RELATIVE MERITS OF FIVE MEASURES OF A DAIRY SIRE'S TRANSMITTING ABILITY 1, 2

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SUMMARY

Lactation milk and fat records of 6,949 daughters, 6,201 different dams, and the contemporary D.H.I.A. herd averages of 2,420 herds were studied, to compare five measures of a dairy sire's transmitting ability. They were the daughter average, daughter-dam difference, equal-parent index, daughter-contemporary herd difference, and daughter-contemporary-herd index. The daughters and dams were included in the D.H.I.A. proofs for 350 Guernsey and 486 Holstein sires used in artificial-breeding associations, and whose proofs were published for 1949–1951. A variance component analysis did not reveal any marked superiority for any of the measures, as determined by the percentage of the total variance comprised by the sire component for each of the measures. Sufficient data for the Holsteins were available for an empirical check of the reliability of these five measures. The simple daughter average appeared to be about as reliable as the equal-parent index or the daughter-herd index to predict future daughters' production for milk or fat. The D.H.I.A. herd average included the daughter in question and reduced the magnitude of the sire component for the herd measures. Use of a contemporary-herd average, which excludes the daughter in question in the two daughter-herd measures, should improve their merit as measures of a dairy sire's breeding value compared to the other measures in this study.

The performance of later daughters of sires selected for use in artificial-breeding associations, on the basis of proofs in one or two herds (natural), usually has reflected little of their sire's original apparent superiority (10, 11). Much of the disappointment in the performance of the artificially sired daughters undoubtedly has resulted because conventional methods of evaluating sire proofs have not adequately accounted for the influence of herd differences and changes in intra-herd environment. The use of the contemporary herd average has been suggested to avoid this glaring weakness (2, 8, 21). Most of the differences between herds are environmental (15, 18, 19) and, presumably, most of the intra-herd environmental changes are reflected by the herd average. Inasmuch as the herd average is readily available, could it be substituted for the dam's average in the daughter-dam difference and in the equal-parent index? If so, many more daughter-herd comparisons than daughter-dam comparisons would be permitted, since about one-half of the tested daughters have tested dams.

For these reasons, five measures of a sire's transmitting ability for milk and fat production, namely, the daughter average ($\bar{O}$), daughter-dam difference

Received for publication December 27, 1957.

1 Contribution from the North Carolina Agricultural Experiment Station and published with the approval of the Director of Research as Paper No. 872 of the Journal Series.

2 The data in this paper were taken from a dissertation presented by the senior author to the Graduate School, North Carolina State College, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, 1955.

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(O-D), equal-parent index (2 O-D), daughter-contemporary herd difference (O-H), and daughter-contemporary herd index (2 O-H) were studied. The latter two measures can be visualized simply by substituting the actual herd average for the dam’s average production in the daughter-dam difference and the equal-parent index.

**EXPERIMENTAL PROCEDURE**

*Data.* The data included lactation milk and fat records of 6,949 daughters, 6,201 different dams, and contemporary D.H.I.A. herd averages for 2,420 herds. The daughters and dams were included in the D.H.I.A. proofs of 350 Guernsey and 486 Holstein sires used in artificial-breeding associations in the United States, whose proofs were published for the years 1949–1951.

To be included in this study, each daughter had to have a contemporary D.H.I.A. herd average for at least one lactation and a dam with a record. The contemporary herd average used was the herd average completed the year following the year the individual cow freshened. This average was chosen after considering that many herds are on a reporting year which does not coincide with the calendar year, that the cow makes a record 10 mo. after freshening, and that the D.H.I.A. average is listed according to the year in which it is completed. Except for the D.H.I.A. herd average, all records were adjusted to a 305-day, 2 × milking, mature equivalent (M.E.) basis.

Naturally and artificially sired daughters of the sires were analyzed separately. The average production of the four groups studied is shown (Table 1).

<table>
<thead>
<tr>
<th>Group</th>
<th>Daughters</th>
<th>Sires</th>
<th>Herds</th>
<th>Milk</th>
<th>%</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>G-N</td>
<td>1,865</td>
<td>636</td>
<td>558</td>
<td>5,677</td>
<td>4.93</td>
<td>426</td>
</tr>
<tr>
<td>G-A</td>
<td>438</td>
<td>324</td>
<td>276</td>
<td>8,066</td>
<td>4.89</td>
<td>392</td>
</tr>
<tr>
<td>H-N</td>
<td>3,582</td>
<td>1,239</td>
<td>1,078</td>
<td>12,901</td>
<td>3.68</td>
<td>472</td>
</tr>
<tr>
<td>H-A</td>
<td>1,064</td>
<td>795</td>
<td>672</td>
<td>12,210</td>
<td>3.59</td>
<td>436</td>
</tr>
</tbody>
</table>


The lower production level for the artificially sired daughters, as compared to the naturally sired animals, is typical of the situation throughout the country as reported from D.H.I.A. summaries (11).

**Analysis.** Each of the five measures was expressed as a linear equation or model which included the effects of herd, sire-within-herd, and within-sire and herd effects on an intra-state basis. The sire-by-herd effect was not included, since previous analysis of similar data had shown it to be small (13) and the sire-by-herd interaction variance could not be estimated with reasonable precision from these data. Using these models, the variances for each of the measures were expressed in terms of the components of variance for the simple daughter average. The details of procedure are described elsewhere (6), but the resulting
expressions for the variances, pertinent to the interpretation of later results, are as follows:

\[ \sigma^2(\bar{y}) = \sigma^2_s + \frac{\sigma^2_h}{\text{No. of herds}} + \frac{\sigma^2_e}{\text{No. of daughters}} \]

\[ \sigma^2(\bar{y} - \bar{\bar{y}}) = \sigma^2_s + \frac{2 \sigma^2_h (1-r)}{\text{No. of herds}} + \frac{\sigma^2_e + \sigma^2\theta}{\text{No. of daughters}} \]

\[ \sigma^2(2 \bar{y} - \bar{\bar{y}}) = 4 \sigma^2_s + \frac{\sigma^2_h (5-4r)}{\text{No. of herds}} + \frac{2 \sigma^2_e + 5 \sigma^2\theta}{\text{No. of pairs}} \]

\[ \sigma^2(\bar{y} - \bar{\bar{y}}) = \sigma^2_s \left( 1 - \frac{2m_{il}}{n_i} + \frac{n^2_{il}}{n^2_{l.}} \right) + \frac{\sum_{ij \neq 1} n_{il} \sigma^2_e}{\text{No. of herds}} + \frac{\sigma^2_e \left( 1 - \frac{1}{n_{il}} \right)}{\text{No. of daughters}} \]

\[ \sigma^2(2 \bar{y} - \bar{\bar{y}}) = \sigma^2_s \left( 4 - \frac{4m_{il}}{n_i} + \frac{n^2_{il}}{n^2_{l.}} \right) + \frac{\sum_{ij \neq 1} n^2_{il} \sigma^2_e}{\text{No. of herds}} + \frac{\sigma^2_e \left( 4 - \frac{3}{n_{il}} \right)}{\text{No. of daughters}} \]

Where: \( \sigma_s^2 \) denotes the variance due to the additive genetic effects of the sire, possibly some epistatic effects (\( \sigma_{e1}^2 \)) and genetic environmental interactions.

\( \sigma_h^2 \) denotes the variance due to the genetic and environmental effects common to a herd but different from these effects on other herds.

\( \sigma_c^2 \) denotes the variance peculiar to the cow. This includes existing errors in measurement of the record and environmental influence not accounted for by the herd effect (\( \sigma^2 \)) and the genetic effects not accounted for by the sire. Hence, \( \sigma_c^2 = \sigma_s^2 + \sigma_i^2 + 3 \sigma_e^2 + \sigma^2 \) where \( \sigma_d^2 \)

represents the dominance variance.

\( \sigma_{e1}^2 \) denotes the variance due to differences in the additive breeding value of the individual cow and, as used, possibly includes some epistatic variance and genotype environmental interaction.

\( \sigma_{e2}^2 \) differs from \( \sigma_{e1}^2 \) in that it does not include the additive genetic variance attributed under random mating to the dam and to chance at segregation (\( \sigma_{e2}^2 = \sigma_d^2 + \sigma_i^2 + \sigma^2 \)).
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r is the correlation between the herd effects for the daughter and her
dam or herd mates.

n_{di} is the number of daughters of the sire under consideration in the
ith herd.

\[ \sum_{ij \neq i} n_{ij} \] is the number of daughters of other sires in the ith herd.

Individual analyses of variance were computed for each of the five measures
for milk and fat production for the two breeds, divided into natural and artificial
groups. From each, estimates of the variance components were derived for herd,
sire-within-herd, and within-herd and sire effects on an intra-state basis using
Method I of Henderson (7).

Since averages of records, differences, and indexes were used in the several
measures, it was necessary to adjust the error variances to a single record basis,
so that the results could be presented independent of the numbers of records per
animal characteristic of these data. The formula used to adjust the error variance
of an average of n records was

\[
\sigma_e^2 = \sigma_s^2 \frac{\bar{n}}{1 + (\bar{n} - 1) r_{dd}}
\]

where \( \bar{n} \) is the harmonic mean of the number of records per cow. The repeat-
ability (\( r_{cd} \)) of successive records of a cow was taken as 0.50 for milk and 0.40
for fat production, as based on values from the literature (1, 9, 12, 14, 20). The
harmonic means in these data were as follows:

<table>
<thead>
<tr>
<th></th>
<th>Daughters</th>
<th>Dams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guernsey, natural</td>
<td>1.32</td>
<td>2.18</td>
</tr>
<tr>
<td>Guernsey, artificial</td>
<td>1.22</td>
<td>2.08</td>
</tr>
<tr>
<td>Holstein, natural</td>
<td>1.32</td>
<td>2.27</td>
</tr>
<tr>
<td>Holstein, artificial</td>
<td>1.22</td>
<td>2.14</td>
</tr>
</tbody>
</table>

Similarly, the error variances for the other measures were adjusted to a single
record or comparison basis with appropriate formulae being derived for each.

The fraction of the total estimated variance in each measure, which was
represented by the sire component estimate, was computed. Since some of the
sires had both naturally and artificially sired daughters, an empirical check was
obtained of the values from the variance component analysis. Correlations for
each of the five measures of a sire’s transmitting ability were computed between
naturally and artificially sired daughters and between a specific number of first
and later artificially sired daughters for the Holstein data.

RESULTS AND DISCUSSION

Variance component analysis. Since the individual lactation milk and fat
records are basic to the interpretation of the other measures, the importance
of the several sources of variation in them is of primary concern. The components
of variance for milk and fat for the daughter average are given in the second,
third, and fourth columns of Table 2. The percentages of the intra-state variance which they represent are given in the second column of Table 3.

Results comparable to those obtained in this study were secured by Legates et al. (13), in an analysis of records of 5,234 Guernsey and 17,581 Holstein daughters of sires used in artificial-breeding associations. The Guernsey sire components accounted for 5.8 and 4.1% of the intra-state variance in milk and fat, respectively, in their data. The comparable percentages for the Holstein sire components were 7.7 and 7.8, respectively. In a study of New York Holstein data (5), the sire component accounted for only 2.8% of the variance in lactation fat records. Carter (3) has since reported that adjustments for year, herd, and season effects removed much nongenetic variation. Following these adjustments, the sire component accounted for 7.7% of the variation.

The differences in the results for the Guernseys and the Holsteins in this study possibly could be explained by sampling, since the number of Guernsey sires was considerably less than the number of Holstein sires. However, lower values for the Guernsey sire components were also obtained in the study by Legates et al. (13).

Values for the herd component of variance are in general agreement with those in the literature (13, 16, 17). Herd differences generally accounted for a larger percentage of the total variance for the artificial groups.

Estimates of the variance components for all five measures for milk and fat are given (Table 2). The variances which are estimated are the functions of the components presented in the investigation for each measure, e.g., for the daughter-dam difference, the \( \sigma_d^2 \) as computed estimates the expected \( 2 \sigma_h^2 (1-r) \). Inspection of the values (Table 2) reveals several circumstances which could be predicted on the basis of the formulae derived for the variances of the measures. The sire variance for the equal-parent index is about four times as large as the corresponding components for the daughter average; likewise, the sire variance for the daughter-herd index is about four times the corresponding component for the daughter-herd difference. The sire variances for the two measures using the herd average were consistently smaller than they were for their counterparts, the daughter-dam difference and the equal-parent index. This was to be expected, since the cow's own record was a part of the herd averages used.

The sire component for the daughter-dam difference was expected to be comparable in size to the component for the daughter average. Values for the daughter-dam difference are higher for the Holsteins. Time trends during the interval the daughters and dams made their records could have contributed to this; but, if they were present, they should have influenced the equal-parent index to as great an extent. The small number of degrees of freedom for sires, however, does not rule out the possibility that sampling may be responsible.

One criterion for evaluating a measure of a sire's transmitting ability is to require the measure to maximize sire differences, thereby permitting more accurate choices among sires. The extent to which this is accomplished can be expressed in terms of the fraction of the total variance which is represented by
TABLE 2

Estimates of variance components for all five measures

<table>
<thead>
<tr>
<th>Group</th>
<th>Herd</th>
<th>Sire</th>
<th>Error*</th>
<th>Herd</th>
<th>Sire</th>
<th>Error*</th>
<th>Herd</th>
<th>Sire</th>
<th>Error*</th>
<th>Herd</th>
<th>Sire</th>
<th>Error*</th>
<th>Herd</th>
<th>Sire</th>
<th>Error*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G-N</td>
<td>9,734</td>
<td>890</td>
<td>20,535</td>
<td>5,722</td>
<td>2,418</td>
<td>37,096</td>
<td>24,662</td>
<td>4,502</td>
<td>94,732</td>
<td>4,414</td>
<td>525</td>
<td>20,628</td>
<td>19,338</td>
<td>2,633</td>
<td>81,641</td>
</tr>
<tr>
<td>G-A</td>
<td>3,067</td>
<td>9,701</td>
<td>15,136</td>
<td>3,317</td>
<td>7,685</td>
<td>33,099</td>
<td>-3,302</td>
<td>37,718</td>
<td>81,154</td>
<td>-20</td>
<td>10,969</td>
<td>13,357</td>
<td>-2,055</td>
<td>40,157</td>
<td>60,481</td>
</tr>
<tr>
<td>H-N</td>
<td>18,871</td>
<td>8,321</td>
<td>42,561</td>
<td>5,870</td>
<td>13,673</td>
<td>38,514</td>
<td>39,429</td>
<td>32,726</td>
<td>199,197</td>
<td>1,078</td>
<td>8,740</td>
<td>44,060</td>
<td>21,615</td>
<td>30,040</td>
<td>171,823</td>
</tr>
<tr>
<td>Fat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G-N</td>
<td>2,588</td>
<td>344</td>
<td>4,830</td>
<td>1,400</td>
<td>561</td>
<td>8,996</td>
<td>6,441</td>
<td>1,285</td>
<td>22,822</td>
<td>841</td>
<td>262</td>
<td>4,861</td>
<td>4,592</td>
<td>1,161</td>
<td>19,221</td>
</tr>
<tr>
<td>G-A</td>
<td>2,371</td>
<td>594</td>
<td>3,647</td>
<td>1,950</td>
<td>28</td>
<td>7,823</td>
<td>4,257</td>
<td>3,180</td>
<td>19,293</td>
<td>1,691</td>
<td>992</td>
<td>3,576</td>
<td>5,800</td>
<td>2,905</td>
<td>13,322</td>
</tr>
<tr>
<td>H-N</td>
<td>2,717</td>
<td>990</td>
<td>5,946</td>
<td>961</td>
<td>1,493</td>
<td>11,066</td>
<td>6,060</td>
<td>3,552</td>
<td>28,078</td>
<td>1,392</td>
<td>771</td>
<td>6,071</td>
<td>3,590</td>
<td>3,045</td>
<td>23,834</td>
</tr>
<tr>
<td>H-A</td>
<td>3,017</td>
<td>806</td>
<td>4,191</td>
<td>1,451</td>
<td>1,173</td>
<td>7,824</td>
<td>6,837</td>
<td>3,652</td>
<td>19,839</td>
<td>996</td>
<td>710</td>
<td>4,254</td>
<td>5,527</td>
<td>2,908</td>
<td>16,748</td>
</tr>
</tbody>
</table>

* Within-sire, within-herd—among paternal sisters in the same herd.
the sire component. Table 4 presents such a comparison for all five measures. Close inspection of this table reveals that no measure has emerged as superior. Although the percentages for the Guernsey natural group are markedly lower than those for the other three groups, there is no consistent trend in any one measure either for milk or for fat.

Using the variance components, repeatability values for each measure can be computed for any number of daughters or herds. For example, the repeatability of the daughter average

\[ \frac{\sigma_s^2}{\sigma_s^2 + \frac{\sigma_h^2}{\text{No. of herds}} + \frac{\sigma_e^2}{\text{No. of daughters}}} \]

for fat for a Holstein sire with five artificially sired daughters in five herds is 0.36 or, for ten daughters in ten herds, 0.53. Usually, natural proofs include daughters in just one or two herds. For a Holstein sire with five daughters all in one herd, the repeatability of the daughter average for fat is 0.20 or for a sire with ten daughters all in one herd it is 0.23. In each case these values indicate the fraction of the superiority of a bull’s first daughters that would be expected to show in a later group of daughters located in different herds. For the other measures considered, such values represent the fraction of the superiority based on that particular measure that one would expect to be exhibited by a later group of progeny, evaluated with that measure.

Much hope has been expressed for the two herd measures. Perhaps their sire components might have represented higher percentages of the total variance if the most contemporary herd average could have been secured in all cases.

Since the cow’s own record could not be separated from the herd average, herd size also introduced another important factor. For herds smaller than the average of 24.2 cows for Holsteins and 26.4 cows for Guernseys in this study, the sire variance of these measures is reduced at an increasing rate as the herd size diminishes; whereas, the sire variance is reduced little for herds larger than those in the study. This is shown by the repeatability estimates for ten daughters in ten herds for the daughter-herd difference for fat production of the Holstein artificial group for 10, 20, 30, and 40 cow herds of 0.44, 0.54, 0.56 and 0.57, re-

### Table 3

<table>
<thead>
<tr>
<th>Breed group</th>
<th>Daughter</th>
<th>Daughter-dam</th>
<th>2 Daughter-dam</th>
<th>Daughter-herd</th>
<th>2 Daughter-herd</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Milk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G-N</td>
<td>2.9</td>
<td>5.3</td>
<td>3.6</td>
<td>2.1</td>
<td>2.5</td>
</tr>
<tr>
<td>G-A</td>
<td>34.8</td>
<td>17.4</td>
<td>31.7</td>
<td>41.7</td>
<td>39.9</td>
</tr>
<tr>
<td>H-N</td>
<td>11.9</td>
<td>14.0</td>
<td>12.1</td>
<td>16.2</td>
<td>13.8</td>
</tr>
<tr>
<td>H-A</td>
<td>11.8</td>
<td>17.2</td>
<td>16.9</td>
<td>12.8</td>
<td>13.2</td>
</tr>
<tr>
<td>Fat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G-N</td>
<td>4.4</td>
<td>5.1</td>
<td>4.2</td>
<td>4.4</td>
<td>4.6</td>
</tr>
<tr>
<td>G-A</td>
<td>9.0</td>
<td>3.3</td>
<td>11.9</td>
<td>15.8</td>
<td>12.6</td>
</tr>
<tr>
<td>H-N</td>
<td>10.2</td>
<td>11.0</td>
<td>9.4</td>
<td>9.4</td>
<td>10.0</td>
</tr>
<tr>
<td>H-A</td>
<td>10.1</td>
<td>11.2</td>
<td>12.0</td>
<td>11.0</td>
<td>11.5</td>
</tr>
</tbody>
</table>
spectively. With the use of a contemporary herd average which excludes the daughter in question, the two daughter-contemporary-herd measures would be likely to give higher percentage values for the sire component than those in this study.

**Empirical analysis.** Correlations between each of the five measures of a sire’s transmitting ability based on naturally or artificially sired daughters, and the performance of a specific number of future artificially sired daughters, were computed. For this analysis, all five of the naturally sired daughters were from the same herd, and each of the artificially sired daughters or comparisons for a sire were from a different herd. With these restrictions, only the Holstein groups had sufficient data to warrant analysis. Correlation values obtained from this phase of the study are given (Table 4).

While the correlations do not show a decisive margin in favor of any one of the measures, the simple daughter average appears to be almost as reliable as any of the other measures. The correlation values involving the daughter average, the equal-parent index, and the daughter-herd index are of approximately the same magnitude. The correlations for the daughter-herd difference were generally slightly lower than these three; whereas, those for the daughter-dam difference were lowest in seven of the eight comparisons. Use of a nonpaternal stablemate’s average instead of the herd average probably would improve the merits of the two daughter-herd measures, because in the average- and small-sized herds a significant portion of the sire effect is removed when the herd average is subtracted from the daughter average.

The empirical correlations between the original natural proof and a later artificial proof were consistently lower than those for an original and a later artificial proof for the one comparable situation. This has been the experience of many in artificial breeding (10). There was no real difference in the ranking of the measures between the artificial and the natural groups.

These results are in partial agreement with those of Carter et al. (4). They found the daughter-dam difference and a daughter-contemporary difference to be 

<table>
<thead>
<tr>
<th>Variables</th>
<th>No. of sires</th>
<th>Measure</th>
<th>Daughter</th>
<th>Daughter-dam</th>
<th>2 Daughter-dam</th>
<th>Daughter-herd</th>
<th>2 Daughter-herd</th>
</tr>
</thead>
<tbody>
<tr>
<td>(X_1) and (X_2)</td>
<td>39</td>
<td>Milk</td>
<td>0.20</td>
<td>-0.11</td>
<td>0.18</td>
<td>0.18</td>
<td>0.19</td>
</tr>
<tr>
<td>(X_2) and (X_3)</td>
<td>47</td>
<td>Milk</td>
<td>0.28</td>
<td>0.08</td>
<td>0.30*</td>
<td>0.21</td>
<td>0.28</td>
</tr>
<tr>
<td>(X_1) and (X_2)</td>
<td>39</td>
<td>Fat</td>
<td>0.26</td>
<td>0.15</td>
<td>0.24</td>
<td>0.27</td>
<td>0.32</td>
</tr>
<tr>
<td>(X_2) and (X_3)</td>
<td>47</td>
<td>Fat</td>
<td>0.34*</td>
<td>0.16</td>
<td>0.35*</td>
<td>0.40**</td>
<td>0.38**</td>
</tr>
</tbody>
</table>

\* Denotes statistical significance at 5% level of probability.
\** Denotes statistical significance at 1% level of probability.
\* Denotes statistical significance at 1% level of probability.

\(X_1\) = First five naturally sired daughters.
\(X_2\) = Next five artificially sired daughters.
about equal in merit. However, in their study the daughter average appeared to be of little value, and the equal-parent index was slightly less dependable than the daughter-dam and the daughter-contemporary comparisons.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to F. J. Verlinden and the staff of the Statistical Laboratory at North Carolina State College. They also wish to acknowledge the assistance of J. F. Kendrick of the Dairy Herd Improvement Section of USDA in assembling the data for the study.

REFERENCES
