THE RELATIONSHIPS BETWEEN HERITABILITY AND TWIN EFFICIENCY VALUES CALCULATED FROM TWIN UNIFORMITY TRIALS[1]

R. LAIRD[2] AND L. O. GILMORE

Department of Dairy Science, Ohio Agricultural Experiment Station, Wooster and Institute of Genetics, The Ohio State University

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

The analysis of variance of a twin uniformity trial

FACTOR	d.f.	MEAN SQUARE		COMPONENTS OF VARIANCE
Between pairs	n-1	M_B	$=$	$2\sigma_H^2 + \sigma_E^2 + \sigma_{HE}^2$
Within pairs	n	M_W	$=$	$\sigma_H^2 + \sigma_{HE}^2$
Total	2n-1			
		$M_B + M_W$	$=$	$2\left(\sigma_H^2 + \sigma_E^2 + \sigma_{HE}^2\right)$

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, M_B = mean square (variance) between pairs, M_W = mean square (variance) within pairs, σ_H^2 = variance due to heredity, σ_E^2 = variance due to the environment

and σ_{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 herdity

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

$$\text{Heritability} = \frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2 + \sigma_{EH}^2}$$

$$= \frac{2\sigma_H^2}{2(\sigma_H^2 + \sigma_E^2 + \sigma_{HE}^2)}$$

$$= \frac{M_B - M_W}{M_B + M_W}$$

The formulae are as follows:

Dick and Whittle (1951) $\qquad E_1 = \frac{1}{2}\left(\frac{M_B}{M_W} - 1\right)$ ....(1)

Carter (1951) $\qquad E_2 = \frac{1}{2}\left(\frac{M_B}{M_W} + 1\right)$ ....(2)

Thoele and Hervey (1952) $\qquad H = \frac{M_B - M_W}{M_B + M_W}$ ....(3)

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,

$$E_1 \quad = \frac{1}{2}\left(\frac{M_B}{M_W} - 1\right) \dots\dots\dots\dots\dots\dots\dots\dots(1)$$

$$\therefore \quad E_1 + 1 = \frac{1}{2}\left(\frac{M_B}{M_W}\right) - \frac{1}{2} + 1$$

$$\therefore \quad E_1 + 1 = \frac{1}{2}\left(\frac{M_B}{M_W}\right) + \frac{1}{2}$$

$$\therefore \quad E_1 + 1 = \frac{1}{2}\left(\frac{M_B}{M_W} + 1\right) = E_2$$

$$E_1 + 1 = E_2, \text{ or } E_1 = E_2 - 1 \dots\dots\dots\dots\dots\dots\dots(4)$$

Relationship between H and E_1 and E_2,

$$E_1 = \frac{1}{2}\left(\frac{M_B}{M_W} - 1\right) \quad\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots (1)$$

$$\therefore \quad E_1 = \frac{1}{2}\left(\frac{M_B - M_W}{M_W}\right)$$

$$\therefore \quad E_1 = \frac{M_B - M_W}{2M_W}$$

$$\therefore \quad M_B - M_W = 2M_W \cdot E_1$$

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,

$$\frac{E_1}{H} = \frac{M_B + M_W}{2M_W}$$

$$\therefore \quad \frac{E_1}{H} = \frac{1}{2}\left(\frac{M_B + M_W}{M_W}\right)$$

$$\therefore \quad \frac{E_1}{H} = \frac{1}{2}\left(\frac{M_B}{M_W} + 1\right)$$

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

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

$$\therefore \quad H = \frac{E_1}{E_1 + 1} \quad\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots (5)$$

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

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

$$E_1 = \frac{H}{1 - H} \quad\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots (7)$$

$$\text{and} \quad E_2 = \frac{1}{1 - H} \quad\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots (8)$$

Summarizing,

$$E_1 = E_2 - 1 \text{ and } E_2 = E_1 + 1 \dotfill (4)$$

$$H = \frac{E_1}{E_1 + 1} \dotfill (5)$$

$$^3H = \frac{E_2 - 1}{E_2} \dotfill (6)$$

_____

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

$$E_1 = \frac{H}{1 - H} \dotfill (7)$$

$$E_2 = \frac{1}{1 - H} \dotfill (8)$$

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.
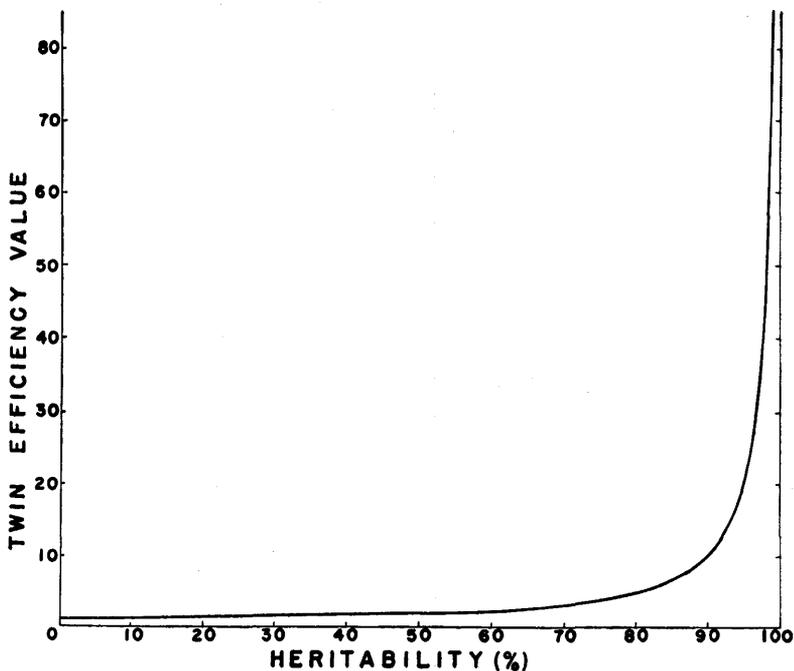

FIGURE 1
Chart showing relationship between heritability and twin efficiency value of Carter (1951).

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

Bonnier, G., A. Hansson, and T. Düring. 1946. Tvillingmetodens Effektivitet. (The efficiency of the twin method.) Kungl. Lantbruksakademiens Tidskrift. 85: 455.

Carter, A. H. 1951. Paper presented at the 7th New Zealand Science Congress. Cited in Hancock.

Dick, I. D. and P. Whittle. 1951. Contributions to the statistical design of identical twin experiments. New Zealand Jour. Sci. Technol. B33(3): 145.

Hancock, J. 1954. Monozygotic twins in cattle. Adv. Genetics 6: 141. Academic Press, New York.

Thoele, H. W. and M. C. Hervey. 1952. Growth uniformity trials with identical twin dairy heifers—estimates of heritability and twin efficiency. Jour. Dairy Sci. 35: 494. Paper presented at Forty-Seventh Annual Meeting Amer. Dairy Sci. Assoc.