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THE RELATIONSHIPS BETWEEN HERITABILITY AND TWIN EFFICIENCY VALUES CALCULATED FROM TWIN UNIFORMITY TRIALS

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Since the inception of experimentation with monozygotic twins the terms "heritability" and "twin efficiency value" have been used widely. Heritability may be defined as the proportion of total variance in a population which is attributable to genetic differences between individuals. Twin efficiency value is defined as the number of pairs of unrelated animals in an experiment which one pair of monozygotic twins can replace without altering the statistical precision of the experiment (Bonnier, et al., 1946). The formula for calculating heritability from twin data has been given by Thoele and Hervey (1952) while formulae for twin efficiency values have been presented by Dick and Whittle (1951) and Carter (1951). It is apparent that the more highly heritable a trait is the more efficient monozygotic twins will be in relation to unrelated animals in experiments involving this trait. Therefore, the two terms must be related in some way but a scrutiny of the literature reveals no presentation of this relationship. In this paper, the relationships between the formulae for heritability (Thoele and Hervey, 1952) and twin efficiency values (Carter, 1951; Dick and Whittle, 1951) will be derived.

Table 1

<table>
<thead>
<tr>
<th>Factor</th>
<th>d.f.</th>
<th>Mean Square</th>
<th>Components of Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between pairs</td>
<td>n-1</td>
<td>MB</td>
<td>2σ_H^2 + σ_E^2 + σ_HE^2</td>
</tr>
<tr>
<td>Within pairs</td>
<td>n</td>
<td>MW</td>
<td>σ_H^2 + σ_E^2</td>
</tr>
<tr>
<td>Total</td>
<td>2n-1</td>
<td>MB + MW</td>
<td>2(σ_H^2 + σ_E^2 + σ_HE^2)</td>
</tr>
</tbody>
</table>

The analysis of variance of a twin uniformity trial, according to Thoele and Hervey (1952), is shown in table 1, where n = the number of pairs of monozygotic twins, MB = mean square (variance) between pairs, MW = mean square (variance) within pairs, σ_H^2 = variance due to heredity, σ_E^2 = variance due to the environment.
and \( \sigma_{HE}^2 \) = variance due to interaction between heredity and environment. It should be pointed out here that the analysis of variance table has been reproduced without change from the paper of Thoele and Hervey (1952). However, a slight correction is required as the interaction between heredity and environment would be found not in the within-pair mean square but would be found entirely in the between-pair mean square. This correction does not influence the results of the present paper.

Variance due to heredity

\[
\sigma_H^2 = \frac{\text{Mean square between pairs} - \text{Mean square within pairs}}{2} = \frac{M_B - M_W}{2}
\]

Heritability

\[
H = \frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2 + \sigma_{EH}^2} = \frac{2\sigma_H^2}{2(\sigma_H^2 + \sigma_E^2 + \sigma_{EH}^2)} = \frac{M_B - M_W}{M_B + M_W}
\]

The formulae are as follows:

Dick and Whittle (1951)

\[
E_1 = \frac{1}{2} \left( \frac{M_B}{M_W} - 1 \right)
\]

Carter (1951)

\[
E_2 = \frac{1}{2} \left( \frac{M_B}{M_W} + 1 \right)
\]

Thoele and Hervey (1952)

\[
H = \frac{M_B - M_W}{M_B + M_W}
\]

where \( E \) = twin efficiency value, the subscript denoting which formula was used.

\( H \) = heritability.

\( M_B \) = mean square (variance) between pairs.

\( M_W \) = mean square (variance) within pairs.

Relationship of \( E_1 \) and \( E_2 \),

\[
E_1 = \frac{1}{2} \left( \frac{M_B}{M_W} - 1 \right)
\]

\[
E_1 + 1 = \frac{1}{2} \left( \frac{M_B}{M_W} - \frac{1}{2} \right) + 1
\]

\[
E_1 + 1 = \frac{1}{2} \left( \frac{M_B}{M_W} + \frac{1}{2} \right)
\]

\[
E_1 + 1 = \frac{1}{2} \left( \frac{M_B}{M_W} + 1 \right) = E_2
\]

\[
E_1 + 1 = E_2, \text{ or } E_1 = E_2 - 1
\]
Relationship between \( H \) and \( E_1 \) and \( E_2 \),

\[
E_1 = \frac{1}{2} \left( \frac{M_B - M_w}{M_w} \right) \tag{1}
\]

\[
\therefore \quad E_1 = \frac{1}{2} \left( \frac{M_B - M_w}{M_w} \right)
\]

\[
\therefore \quad E_1 = \frac{M_B - M_w}{2M_w}
\]

\[
\therefore \quad M_B - M_w = 2M_w \cdot E_1
\]

Substituting, \( 2M_w \cdot E_1 \) for \( M_B - M_w \) in equation (3).

\[
H = \frac{2M_w \cdot E_1}{M_B + M_w}
\]

Rearranging,

\[
\frac{E_1}{H} = \frac{M_B + M_w}{2M_w}
\]

\[
\therefore \quad \frac{E_1}{H} = \frac{1}{2} \left( \frac{M_B + M_w}{M_w} \right)
\]

\[
\therefore \quad \frac{E_1}{H} = \frac{1}{2} \left( \frac{M_B + M_w}{M_w} + 1 \right)
\]

\[
\therefore \quad \frac{E_1}{H} = E_2 \quad \text{from equation (2)}
\]

\[
\therefore \quad \frac{E_1}{H} = E_1 + 1 \quad \text{from equation (4)}
\]

\[
\therefore \quad H = \frac{E_1}{E_1 + 1} \quad \text{(5)}
\]

and \( H = \frac{E_1 - 1}{E_2} \quad \text{(6)} \)

The solution of equations (5) and (6) for \( E \) gives

\[
E_1 = \frac{H}{1 - H} \quad \text{(7)}
\]

and \( E_2 = \frac{1}{1 - H} \quad \text{(8)} \)
Summarizing,

\[ E_1 = E_2 - 1 \quad \text{and} \quad E_2 = E_1 + 1 \] .......................... (4)

\[ H = \frac{E_1}{E_1 + 1} \] .......................... (5)

\[ \delta H = \frac{E_2 - 1}{E_2} \] .......................... (6)

*This formula was in error in the abstract in Jour. Dairy Sci. 38(6): 616. 1955.

\[ E_1 = \frac{H}{1 - H} \] .......................... (7)

\[ E_2 = \frac{1}{1 - H} \] .......................... (8)

Figure 1 shows the relationship between Carter's efficiency value and heritability. Carter's formula (1951) was selected in preference to that of Dick and Whittle (1951) because the former gives a value of one if heritability is zero, whereas the latter formula gives a value of zero. A value of one should be expected as a pair of monozygotic twins would be as useful as a pair of unrelated animals when heritability was zero, provided maternal effects were negligible.
It will be seen that the efficiency changes but little (1 to 10) over the range 0 to 90 percent heritability while at heritabilities higher than 95 percent the change in efficiency is great per percentage unit of heritability. As heritability approaches 100 percent the efficiency value approaches infinity. Figure 1 could be enlarged if it were desired to find efficiency values graphically from heritability estimates.

**SUMMARY**

The relationships between the heritability and twin efficiency values in twin uniformity trials have been derived.

It has been shown that the twin efficiency value changes slowly with changes in heritability below 70 or 80 percent and thereafter much more rapidly, especially at heritabilities of 95 percent and above.

**REFERENCES**


