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Effect of ignoring full sib relationships when making half sib estimates of heritability

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Summary. Heritability estimated from sire family variance components, ignoring dams, pools conventional paternal and maternal half sib estimates, in a way which is biased upward, and sub-optimal for minimizing the sampling variance. Standard error of a sire family estimate will be smaller than that of the equivalent paternal half sib estimate, but not as small as that of an estimate obtained by optimal pooling of paternal and maternal half sib estimates. If only additive genetic variance components are significant, the bias may be removed by use of a computed average genetic relationship for sire families, in place of a nominal R = 0.25. Average genetic relationship may be computed from mean and variance of dam family size within sire families. If dominance, epistatic, or maternal components are significant, this simple correction is not appropriate. In situations likely to be encountered in large domestic species such as sheep and cattle (dam family size small and uniform) bias will be negligible. The method could be useful where cost of dam identification is a limiting factor.

Key words: Heritability – Family size – Genetic relationship – Analysis of variance – Sheep

Introduction

In species such as sheep and cattle, where the frequencies of twin and multiple births are low, it has been common practice to estimate heritability by the analysis of variance method, using only between and within sire family variance components, and assuming that presence of a small number of full sibs in some paternal half sib families will have a negligible effect on the estimations. This approach has advantages of a simpler analysis of variance and of enabling data in which the dam's identification is unknown to be utilized.

Some workers (Hazel and Terrill 1945; Rendel 1956; McGuirk 1973) have considered whether a low frequency of full sib groups in their particular data set would be likely to bias heritability estimates. Their conclusions were all negative. This paper attempts to outline the general conditions under which sire family heritability estimates would be seriously biased by presence of full sib progeny. The effect on standard errors of estimates is also considered. The results should be of interest in experimental design, in the case where cost of dam identification is a limiting factor.

Average genetic relationship within a sire family

1 One progeny per dam

If each dam has exactly one offspring, all progeny of a sire are half sibs, their average genetic relationship is R = 0.25 (Fisher 1918), and heritability in the narrow sense (Lush 1940) is estimated as:

$$\hat{h}^2 = \frac{\hat{\sigma}_S^2}{R\,(\hat{\sigma}_S^2 + \hat{\sigma}_W^2)}$$

where $\hat{\sigma}_S^2$ and $\hat{\sigma}_W^2$ are estimates of between and within sire family variance components. Most workers proceed on this basis, assuming that the occasional dam with multiple progeny will not significantly alter R or the resultant heritability estimate.

2 One or two progeny per dam

In the simple case where each dam has either 1 or 2 progeny, let the N progeny of a sire consist of

f dam families of size 2
and (N – 2 f) dam families of size 1.

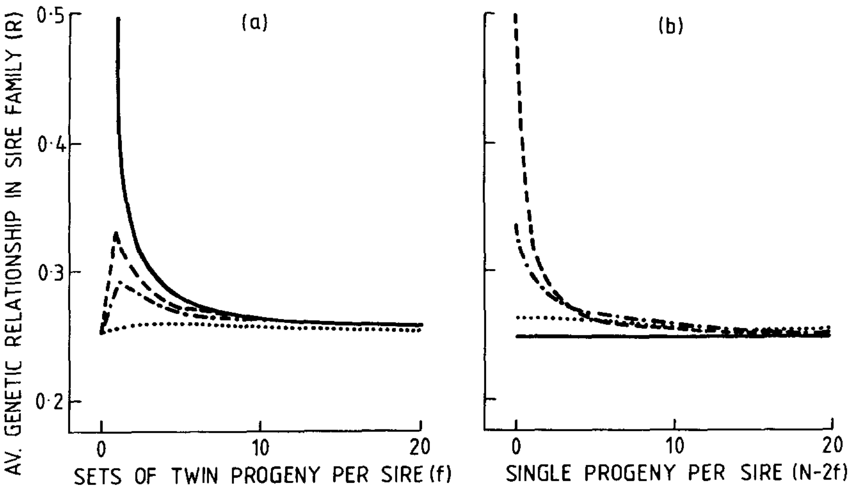

Fig. 1 a, b. Average genetic relationship within a sire family when dams have either 1 or 2 progeny. Graph (**a**) —— zero single progeny, – – – 1 single progeny, –·–·– 2 single progeny, ···· 10 single progeny; Graph (**b**) —— zero sets of twin progeny, – – – – one set of twin progeny, –·–·– 2 sets of twin progeny, ···· 10 sets of twin progeny

The average genetic relationship among offspring of this sire is then:

$$R = \left(1 - \frac{f}{N(N-1)/2}\right) 0.25 + \left(\frac{f}{N(N-1)/2}\right) 0.5$$

$$= \left(1 + \frac{2f}{N(N-1)}\right) 0.25. \qquad (1)$$

Expression (1) is equivalent to that of Rendel (1956) when dams have either single or twin progeny. In this case R cannot exceed 0.50, and in most practical circumstances would rarely exceed 0.27 (Fig. 1).

3 Multiple progeny per dam

Let the progeny of one sire have an arbitrary distribution of dam family sizes

f_1 dam families of size 1
f_2 dam families of size 2
·
·
f_n dam families of size n

and let N = number of progeny per sire = $\sum_{r=1}^{n} r\, f_r$

The average genetic relationship within this sire family will be of the form

$$R = (1 + Q)\, 0.25 \qquad (2)$$

where

$$Q = \frac{\text{number of full sib pairs of progeny}}{\text{total number of pairs of progeny}}$$

$$= \frac{\sum_{r=2}^{n} \binom{r}{2} f_r}{N(N-1)/2}$$

$$= \frac{\frac{1}{2}\left[\sum_{r=1}^{n} r^2 f_r - \sum_{r=1}^{n} r\, f_r\right]}{N(N-1)/2}$$

$$= \frac{\frac{1}{2} f.\, [\varepsilon(r^2) - \varepsilon(r)]}{\frac{1}{2} f.\, \varepsilon(r)\, [f.\, \varepsilon(r) - 1]}$$

where $f. = \sum_r f_r$ is total number of dam families and $\varepsilon(r) = N/f.$ is expected value of dam family size. With some algebra, this rearranges to give

$$Q = \frac{\mathrm{Var}(r) + \bar{r}(\bar{r} - 1)}{\bar{r}(N-1)} \qquad (3)$$

where Var(r) is variance of dam family size within sire group and $\bar{r}$ is mean dam family size.

If the distribution of dam family sizes within sire is Poisson, expression (3) simplifies to:

$$Q = \frac{\bar{r}}{N-1}.$$

Expressions (2) and (3) are equivalent to the seemingly different formula of Rendel (1956), but have the advantage that individual dam family sizes are not required, only an estimate of their mean and variance, which could perhaps come from a subset of the data, or even a separate experiment.

Figure 2 shows that the average relationship within a sire family is appreciably greater than R = 0.25 whenever the mean ($\bar{r}$) or variance (Var(r)) of dam family size is greater than 2. The deviation from R = 0.25 is also more pronounced when sire family size (N) is small.

Effect of ignoring dam families on analysis of variance, variance components, and heritability estimation

1 Including dams

A common procedure is to mate s sires to a random sample of d. dams (d_i dams for sire i) and obtain $n_{..}$ progeny (n_{ij} progeny from jth dam mated to ith sire). If data arising from measurement of these progeny are subjected to a 3 level nested analysis of variance, as outlined in Table 1, Kempthorne (1955) shows that

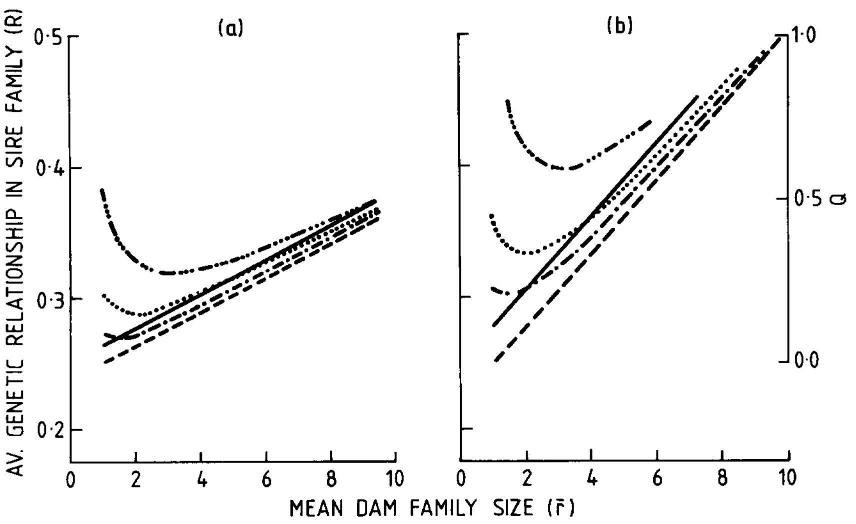

Fig. 2 a, b. Average genetic relationship within a sire family when dams have multiple progeny. Graph (**a**) N = 20 progeny per sire; Graph (**b**) N = 10 progeny per sire. Variance of dam family size equal to mean dam family size (——), zero (– – – –), 2 (–·–·–), 4 (· · ·) or 10 (–· · ·– · · ·)

variance components have the following expectations in terms of covariances between collateral relatives

$$\sigma^2_W = \sigma^2_P - \mathrm{Cov\,(FS)}$$

$$\sigma^2_D = \mathrm{Cov\,(FS)} - \mathrm{Cov\,(HS)}$$

$$\sigma^2_S = \mathrm{Cov\,(HS)} \tag{4}$$

where Cov (FS) = covariance of full sibs
Cov (HS) = covariance of half sibs.

Given the following theoretical results for covariances between relatives in terms of additive genetic (A_0), dominance (D_0), epistatic (A_0A_0, etc.), maternal genetic (A_M, D_M, A_0A_M) and maternal environmental (E_M) variances and covariances (Kempthorne 1955; Willham 1963).

$$\begin{aligned}\mathrm{Cov\,(FS)} = {} & \frac{1}{2}\sigma^2_{A_0} + \frac{1}{4}\sigma^2_{D_0} + \frac{1}{4}\sigma^2_{A_0A_0} + \frac{1}{8}\sigma^2_{A_0D_0} \\ & + \frac{1}{16}\sigma^2_{D_0D_0} + \frac{1}{8}\sigma^2_{A_0A_0A_0} + \ldots \\ & + \sigma^2_{A_M} + \sigma^2_{D_M} + \ldots \\ & + \sigma_{A_0A_M} + \ldots \\ & + \sigma^2_{E_M} \\ \mathrm{Cov\,(HS)} = {} & \frac{1}{4}\sigma^2_{A_0} + \frac{1}{16}\sigma^2_{A_0A_0} + \frac{1}{64}\sigma^2_{A_0A_0A_0} + \ldots \end{aligned} \tag{5}$$

and, knowing that the covariances within a full or half sib family are equal to the complement of (5) plus an individual environmental (E_0) component, it is usual to equate sire and dam variance component estimates directly to their compositions, viz.

Table 1. Analysis of variance, including dams as a source of variation

Source	D.F.	Mean square	Expected mean square
Sires	$f_S = s - 1$	S	$\sigma^2_W + k_2\,\sigma^2_D + k_3\,\sigma^2_S$
Dams with sires	$f_D = d. - s$	D	$\sigma^2_W + k_1\,\sigma^2_D$
Progeny within dams	$f_W = n.. - d.$	W	σ^2_W
Total	$n.. - 1$	P	σ^2_P

Table 2. Analysis of variance, ignoring dams as a source of variation

Source	D.F.	Mean source	Expected mean square
Sires	$f_s = s - 1$	S	$\sigma^2_{W^1} + k_3\,\sigma^2_{S^1}$
Progeny within sires	$f_{w^1} = n.. - s$	W^1	$\sigma^2_{W^1}$
Total	$n.. - 1$	P	σ^2_P

$$\begin{aligned}\hat\sigma^2_S = {} & \frac{1}{4}\left[\hat\sigma^2_{A_0} + \frac{1}{4}\sigma^2_{A_0A_0} + \frac{1}{16}\sigma^2_{A_0A_0A_0} + \ldots\right] \\ \hat\sigma^2_D = {} & \frac{1}{4}\left[\sigma^2_{A_0} + \sigma^2_{D_0} + \frac{3}{4}\sigma^2_{A_0A_0} + \frac{1}{2}\sigma^2_{A_0D_0} + \frac{1}{4}\sigma^2_{D_0D_0}\right. \\ & + \frac{7}{16}\sigma^2_{A_0A_0A_0} + \ldots \\ & \left. + 4\,(\sigma^2_{A_M} + \sigma^2_{D_M} + \sigma_{A_0A_M} + \sigma^2_{E_M})\right] \end{aligned} \tag{6}$$

and to define two heritability estimates

$$\hat h^2_S = \frac{4\,\hat\sigma^2_S}{\hat\sigma^2_P}$$

$$\text{and } \hat h^2_D = \frac{4\,\hat\sigma^2_D}{\hat\sigma^2_P} \tag{7}$$

of which $\hat h^2_S$ is the more commonly used since its numerator contains only additive genetic components and their interactions.

2 Ignoring dams

If analysis of variance is performed on the data set defined above, ignoring dams a source of variation, the statistical consequences are as summarized in Table 2.

By equating expected sums of squares from Tables 1 and 2, it is easily shown that

$$\hat{\sigma}^2_{W_1} = \hat{\sigma}^2_W + (1 - Q)\,\hat{\sigma}^2_D$$

and

$$\hat{\sigma}^2_{S_1} = \hat{\sigma}^2_S + Q\,\hat{\sigma}^2_D \tag{8}$$

where, using the notation of Table 1,

$$Q = 1 - k_1\left(\frac{f_D}{f_D + f_W}\right). \tag{9}$$

This use of Q will be shown (section iii) to be equivalent to that of equations (1) and (2). Substitution of equations (8) into (6) leads to an expression for the composition of the sire ignoring dam variance component.

$$\hat{\sigma}^2_{S_1} = \frac{1}{4}\Bigg[(1+Q)\,\sigma^2_{A_0} + Q\,\sigma^2_{D_0} + \left(\frac{1+3Q}{4}\right)\sigma^2_{A_0A_0} + \frac{Q}{2}\,\sigma^2_{A_0D_0} + \frac{Q}{4}\,\sigma^2_{D_0D_0} + \left(\frac{1+7Q}{16}\right)\sigma^2_{A_0A_0A_0} + \ldots + 4Q\,(\sigma^2_{A_M} + \sigma^2_{D_M} + \sigma^2_{A_0A_M} + \sigma^2_{E_M})\Bigg]. \tag{10}$$

If heritability is estimated (using a nominal R = 0.25) from this component as

$$\hat{h}^2_{S_1} = \frac{4\,\hat{\sigma}^2_{S_1}}{\sigma_{P^2}} = \frac{4\,(\hat{\sigma}^2_S + Q\,\hat{\sigma}^2_D)}{\hat{\sigma}^2_P} = \hat{h}^2_S + Q\,\hat{h}^2_D \tag{11}$$

its numerator is seen from (10) to contain various non-additive and maternal contributions to an extent dependent on the magnitude of Q. Using a computed R to "correct" $\hat{h}^2_{S_1}$ for bias (using $\hat{h}^2_S = \hat{h}^2_{S_1}/4R$) is clearly only appropriate in cases where $\sigma^2_{A_0}$ can be assumed to be the sole significant component of $\hat{\sigma}^2_{S_1}$. There is evidence in cattle (for example Hohenboken and Brinks 1973) that non additive and maternal contributions cannot always be ignored, but the situation in sheep has not been investigated.

3 *Magnitude of Q*

If (9) is rewritten as

$$Q = 1 - \frac{n_{..} - \sum_i \left(\frac{\sum_j n^2_{ij}}{n_{i.}}\right)}{n_{..} - s} = \sum_i \left(\frac{\sum_j n^2_{ij}}{n_{i.}} - 1\right) \Bigg/ \sum_i (n_{i.} - 1)$$

letting $\bar{n}_{i.} = \frac{n_{i.}}{d_i}$ = mean dam family size for sire group i and $\mathrm{Var}_i(n_{ij})$ = variance of dam family sizes for sire group i leads to

$$Q = \sum_i \left(\frac{\mathrm{Var}_i(n_{ij}) + \bar{n}_{i.}(\bar{n}_{i.} - 1)}{\bar{n}_{i.}}\right) \Bigg/ \sum_i (n_{i.} - 1). \tag{12}$$

Equation (3) is equivalent to (12) for one sire group. For more than one sire group (12) indicates the method of pooling. The nature of Q and its likely magnitude in various circumstances, is thus as discussed for R in equations (2) and (3), since Q = 4R − 1. As Q is also shown in Figure 2 there is no need to repeat the example.

4 *Standard error of heritability estimate*

From equation (11), it follows, if Q is known without error, that

$$\mathrm{Var}(\hat{h}^2_{S_1}) = \mathrm{Var}(\hat{h}^2_S) + Q^2\,\mathrm{Var}(\hat{h}^2_D) + 2Q\,\mathrm{Cov}(\hat{h}^2_S, \hat{h}^2_D) \tag{13}$$

so that $\mathrm{Var}(\hat{h}^2_{S_1})$ may or may not exceed $\mathrm{Var}(\hat{h}^2_S)$ depending on the sign of $\mathrm{Cov}(\hat{h}^2_S, \hat{h}^2_D)$ and its magnitude relative to $\mathrm{Var}(\hat{h}^2_D)$. It is of some interest to determine whether there are cases when $\hat{h}^2_{S_1}$ would be preferred to $\hat{h}^2_S$ from the point of view of precision. The methods developed by Osborne and Paterson (1952) can be used to extend expressions for the sampling variances of $\hat{h}^2_S$ and $\hat{h}^2_D$, to $\mathrm{Cov}(\hat{h}^2_S, \hat{h}^2_D)$ and hence using (13) to $\mathrm{Var}(\hat{h}^2_{S_1})$. A summary of these results is given in Table 3, each result being of the general form

$$\frac{1}{\sigma^4_P} \sum_i \alpha_i\,\mathrm{Var}(\varphi_i) \tag{14}$$

where φ_i are mean squares and α_i the coefficients defined in Table 3. In deriving these results, the usual assumptions of mean squares independent, but components correlated, are involved. Also high order terms are neglected in expressions such as

$$\mathrm{Var}\left(\frac{X}{Y}\right) \approx \frac{1}{\bar{Y}^4} \cdot [\bar{Y}^2\,\mathrm{Var}(X) + \bar{X}^2\,\mathrm{Var}\,Y - 2\bar{X}\bar{Y}\,\mathrm{Cov}(X,Y)]$$

an approximation which holds provided the coefficient of variation of Y is small.

In application, the expression

$$\mathrm{Var}(\varphi_i) = \frac{2\varphi^2_i}{f_i + 2} \tag{15}$$

developed by Fisher (1928) is used in conjunction with (14).

Table 3. Sampling variances and covariances of heritability estimates expressed as linear functions of variances of mean squares *S*, *D*, *W*, and *W*^{1}, as defined in Tables 1 and 2. For brevity, the following functions of k values are defined: $a = \frac{4}{k_3}$, $b = \frac{-4k_2}{k_1 k_3}$, $c = \frac{4(k_2 - k_1)}{k_1 k_3}$, $d = 0$, $e = \frac{4}{k_1}$, $f = \frac{-4}{k_1}$, $x = \frac{1}{k_3}$, $y = \left(\frac{1}{k_1} - \frac{k_2}{k_1 k_3}\right)$, $z = \left(1 - \frac{1}{k_1} + \frac{k_2 - k_1}{k_1 k_3}\right)$, these quantities being coefficients in equations defining relevant components as functions of mean squares, viz.: $4\hat{\sigma}_S^2 = aS + bD + cW$, $4\hat{\sigma}_D^2 = dS + eD + fW$, $\hat{\sigma}_P^2 = xS + yD + zW, = xS + (1 - x)W^1$, $4\hat{\sigma}_{S_1}^2 = aS - aW^1$

	Constant multiplier	Coefficients of linear function of variances of mean squares			
		Var (S)	Var (D)	Var (W)	Var (W^1)
1. Var $(\hat{h}_S^2)$	$\frac{1}{\sigma_P^4}$	$(a - x h_S^2)^2$	$(b - y h_S^2)^2$	$(c - z h_S^2)^2$	–
2. Var $(\hat{h}_D^2)$	$\frac{1}{\sigma_P^4}$	$(d - x h_D^2)^2$	$(e - y h_D^2)^2$	$(f - z h_D^2)^2$	–
3. Cov $(\hat{h}_S^2, \hat{h}_D^2)$	$\frac{1}{\sigma_P^4}$	$(a - x h_S^2)(d - x h_D^2)$	$(b - y h_S^2)(e - y h_D^2)$	$(c - z h_S^2)(f - z h_D^2)$	–
4. Var $(\hat{h}_{S_1}^2)$	$\frac{1}{\sigma_P^4}$	$[(a - x h_S^2) + Q(d - x h_D^2)]^2$	$[(b - y h_S^2) + Q(e - y h_D^2)]^2$	$[(c - z h_S^2) + Q(f - z h_D^2)]^2$	–
5. Var $(\hat{h}_{S_1}^2)$	$\frac{1}{\sigma_P^4}$	$(a - x h_{S_1}^2)^2$	–	–	$(-a - (1 - x) h_{S_1}^2)^2$

Var $(\hat{h}_{S_1}^2)$ may also be obtained directly using these methods, instead of substituting in (13), and this approach leads to the expression shown in line 5 of Table 3. Lines 4 and 5 are, of course, equivalent, but it is line 5 which would be used in practice.

Comparing lines 1 and 4 of Table 3 shows that:

1. Q will influence the magnitude of the difference between Var $(\hat{h}_S^2)$ and Var $(\hat{h}_{S_1}^2)$, but not its sign.

2. In the expression for Var $(\hat{h}_{S_1}^2)$, compared with that for Var $(\hat{h}_S^2)$, the coefficient of Var (S) will be smaller, since $d < x h_D^2$; the coefficient of Var (D) will be larger, since $e > y h_D^2$; and the coefficient of Var (W) will be smaller, since $f < z h_D^2$. Since

$$\text{Var}(S) > \text{Var}(D) > \text{Var}(W)$$

it is likely that the first inequality will dominate the situation and that Var $(\hat{h}_{S_1}^2)$ will be smaller than Var $(\hat{h}_S^2)$.

A numerical investigation, results of which are summarized in Fig. 3, confirmed that under a range of likely practical conditions Var $(\hat{h}_{S_1}^2)$ was always less than or equal to Var $(\hat{h}_S^2)$, and that the increase in precision could be as much as a 12% lower standard error. For the conditions investigated, Cov $(\hat{h}_S^2, \hat{h}_D^2)$ was al-

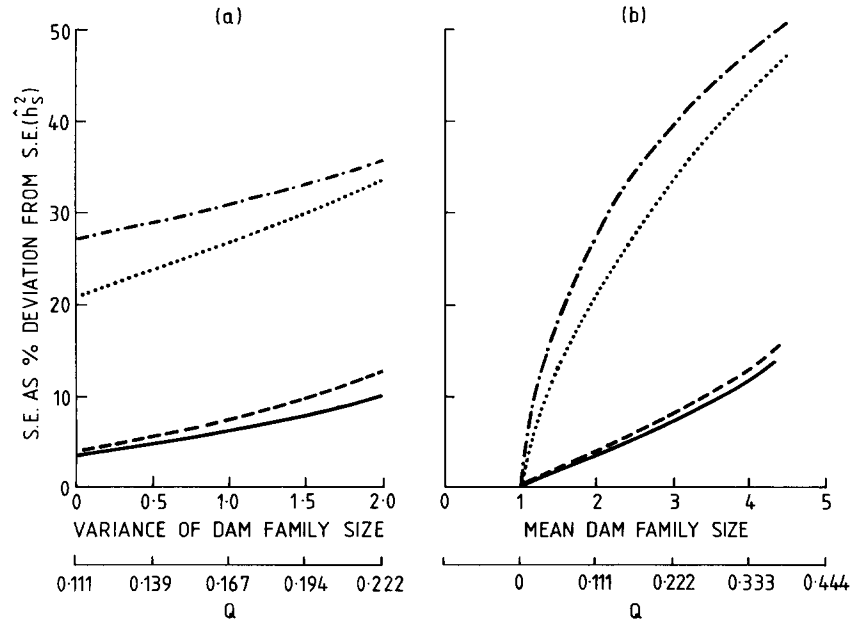

Fig. 3 a, b. Percentage *decrease* in standard error comparing SE $(\hat{h}_{S_1}^2)$ and SE $(\hat{h}_{S+D}^2)$ with SE $(\hat{h}_S^2)$, for data on 1,000 progeny from 100 sire families. Graph (**a**) mean dam family size = 2.0; Graph (**b**) variance of dam family size = 0.0. —— $h^2 = 0.40$, SE $(\hat{h}_{S_1}^2)$; – – – – $h^2 = 0.20$, SE $(\hat{h}_{S_1}^2)$; –·–·– $h^2 = 0.40$, SE $(\hat{h}_{S+D}^2)$; ···· $h^2 = 0.20$, SE $(\hat{h}_{S+D}^2)$

ways negative, the corresponding correlation varying from -0.02 to -0.49. It is apparent from equation (11) that $\hat{h}^2_{S1}$ in effect pools the paternal and maternal half sib estimates in a way which is

1. biased and
2. not optimal in the sense of weighting $\hat{h}^2_S$ and $\hat{h}^2_D$ according to their variances and covariance.

It is therefore of some interest to ask how much better again the standard error of an optimally pooled estimate would be. If $\hat{h}^2_S$ and $\hat{h}^2_D$ are unbiased estimates of the same parameter, the optimum pooled estimator is (following Aitken 1935)

$$\hat{h}^2_{S+D} = \frac{[\mathrm{Var}\,(\hat{h}^2_D) - \mathrm{Cov}\,(\hat{h}^2_S, \hat{h}^2_D)]\,\hat{h}^2_S + [\mathrm{Var}\,(\hat{h}^2_S) - \mathrm{Cov}\,(\hat{h}^2_S, \hat{h}^2_D)]\,\hat{h}^2_D}{\mathrm{Var}\,(\hat{h}^2_S) + \mathrm{Var}\,(\hat{h}^2_D) - 2\,\mathrm{Cov}\,(\hat{h}^2_S, \hat{h}^2_D)}$$

and its sampling variance is

$$\mathrm{Var}\,(\hat{h}^2_{S+D}) = \frac{\mathrm{Var}\,(\hat{h}^2_S)\,\mathrm{Var}\,(\hat{h}^2_D) - \mathrm{Cov}^2\,(\hat{h}^2_S, \hat{h}^2_D)}{\mathrm{Var}\,(\hat{h}^2_S) + \mathrm{Var}\,(\hat{h}^2_D) - 2\,\mathrm{Cov}\,(\hat{h}^2_S, \hat{h}^2_D)}\,.$$

Corresponding standard errors of $\hat{h}^2_{S+D}$ are summarized in Fig. 3, for comparison with those of $\hat{h}^2_{S1}$ and $\hat{h}^2_S$ under the same range of conditions. It is clear that the standard error of $\hat{h}^2_{S1}$ will not be as small as that of $\hat{h}^2_{S+D}$, and that the superiority of the latter will be greatest at a high heritability and a high mean dam family size. It should be noted that while $\hat{h}^2_{S+D}$ is optimal in the sense of minimising standard error, it will be biased in a similar way to $\hat{h}^2_{S1}$ if non additive or maternal variances are significant.

Example

In an Australian Merino sheep flock a typical sire family would consist of 50 dam families of mean size 1.10 and variance 0.092 (based on 45 dam families of size 1 and 5 families of size 2). In this case

$Q = [0.092 + 1.10\,(0.10)]/[1.10\,(55 - 1)] = 0.034$ and
$R = (1 + 0.034)\,0.25 = 0.2508$.

For a trait such as hogget fleece weight with a nominal heritability of $h^2_S = h^2_D = 0.4$, a sire family estimate of heritability would have the expectation $0.4 + (0.0034)\,(0.4) = 0.4014$. If non-additive and/or maternal components were significant to the extent that $h^2_D/h^2_S = 2.0$, a sire family estimate would have the expectation $0.4 + 0.0034\,(2.0)\,(0.4) = 0.4027$. The sire family method is thus negligably biased for this type of flock structure.

Conclusion

The sire family method ignoring dams leads to slightly biased and reduced but not minimum variance heritability estimates, for a range of conditions commonly encountered in sheep and cattle populations. Where additive genetic variance is the only component of concern, use of a computed genetic relationship in place of a nominal $R = 0.25$ is appropriate and would remove the slight bias. This approach is an acceptable alternative to more complex methods, and has the advantage that dam identity is not required.

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