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Heritability Estimates of Milk Production from Daughter on Dam Regression by Year and Management Level

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ABSTRACT

Heritability estimated by year of freshening for first-lactation milk records of artificially sired Holstein cows in the northeastern United States from daughter on dam regression averaged about .34 on the linear scale and .31 on the logarithmic scale. Little change could be detected from 1965 to 1982. Number of daughter-dam pairs was 197,338. Heritability estimates on the .5 and .4 power scales always were bounded by estimates on the linear and log scales. Heritability estimates were smallest in low management levels. Residual standard deviations for measurements to the .4 power were similar for all levels of management for a particular year, although a tendency was for the residual standard deviation to be larger in the low management level and smaller in the high management level.

INTRODUCTION

Mirande and Van Vleck (7) presented evidence that heritability of milk yield of Holstein cows as estimated from among sire variation has been decreasing in the northeastern United States. Their results also indicated smaller heritability for low and high levels of management as compared to middle levels of management. They, along with Danell (1) and Powell and Norman (9), have reviewed previous studies. Powell and Norman (9) presented estimates from daughter on dam regression by level of production typical of results for records expressed as deviations from herdmate averages. Norman et al. (8), however, found estimates obtained from herdmate deviations often are not in agreement with estimates obtained from nondeviated records.

The purpose of this analysis was to estimate heritability from daughter on dam regression using residuals from a Method 3 analysis (3) for variance components to determine whether heritability has decreased with time and whether heritability is the same for different management levels. Selection of dams is not expected to reduce the estimates as selection of parents would reduce estimates of heritability from among sire variance. To compare the effect of transformations on heritability estimates, analyses for milk records were carried out on the linear (nontransformed) scale and three transformed scales — the logarithmic, square root, and .4 power scales.

MATERIALS AND METHODS

The data set was chosen to be the same as that used by Mirande and Van Vleck (7) so that the two sets of estimates could be compared but the data set was limited to records for which daughters and dams were matched within a herd. The records included first-lactation milk, fat, and fat test records [mature equivalent (ME), 2×, 305-d] of artificially sired (AI) Holstein cows obtained from the Northeast Dairy Records Processing Laboratory (DRPL) at Ithaca, NY. Records for each year included records of up to the first 80 daughters of each sampling bull freshening in that year and records of daughters of proven bulls resulting after the sampling proof was available also freshening in that year. Number of records was 667,913 from which 197,338 daughter-dam pairs were obtained. Each year from 1960 through 1982 was broken into two seasons of freshening to create herd-year-season effects. Seasons were December of the preceding calendar year through April and May through November. To assign records to four management groups we used the associated rolling herd average as of May of the same year as calculated
The three dividing points for each year were those used by Mirande and Van Vleck (7) and were the average rolling herd average for that year and the average plus or minus the standard deviation of the associated rolling herd averages. Although the distribution of records might be expected to be 1/6, 1/3, 1/3, and 1/6 in the four groups, there were, in fact, fewer than expected in the low management group.

The model used for estimation of residual variance and covariance components was:

\[
\begin{bmatrix}
y_1 \\
y_2 \\
y_1+y_2
\end{bmatrix} =
\begin{bmatrix}
X & 0 & 0 \\
0 & X & 0 \\
0 & 0 & X
\end{bmatrix}
\begin{bmatrix}
h_1 \\
h_1^* \\
h_1 + h_1^*
\end{bmatrix} +
\begin{bmatrix}
Z & 0 & 0 \\
0 & Z & 0 \\
0 & 0 & Z
\end{bmatrix}
\begin{bmatrix}
s_1 \\
s_1^* \\
s_1 + s_1^*
\end{bmatrix} +
\begin{bmatrix}
e_1 \\
e_2 \\
e_1 + e_2
\end{bmatrix}
\]

where \( y_1, y_2 \) are vectors of daughter and dam records; \( h_1 \) is the vector of herd-year-season effects associated with daughter records; \( h_1^* \) is the vector that approximates herd-year-season effects associated with dam records; \( s_1 \) is the vector of sire effects associated with daughter records; \( e_1, e_2 \) are corresponding vectors of random residual effects; and \( X, Z \) are matrices associating effects with records.

The \( s_1^* \) vector in the model for dam records is a vector of dummy variables to allow for estimating the residual covariance from separate analyses of \( y_1, y_2, \) and \( y_1 + y_2 \). The \( h_1^* \) vector is an approximation, because with the same incidence matrix, \( X \), for both \( h_1 \) and \( h_1^* \) (also to allow for covariance estimation), the implied assumption is that all dams of daughters freshening in a herd-year-season also freshen in the same herd-year-season (although different from herd-year-season of the daughter). The approximation probably increases residual variance of dam records and thus decreases the estimate of heritability. Nevertheless, the approximation seems preferable to assuming herd-year-season effect (or herd effect only) on daughter record is identical to herd-year-season effect on dam record or to analyzing herdmate deviations where herdmates of records of daughter and dam members of each pair are likely to consist of mostly different cows. In contrast to Van Vleck (12), who used a random effects model, the estimates of residual components of variance and covariance were computed by Method 3 of Henderson (3):

\[
V_{e_1} = \frac{(y_1^2 - R(h_1, s_1))}{d},
\]

\[
V_{e_2} = \frac{(y_2^2 - R(h_1^*, s_1^*))}{d},
\]

\[
Ve_1 + e_2 = \frac{(y_1 + y_2)'(y_1 + y_2) - R(h_1 + h_1^*, s_1 + s_1^*)}{d}
\]

\[
Ve_1 + e_2 = \frac{(y_1 + y_2)'(y_1 + y_2) - R(h_1 + h_1^*, s_1 + s_1^*)}{d}
\]

\[
Ve_1 + e_2 = \frac{(y_1 + y_2)'(y_1 + y_2) - R(h_1 + h_1^*, s_1 + s_1^*)}{d}
\]

The \( R(\ ) \) indicates reduction in sum of squares due to fitting the model and \( d = N - r(X,Z) \) with \( N \), the total number of pairs, and \( r(X,Z) \), the rank of the coefficient matrix for ordinary least squares equations for the model.

Heritability then was estimated as:

\[
h^2 = \frac{2C_{e_1} e_2}{Ve_2}.
\]

Number of records and degrees of freedom are in Table 1. Analyses of records from before 1965 are not shown because of the limited number of degrees of freedom.

**RESULTS AND DISCUSSION**

Estimates of heritability are in Figure 1 for first-lactation milk yield on linear and logarithmic scales by year of freshening of the daughters. A smoothing procedure was employed to eliminate yearly fluctuations. The median for each consecutive set of five estimates was chosen to represent a year. For example, the median from estimates for 1969, 1970, 1971, 1972, 1973 represents 1971 and the median from estimates for 1970, 1971, 1972, 1973, 1974 represents 1972. Smoothed estimates are in Figure 2. Neither representation indicates that heritability has decreased. If any trend is detectable, the trend seems to be for a slight increase in later years.

In all cases the heritability estimate for the linear scale was greater than the estimate for...
TABLE 1. Summary statistics of data used for estimating heritability from daughter on dam regression by year of first freshening for milk yield and fat test.

<table>
<thead>
<tr>
<th>Year of freshening</th>
<th>No. of records</th>
<th>Degrees of freedom</th>
<th>Daughter means (kg)</th>
<th>Standard errors of heritability</th>
<th>Daughter residual variance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Milk</td>
<td>Test</td>
<td>Milk</td>
</tr>
<tr>
<td>1965</td>
<td>2097</td>
<td>791</td>
<td>7078</td>
<td>3.66</td>
<td>.073</td>
</tr>
<tr>
<td>1966</td>
<td>2910</td>
<td>1284</td>
<td>7131</td>
<td>3.67</td>
<td>.054</td>
</tr>
<tr>
<td>1967</td>
<td>3568</td>
<td>1662</td>
<td>7022</td>
<td>3.67</td>
<td>.046</td>
</tr>
<tr>
<td>1968</td>
<td>4474</td>
<td>2244</td>
<td>7012</td>
<td>3.66</td>
<td>.039</td>
</tr>
<tr>
<td>1969</td>
<td>5959</td>
<td>3237</td>
<td>7089</td>
<td>3.65</td>
<td>.033</td>
</tr>
<tr>
<td>1970</td>
<td>6877</td>
<td>3932</td>
<td>7244</td>
<td>3.64</td>
<td>.029</td>
</tr>
<tr>
<td>1971</td>
<td>7711</td>
<td>4521</td>
<td>7248</td>
<td>3.64</td>
<td>.028</td>
</tr>
<tr>
<td>1972</td>
<td>8722</td>
<td>5261</td>
<td>7142</td>
<td>3.64</td>
<td>.027</td>
</tr>
<tr>
<td>1973</td>
<td>9780</td>
<td>5949</td>
<td>6979</td>
<td>3.60</td>
<td>.025</td>
</tr>
<tr>
<td>1974</td>
<td>11048</td>
<td>6830</td>
<td>7222</td>
<td>3.63</td>
<td>.022</td>
</tr>
<tr>
<td>1975</td>
<td>12279</td>
<td>7767</td>
<td>7339</td>
<td>3.64</td>
<td>.022</td>
</tr>
<tr>
<td>1976</td>
<td>13557</td>
<td>8835</td>
<td>7415</td>
<td>3.70</td>
<td>.023</td>
</tr>
<tr>
<td>1977</td>
<td>14608</td>
<td>9715</td>
<td>7612</td>
<td>3.73</td>
<td>.023</td>
</tr>
<tr>
<td>1978</td>
<td>15351</td>
<td>10178</td>
<td>7878</td>
<td>3.69</td>
<td>.023</td>
</tr>
<tr>
<td>1979</td>
<td>18268</td>
<td>12607</td>
<td>8052</td>
<td>3.62</td>
<td>.019</td>
</tr>
<tr>
<td>1980</td>
<td>20149</td>
<td>14239</td>
<td>8281</td>
<td>3.62</td>
<td>.016</td>
</tr>
<tr>
<td>1981</td>
<td>22905</td>
<td>16385</td>
<td>8334</td>
<td>3.63</td>
<td>.016</td>
</tr>
<tr>
<td>1982</td>
<td>13895</td>
<td>8784</td>
<td>8287</td>
<td>3.64</td>
<td>.023</td>
</tr>
</tbody>
</table>

1 kg²/1000.

The logarithmic scale. Smoothed estimates indicate that on the linear scale heritability may be 10% (.34 vs. .31) greater. This result contrasts to among-sire estimates of Mirande and Van Vleck (7), who found no difference on linear and log scales and Hill et al. (4), who reported a higher estimate for the log scale. Heritability estimates on the square root and .4 power scales in all years were bounded by estimates on the linear and log scales and thus are not shown. Standard errors of heritability estimates for unsmoothed estimates on the linear scale

![Figure 1](https://example.com/figure1.png)  
Figure 1. Heritability estimates from daughter on dam regression for first-lactation milk yield by year of freshening on the linear and logarithmic scales. Estimates on the square root and .4 power scales were bounded by the estimates on the linear and log scales.

![Figure 2](https://example.com/figure2.png)  
Figure 2. Smoothed estimates of heritability from daughter on dam regression for first-lactation milk yield by year of freshening on linear and logarithmic scales. Smoothed estimates are medians of five consecutive estimates.
TABLE 2. Ratios of daughter to dam residual variances for milk records (X) on the linear, logarithmic, and .5 and .4 power scales.

<table>
<thead>
<tr>
<th>Year of freshening</th>
<th>Scale</th>
<th>X</th>
<th>log X</th>
<th>X⁻⁰⁵</th>
<th>X⁻⁰⁴</th>
</tr>
</thead>
<tbody>
<tr>
<td>1965</td>
<td></td>
<td>1.23</td>
<td>1.24</td>
<td>1.21</td>
<td>1.21</td>
</tr>
<tr>
<td>1966</td>
<td></td>
<td>1.09</td>
<td>1.00</td>
<td>1.05</td>
<td>1.04</td>
</tr>
<tr>
<td>1967</td>
<td></td>
<td>1.09</td>
<td>1.17</td>
<td>1.12</td>
<td>1.12</td>
</tr>
<tr>
<td>1968</td>
<td></td>
<td>1.13</td>
<td>1.31</td>
<td>1.21</td>
<td>1.23</td>
</tr>
<tr>
<td>1969</td>
<td></td>
<td>1.09</td>
<td>1.17</td>
<td>1.12</td>
<td>1.13</td>
</tr>
<tr>
<td>1970</td>
<td></td>
<td>1.16</td>
<td>1.24</td>
<td>1.19</td>
<td>1.19</td>
</tr>
<tr>
<td>1971</td>
<td></td>
<td>1.21</td>
<td>1.35</td>
<td>1.26</td>
<td>1.28</td>
</tr>
<tr>
<td>1972</td>
<td></td>
<td>1.04</td>
<td>1.16</td>
<td>1.08</td>
<td>1.10</td>
</tr>
<tr>
<td>1973</td>
<td></td>
<td>0.99</td>
<td>1.13</td>
<td>1.05</td>
<td>1.06</td>
</tr>
<tr>
<td>1974</td>
<td></td>
<td>1.03</td>
<td>1.16</td>
<td>1.08</td>
<td>1.09</td>
</tr>
<tr>
<td>1975</td>
<td></td>
<td>1.13</td>
<td>1.28</td>
<td>1.18</td>
<td>1.19</td>
</tr>
<tr>
<td>1976</td>
<td></td>
<td>1.16</td>
<td>1.23</td>
<td>1.18</td>
<td>1.19</td>
</tr>
<tr>
<td>1977</td>
<td></td>
<td>1.29</td>
<td>1.36</td>
<td>1.30</td>
<td>1.31</td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td>1.38</td>
<td>1.44</td>
<td>1.39</td>
<td>1.39</td>
</tr>
<tr>
<td>1979</td>
<td></td>
<td>1.38</td>
<td>1.36</td>
<td>1.35</td>
<td>1.33</td>
</tr>
<tr>
<td>1980</td>
<td></td>
<td>1.37</td>
<td>1.33</td>
<td>1.33</td>
<td>1.33</td>
</tr>
<tr>
<td>1981</td>
<td></td>
<td>1.27</td>
<td>1.32</td>
<td>1.27</td>
<td>1.27</td>
</tr>
<tr>
<td>1982</td>
<td></td>
<td>1.10</td>
<td>1.18</td>
<td>1.12</td>
<td>1.13</td>
</tr>
</tbody>
</table>

The residual variance for dam records is expected to be smaller than for daughter records if any selection has occurred. The reduction in variance due to selection is well known not to bias the regression coefficient. If variation has been increasing with time, however, estimates of heritability may be biased downward (12) because for data with daughters freshening in a particular year the dam variance would be expected to be reduced more than the covariance. If the increase in variation with time is less on one measurement scale than another, then estimates for that scale would be less biased. To examine whether larger estimates on the linear scale as compared to the log scale may be due to the change in variance with time, ratios of residual variances of daughter to dam were calculated and are in Table 2. Ratios suggest that heritability estimates on the linear scale are less biased than on the transformed scales by increase in variance with time – for 3 yr the ratio is larger on the linear scale and for 15 yr the ratio is larger on the log scale.

Heritability estimates for fat test are in Figure 3. Daughter-dam estimates fluctuate much less over time than paternal half-sib estimates of Mirande and Van Vleck (7). Estimates are on or above the upper end of the range of previous estimates (5).

Residual variance of fat test increased by 30 to 50% after 1975 (Table 1), although the increase does not seem related to an increase in mean fat test.

Smoothed heritability estimates for milk yield by management group are in Figure 4. Except for estimates for low management

Figure 3. Heritability estimates from daughter on dam regression for first-lactation fat test by year of freshening.

Figure 4. Smoothed heritability estimates from daughter on dam regression for first-lactation milk yield by year of freshening and herd management group.
prior to 1974, the pattern is for lower estimates of heritability with low management and higher estimates for medium and high management groups. Heritability seems to be somewhat larger for high management than middle management. Degrees of freedom for low management were less than 100 before 1969 and less than 250 before 1972, which may explain the pattern of high estimates early in the period and low estimates late in the period. Smoothed heritability estimates by management for fat test are in Figure 5.

Analyses of Mirande and Van Vleck (7) suggested that a power transformation slightly less than the square root transformation (power of .5) for milk records might equalize variation over management groups because the square root transformation equalized residual variation for different management groups better than on the linear or log scales. Smoothed residual standard deviations for the four management groups for milk to the .4 power are in Figure 6 expressed as a percentage of the largest residual standard deviation (low management level in 1977, 2.55 kg$^4$).

The pattern is similar to that for the square root scale for the analyses of Mirande and Van Vleck (7), although residual standard deviations are smaller for the high than for the low management group. This transformation and the square root transformation seem to equalize residual variation across management groups better than the logarithmic transformation, although the log transformation seems to equalize variation over time better than the .5 and .4 power scales.

**CONCLUSIONS**

Heritability of first-lactation milk yield and fat test has not decreased in the AI population of Holstein cows in the northeastern United States. The decrease in heritability estimates obtained from variation among sampling sires in the earlier study must reflect something other than an overall reduction in genetic variation. Selection of parents of sampling sires, however, cannot explain all of the reduction.

Heritability for milk yield measured on the usual (linear) scale is apparently about 10% greater than for measurements on the logarithmic scale (approximately .34 vs .31). Heritability for milk yield seems lower in low management than in medium or high management groups.

These results and the results of the previous study, that the residual variance on the log scale is greatest in the low management groups, suggest that more research is needed to find an appropriate transformation to equalize residual variation and at the same time properly weight records according to heritability for that environment. One possibility would be a multiple trait genetic evaluation considering milk yield to be a different trait in different management groups as suggested by Falconer (2) and other studies (6, 10, 11). Difficulties with such a procedure are numerous: 1) the

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**Figure 5.** Smoothed heritability estimates from daughter on dam regression for first-lactation fat test by year of freshening and herd management group.

**Figure 6.** Smoothed residual standard deviations for first-lactation milk yield to the .4 power by year of freshening and herd management group expressed as a percentage of the residual standard deviation for the low management group in 1977, 2.55 kg$^4$. 

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problem of defining the optimum number of management groups as well as how to assign records to those groups; 2) the computational requirements for a multiple trait evaluation and, 3) how to obtain reliable estimates of the genetic correlations across herd groups. A last difficulty may be in explaining to dairy producers how to use four or more correlated evaluations on each bull for milk yield (or dollar value) in their specific herd.

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