| Guernsey       | .41          | (.028)  | .40             | (.046)   | .17                  | (.048) |  |
| Holstein       | .42          | (.010)  | .43             | (.016)   | .24                  | (.023) |  |
| Grandsires     |              |         | .49             | (.018)   | .27 <sup>b</sup>     | (.047) |  |
| Jersey         | .36          | (.034)  | .39             | (.060)   | .18                  | (.066) |  |
| Brown Swiss    | .29          | (.074)  | .46             | (.126)   | .41                  | (.174) |  |

a Standard error of the estimate.

b Estimate from grand paternal correlation.

Even though the daughter-dam regressions are nearly the same for all breeds, there are differences among the breeds in the total amount of available genetic variation. This is seen in Table 1. The total variance of Jersey and Guernsey records is half that of Holstein records. On this basis alone, genetic progress can be only two-thirds as fast for those breeds as for the Holstein breed.

Van Vleck and Bradford (5) also reported for records analyzed as mature equivalent records and not as deviations that the heritability estimates were nearly equal for both the daughter-dam and the paternal half-sib methods. The analysis was for a sire by herd model for which components of variance were estimated. Similar analyses were performed on the larger number of records of artificially bred Holstein cows available in the current study. Results are shown in Table 4.

The general results are the same as reported earlier (5). The analyses of deviations by the more complex model lowered the daughter-dam estimates of heritability slightly but had little effect on the estimates from sire components of variance. Interestingly, the heritability estimates from grandsire components were nearly the same as those from sire components. Dropping the interaction effects out of the model changed the estimates only a small amount.

The comparison of the estimates for deviations and for mature equivalent records was

striking. The daughter-dam regressions were similar for both ways of expressing a record. Results of the variance component analysis were similar to those found earlier, except that with more data the mature equivalent estimates of heritability from sire components were even higher than those found for the trios of records. Instead of being the same magnitude as the daughter-dam estimates, the sire component estimates for the mature equivalent records were more than half again larger than the daughter-dam estimates. Perhaps a clue concerning the reason for this result was given in the analyses of grandsires by herds. The heritability estimates from grandsire components exceeded unity!

There is undoubtedly confounding of years or seasons with sires, which probably increases the sire component. This confounding could be greater with grandsires, thus biasing the grandsire component of variance upward even more than the sire component. Analyses (7) which also included year-season effects in the model have shown the within-herd estimate of heritability for mature equivalent records from sire components to be about 0.40. The year-season effects accounted for only about 2% of the total variation. However, the likelihood that all of the year-season variance would go into the sire component when year-seasons are ignored seems rather remote. A sizeable (7%) herd by vear-season interaction was reported by Van Vleck et al. (7). This interaction should increase

TABLE 4

Fraction of variance accounted for by sire (grandsire), herd, and sire (grandsire) by herd effects for mature equivalent records and deviations from herd-mate averages for A.I. Holstein daughters

|                            | Fraction of total variance |                |                 |                  |                       | Within<br>subclass<br>daugh-<br>ter-dam     | Four<br>times<br>within<br>herd<br>intra-<br>class |
|----------------------------|----------------------------|----------------|-----------------|------------------|-----------------------|---|--|
| Model includes             | $\sigma^2_s$               | $\sigma^2_h$   | $\sigma^2_{sh}$ | $\sigma^2_{\ e}$ | $\sigma^2{}_T$        | regres-<br>sion                             | corre-<br>lation                                   |
| Sires                      |                            |                | Deviations      |                  |                       |   |  |
| (S, H, SH, E)<br>(S, H, E) | $060 \\ .060$              | $.045 \\ .048$ | .046            | .841<br>.892     | 57,577<br>57,777      | .151<br>.183                                | .249 $.253$  |
| Grandsires                 |                            |                |                 |                  |                       |   |  |
| (S, H, SH, E)<br>(S, H, E) | 0.015 $0.016$              | .047<br>.053   | .050            | .888<br>.931     | $58,710 \\ 58,712$    | $\begin{array}{c} .177 \\ .196 \end{array}$ | $.244^{a}$ $.264^{a}$                              |
| Sires                      |                            | Mature         | equivalent      | records          |                       |   |  |
| (S, H, SH, E)<br>(S, H, E) | $083 \\ 008$               | .265<br>.266   | .013            | .614 $.626$      | $78,\!465$ $78,\!465$ | .158 $.160$                                 | $.588 \\ .590$                                     |
| Grandsires                 |                            |                |                 |                  |                       |   |  |
| (S, H, SH, E)<br>(S, H, E) | .054<br>.054               | .276<br>.278   | .023            | .647<br>.667     | 81,016<br>81,017      | .195<br>.170                                | 1.174 <sup>a</sup><br>1.203 <sup>a</sup>           |

<sup>&</sup>lt;sup>a</sup> Sixteen times the grandparental correlation.

the herd component for the present analyses, but does not appear to do so. This interaction may increase the sire component if the interaction is ignored. If this were the case, the size of the grandsire component should not be biased any more than the sire component. Yet the grandsire component appears to be inflated by a larger amount than does the sire component.

#### CONCLUSIONS

There is a marked difference in heritability estimates for first-lactation deviations from herd-mate averages between daughter-dam regression and paternal half-sib correlation. If this is a true difference and not a statistical artifact, about 18% of the within-herd variation in first-lactation milk records is due to maternal effects.

Analyses of both deviations and mature equivalent records with a sire by herd components of variance model gave different results for the paternal half-sib correlation. The daughter-dam regression estimates remained about 0.35 to 0.40. The heritability estimates derived from sire and grandsire components of variance for deviations by this model were not different from those obtained by ignoring herd effects. The corresponding estimates for mature equivalent records are outside the probable range of heritability, being much higher than the daughter-dam regressions.

Some factors either are biasing the heritability estimates from sire components downward for deviations or upward for mature equivalent records, or both. Further work should be done to discover the reasons for the differences between analyses of deviations from herd-mate averages and mature equivalent records.

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