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Adjustment of Heritabilities Estimated by Correlation Coefficients for Typical Forest Tree Breeding Experiments

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The coefficient of the regression of offspring values on parental values for measurable traits has been widely used as an estimator of heritability. Use of the correlation coefficient eliminates certain biases which are characteristic of the regression coefficient as an estimator (Frey and Horner, 1957), but the correlation coefficient has some biases associated with it which are related to number of trees per family and the coefficient of relationship among family members. The discussion presented here shows that the genetic interpretation of the correlation coefficient is usually quite different from that of the regression coefficient. Equations and tabulations are derived for empirical adjustment of the correlation coefficient as an estimator of heritability.

The concept of heritability as the ratio of additive genetic variance to total phenotypic variance is widely accepted (Lush, 1940, Falconer, 1960; Hanson, 1963). The concept of estimating heritability by the regression coefficient for offspring values regressed on parent values has been generally adopted (Kempthorne and Tanden, 1953; Falconeh, 1960; Hill, 1970; Ollivier, 1974).

Theory behind the use of the regression coefficient as an estimator of heritability was first developed by R. A. Fisher (1918) based on earlier work by Galton (1889), and Weinberg (1910). Falconer's (1960) outline of the application of this concept to animal breeding can be directly applied to forestry in many instances. Falconer's notation, therefore, will be used throughout the present paper so that the reader may refer to a readily available and understandable text. Page numbers without references are from Falconer (1960).

Genetic covariance between an offspring and one of its parents is equal to $\frac{1}{2}$ the additive genetic variance (V_A) for the random mating population (p. 162). If an array of family means for a particular trait was derived from half-sib families, and these means were regressed on the corresponding single-parent values for the same trait, then the estimated regression coefficient (b_{OP}) would be interpreted as:

$$b_{OP} = \frac{\sigma_{XY}}{\sigma^2_X} = \frac{\frac{1}{2}V_A}{V_P} \qquad (1)$$

where σ_{XY} = covariance of parents and offspring,
σ^2_X = variance of parental values,
V_A = additive genetic variance, and
V_P = phenotypic variance of parents.

If values for both parents were known for a series of full-sib families, the regression coefficient for full-sib family means regressed on mid-parent values (the mean of the 2 parents of a full-sib family) would be interpreted as:

$$b_{OP}\frac{\sigma_{XY}}{\sigma^2_X} = \frac{\frac{1}{2}V_A}{\frac{1}{2}V_P} = \frac{V_A}{V_P} \qquad (2)$$

where terms are as defined for equation (1).

Two points to note from equations (1) and (2) are that the covariance of family means with single-parent values is the same as with mid-parent values (p. 154), and that the variance of mid-parent values (σ^2_X) is only $\frac{1}{2}$ that for single-parent values.

Heritability (h^2) is defined as:

$$h^2 = \frac{V_A}{V_P} \qquad (3)$$

Therefore, two times the regression coefficient for half-sib family means regressed on single-parent values has

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been used as an estimate of heritability. Also, the regression coefficient for full-sib family means regressed on mid-parent values has been used as a direct estimate of heritability (p. 169).

The regression coefficient (b_{OP}) is not an appropriate estimator of heritability when there are differences in variances and/or means between offspring and parent generations. Such a situation is often encountered in forest tree breeding when offspring are grown on different sites than those of their parents and are measured at younger ages than their parents. The problem was recognized by FREY and HORNER (1957) who suggested that scales of both the offspring and parental values be coded into units of standard deviations. The regression coefficient for coded arrays is equivalent to the correlation coefficient (r_P) for the uncoded scales. When there are no differences in variances or means of uncoded arrays, (r_P) and (b_{OP}) will be identical:

$$r_P = \frac{\sigma_{XY}}{\sqrt{\sigma^2_X\sigma^2_Y}} = \frac{\sigma_{XY}}{\sqrt{\sigma^2_X\sigma^2_X}} = \frac{\sigma_{XY}}{\sigma^2_X} = b_{OP} \qquad (4)$$

if $\sigma^2_Y = \sigma^2_X$, and $\bar{Y} = \bar{X}$

The correlation coefficient (r_P) as an estimator of heritability would seem to be the best choice because if scaling is needed, the correlation coefficient does the job; if scaling is not needed, it does no harm. When (r_p) is used to estimate (h^2), biases associated with the number of offspring per parent and the phenotypic intraclass correlation can be eliminated as shown below.

If a correlation coefficient (r_1) is derived from half-sib family means regressed on single-parent values of non-inbred, unrelated parents, it should be interpretedd as:

$$r_1 = \frac{\sigma_{XY}}{\sqrt{\sigma^2_X\sigma^2_Y}} = \frac{\frac{1}{2}V_A}{\sqrt{V_P \cdot \left[\frac{1+(n-1)t}{n}\right]V_P}} \qquad (5)$$

where $\sigma^2_Y = \left[\frac{1+(n-1)t}{n}\right]V_P$ = phenotypic variance of family means (p. 179), n = number of offspring per family, and t = the phenotypic intraclass correlation for families (p. 151). Equation *(5)* shows that two times (r_P) will estimate heritability when there is one offspring per parent ($n = 1$). Otherwise, the appropriate coefficient for (r_P) to estimate (h^2) is a function of (t) as well as (n) when $n > 1$ and $0 < t < 1$ as shown in equation *(6)*.

$$r_1 = \frac{\frac{1}{2}}{\sqrt{\frac{1+(n-1)t}{n}}} \cdot \frac{V_A}{V_P} \qquad (6)$$

$$\text{If we let } K_1 = \frac{\sqrt{\frac{1+(n-1)t}{n}}}{\frac{1}{2}}, \text{ then}$$

$$h^2 = K_1 r_1 = \frac{V_A}{V_P}$$

Table 1A shows adjustment coefficients (K_1) for a range of values of (n) and (t). In all cases where n is greater than 1, the adjustment coefficient (K_1) is less than 2 and decreases sharply with higher numbers of siblings per family and lower values of the phenotypic intraclass correlation *(Table 1A)*.

Table 1.--Adjustment coefficients (K) for estimating heritability based on correlation coefficients from (A) the half-sib offspring:parent correlation, (B) the full-sib offspring:parent correlation, (C) the ramet:ortet correlation with varying values of number of siblings per family, or ramets per ortet (n), and the phenotypic intraclass correlation (t).

	n									
t	1	2	3	5	10	20	40	60	80	100
A										
.0125	2	1.42	1.17	.92	.67	.50	.39	.34	.32	.30
.050	2	1.45	1.21	.98	.76	.62	.54	.51	.50	.49
.100	2	1.48	1.26	1.06	.87	.76	.70	.68	.67	.66
.150	2	1.52	1.32	1.13	.97	.88	.83	.81	.80	.80
.200	2	1.55	1.37	1.20	1.06	.98	.94	.92	.92	.91
.250	2	1.58	1.41	1.26	1.14	1.07	1.04	1.02	1.02	1.01
B										
.0125	1.41	1.01	.83	.65	.47	.35	.28	.24	.22	.21
.050	1.41	1.03	.86	.69	.54	.44	.38	.36	.35	.35
.100	1.41	1.05	.89	.75	.62	.54	.49	.48	.47	.47
.150	1.41	1.07	.93	.80	.69	.62	.59	.57	.57	.56
.200	1.41	1.10	.97	.85	.75	.69	.66	.65	.65	.64
.250	1.41	1.12	1.00	.89	.81	.76	.73	.72	.72	.72
C										
.0125	1	.712	.584	.458	.334	.249	.193	.170	.158	.150
.050	1	.725	.606	.490	.381	.312	.272	.257	.249	.244
.100	1	.742	.632	.529	.436	.381	.350	.339	.334	.330
.150	1	.758	.658	.566	.485	.439	.414	.405	.401	.398
.200	1	.775	.683	.600	.529	.490	.469	.462	.458	.456
.250	1	.791	.707	.632	.570	.536	.518	.512	.509	.507

If a correlation coefficient (r_2) is derived from full-sib family means regressed on mid-parent values of non-inbred, unrelated parents, it should be interpreted as:

$$r_2 = \frac{\sigma_{XY}}{\sqrt{\sigma^2_X\sigma^2_Y}} = \frac{\frac{1}{2}V_A}{\sqrt{\frac{V_P}{2} \cdot \left[\frac{1+(n-1)t}{n}\right]V_P}} \qquad (7)$$

where $\sigma^2_X = \frac{V_P}{2} = \frac{1}{2}$ of the phenotypic variance of parents, (p. 179), and other terms are as defined in equation *(5)*. Simplifying, we have:

$$r^2 = \frac{\frac{1}{2}}{\sqrt{\frac{1}{2}\left[\frac{1+(n-1)t}{n}\right]}} \cdot \frac{V_A}{V_P} \qquad (8)$$

$$\text{If we let } K_2 = \frac{\sqrt{\frac{1}{2}\left[\frac{1+(n-1)t}{n}\right]}}{\frac{1}{2}}, \text{ then} \qquad (9)$$

$$h^2 = K_2 r_2 = \frac{V_A}{V_P}$$

Table 1B shows adjustment coefficients (K_2) computed for a range of values of (n) and (t). The adjustment coefficient (K_2) may be equal to, greater than, or less than one depending on (n) and (t) *(Table 1B)*. In most cases, the correlation coefficient (r_2) overestimates heritability.

The application of coefficients K_1 and K_2 to estimate (h^2) is complicated by the fact that an estimate of the phenotypic intraclass correlation (t) is needed. In the case of half-sib families,

$$t = \frac{1}{4} h^2 \text{ (p. 169).}$$

In the case of full-sibs,

$$t > \frac{1}{2} h^2,$$

since h^2 is defined as containing only additive genetic variance, but (t) may contain elements of genetic dominance variance plus environmental covariance (p. 169). If as an approximation we take

$$t = h^2\varrho \qquad (10)$$

where ϱ is the coefficient of relationship, then an iterative procedure will yield an adjusted estimate of h^2 based on r_1 or r_2 as the case may be. The procedure is to multiply the correlation coefficient (say r_1) times (ϱ), the coefficient of relationship. The resulting estimate of (t) is then used to enter *Table 1A,* according to n, the number of offspring per family. The adjustment coefficient K_1 which is obtained from *Table 1A* is then multiplied by r_1 to obtain an adjusted estimate of (h^2). The adjusted estimate of (h^2) is then used to re-estimate (t) and the procedure is repeated until the product ($r_1 \times K_1$) = h^2 becomes an iterative constant. For example, if n = 40, r_1 = .5 and ϱ = .25, the final estimate of (t) is 0.081 and adjusted h^2 = .32 *(Table 2).*

Table 2.--Estimated values of the phenotypic intraclass correlation (t) and adjusted heritability (h^2) obtained by iteration. (Correlation coefficient r_1 = .5 and number of trees per half-sib family n = 40).

Cycle No.	t	h^2
1	0.125	0.38
2	.096	.35
3	.086	.33
4	.082	.32
5	.081	.32

A third estimator of heritability is sometimes used: the correlation coefficient (r_0) between ortets and means of ramets. In this case, the following interpretation of (r_0) is appropriate:

$$r_0 = \frac{\sigma_{XY}}{\sqrt{\sigma^2{}_X\sigma^2{}_Y}} = \frac{V_G}{\sqrt{V_P \cdot \left[\dfrac{1+(n-1)t}{n}\right] V_P}} \qquad (11)$$

$$= \frac{1}{\sqrt{\left[\dfrac{1+(n-1)t}{n}\right]}} \cdot \frac{V_G}{V_P}$$

If we let $K_0 = \sqrt{\left[\dfrac{1+(n-1)t}{n}\right]}$, then

$$h^2 = K_0 r_0 = \frac{V_G}{V_P}$$

where V_G = total genetic variance.

Note that in the case of clones, adjusted r_0 estimates broad sense rather than narrow sense heritability as in the previous two cases (Hanson, 1963).

Values of K_0 can be read directly from *Table 1C* because in the case of clones, (ϱ), the coefficient of relationship among ramets is 1, so t = h^2 according to *(10).* Iteration then proceeds as in the cases outlined above.

To avoid having to go through an iterative procedure to estimate adjusted heritabilities for the most frequently encountered situations, *Tables 3, 4, 5, and 6* have been prepared which permit adjusted heritabilities to be read directly. Estimates of three parameters are required to enter the appropriate table:

ϱ = the coefficient of relationship among siblings or ramets,

r = the correlation coefficient from an offspring-parent or a ramet-ortet analysis, and

n = the number of offspring per family, or ramets per clone.

Each table represents one of four values of ϱ: 0.25, 0.33, 0.50 and 1.0. While a value of ϱ = 0.33 has not been frequently used, in many cases it may be more appropriate for open-pollinated families than ϱ = 0.25. This is because a relatively small amount of natural self-fertilization, or a limited number of effective male parents can substantially increase the coefficient of relationship (Squillace, 1974). When the proper table is chosen according to (ϱ), it can be entered from the left margin in the row appropriate to the value of the correlation coefficient. Adjusted heritability

Table 3.--Adjusted narrow-sense heritability from offspring single-parent analysis (sibling coefficient of relationship of 0.25) for specified numbers of siblings per family (n), and estimated correlation coefficient (r_1).

	n									
r_1	1	2	3	4	5	7	10	20	40	100
.05	.10	.07	.06	.05	.05	.04	.03	.02	.02	.01
.10	.20	.14	.12	.10	.09	.08	.07	.05	.04	.03
.15	.30	.22	.18	.16	.14	.12	.11	.08	.06	.04
.20	.40	.29	.24	.22	.20	.17	.15	.11	.09	.07
.25	.50	.37	.31	.27	.25	.22	.19	.15	.12	.09
.30	.60	.45	.38	.34	.31	.27	.24	.19	.15	.12
.35	.70	.53	.45	.40	.37	.32	.28	.23	.19	.16
.40	.80	.61	.52	.46	.43	.38	.34	.27	.23	.20
.45	.90	.69	.59	.53	.49	.44	.39	.32	.27	.24
.50	1.00	.77	.67	.60	.56	.50	.45	.37	.32	.29
.55		.86	.74	.67	.63	.56	.51	.43	.38	.34
.60		.94	.82	.75	.70	.63	.58	.49	.44	.40
.65			.90	.83	.77	.70	.65	.56	.50	.46
.70			.99	.91	.85	.78	.71	.63	.57	.53
.75				.99	.93	.86	.79	.70	.64	.60
.80						.94	.87	.78	.72	.68
.85							.95	.85	.80	.76
.90								.94	.89	.84
.95									.97	.94

will then be found in the column headed by the appropriate value of (n). Numbers of offspring per family or ramets per clone will often vary within an experiment. If this is the case, the harmonic mean of $(\bar{n})$ should be computed according to:

$$\frac{1}{n} = \frac{1}{i}\left(\frac{1}{n_1} + \frac{1}{n_2} + \dots \frac{1}{n_2}\right)$$

where n_i is the number of siblings or ramets in the ith family or clone.

It must be emphasized that adjusting the correlation coefficient removes a bias from the estimate of heritability based on offspring : parent correlations, but it does not make the estimate more precise. That is, the variance of the estimate is not reduced, but the expected value of the estimate is equal to heritability if other related assumptions are valid (p. 168 ff.). In some arrays of data where adjusted heritability can be used to estimate genetic gain, and that estimate can be compared with realized gain, considerable improvement in the predictive value of heritability may be shown. But if the assumed genetic model is in error, or if the standard error of the estimate is high, then large differences between adjusted estimates and expected values based on realized gain may remain even after adjustment.

Table 4.--Adjusted narrow-sense heritability from offspring single-parent correlation analysis (sibling coefficient of relationship of 0.33) for specified numbers of siblings per family (n), and estimated correlation coefficient (r_1).

	n									
r_1	1	2	3	4	5	7	10	20	40	100
.05	.10	.07	.06	.05	.05	.04	.03	.02	.02	.01
.10	.20	.14	.12	.10	.10	.08	.07	.05	.04	.03
.15	.30	.22	.18	.16	.15	.13	.11	.08	.07	.05
.20	.40	.30	.25	.22	.20	.18	.15	.12	.10	.08
.25	.50	.37	.32	.28	.26	.23	.20	.16	.13	.11
.30	.60	.45	.39	.35	.32	.29	.25	.20	.17	.15
.35	.70	.54	.46	.42	.38	.34	.31	.25	.22	.19
.40	.80	.62	.54	.49	.45	.41	.37	.31	.27	.24
.45	.90	.71	.62	.56	.52	.47	.43	.37	.33	.30
.50	1.00	.79	.70	.64	.60	.55	.50	.44	.39	.36
.55		.88	.78	.72	.68	.62	.57	.51	.46	.43
.60		.98	.87	.80	.76	.70	.65	.58	.54	.51
.65			.96	.89	.85	.79	.73	.66	.62	.59
.70				.98	.94	.88	.82	.75	.70	.68
.75						.97	.92	.84	.80	.77
.80								.94	.90	.87
.85										.98
.90										

Table 5.--Adjusted narrow-sense heritability from offspring mid-parent correlations analysis (sibling coefficient of relationship of 0.50) for specified numbers of siblings per family (n), and estimated correlation coefficient (r_2).

	n									
r_1	1	2	3	4	5	7	10	20	40	100
.05	.07	.05	.04	.04	.03	.02	.02	.02	.01	.01
.10	.14	.10	.09	.07	.07	.06	.05	.04	.03	.02
.15	.21	.16	.13	.12	.10	.09	.08	.06	.05	.04
.20	.28	.21	.18	.16	.14	.13	.11	.09	.07	.06
.25	.35	.27	.23	.20	.19	.16	.14	.12	.10	.08
.30	.42	.32	.28	.25	.23	.20	.18	.15	.13	.11
.35	.49	.38	.33	.30	.28	.25	.22	.19	.16	.14
.40	.57	.44	.39	.35	.33	.29	.27	.23	.20	.18
.45	.64	.50	.44	.40	.38	.34	.31	.27	.24	.22
.50	.71	.57	.50	.46	.43	.40	.37	.32	.29	.27
.55	.78	.63	.56	.52	.49	.45	.42	.37	.34	.32
.60	.85	.70	.62	.58	.55	.51	.48	.43	.40	.38
.65	.92	.76	.69	.65	.62	.58	.54	.49	.46	.44
.70	.99	.83	.76	.71	.68	.64	.61	.56	.53	.51
.75		.90	.83	.78	.75	.71	.68	.63	.60	.58
.80		.97	.90	.85	.82	.79	.75	.70	.68	.66
.85			.97	.93	.90	.86	.83	.78	.76	.74
.90					.98	.94	.90	.87	.84	.83
.95							.99	.95	.93	.92
1.00										1.00

Table 6.--Adjusted broad-sense heritability from ramet-ortet correlation analysis (ramet coefficient of relationship of 1.0) for specified numbers of ramets per clone (n), and estimated correlation coefficient (r_o).

	n									
r_1	1	2	3	4	5	7	10	20	40	100
.05	.05	.04	.03	.03	.02	.02	.02	.01	.01	.01
.10	.10	.07	.06	.05	.05	.04	.04	.03	.02	.02
.15	.15	.11	.09	.08	.08	.07	.06	.05	.04	.03
.20	.20	.15	.13	.12	.11	.10	.09	.07	.06	.05
.25	.25	.19	.17	.15	.14	.13	.11	.10	.08	.07
.30	.30	.24	.21	.19	.18	.16	.15	.12	.11	.10
.35	.35	.28	.25	.23	.21	.20	.18	.16	.14	.13
.40	.40	.33	.29	.27	.26	.24	.22	.20	.18	.17
.45	.45	.37	.34	.31	.30	.28	.26	.24	.22	.21
.50	.50	.42	.39	.36	.35	.33	.31	.29	.27	.26
.55	.55	.47	.44	.41	.40	.38	.36	.34	.32	.31
.60	.60	.52	.49	.47	.45	.43	.41	.39	.38	.37
.65	.65	.58	.54	.52	.51	.49	.47	.45	.44	.43
.70	.70	.63	.60	.58	.57	.55	.54	.52	.51	.50
.75	.75	.69	.66	.64	.63	.62	.60	.59	.58	.57
.80	.80	.75	.72	.71	.70	.69	.68	.66	.65	.65
.85	.85	.81	.79	.78	.77	.76	.75	.74	.73	.73
.90	.90	.87	.86	.85	.84	.84	.83	.82	.82	.82
.95	.95	.94	.93	.92	.92	.92	.92	.91	.91	.91
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Summary

The correlation coefficient as an estimator of heritability must in some cases be interpreted quite differently than the regression coefficient because magnitude of the correlation coefficient is influenced by the number of offspring per family and the size of the phenotypic intraclass correlation. In most cases, the bias in the correlation coefficients causes an overestimate of heritability which can be large when there are many trees per family. Methods and tables are provided to derive adjusted estimates according to the number of trees per family so that the expected value of the estimator is equal to heritability.

Key words: Tree breeding, heritability, correlation coefficients.

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