

## **A New Approach to the Estimation of Variance of Sample Heritability from Full-Sib Analysis**

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### **SUMMARY**

Heritability ( $h^2$ ) is an important genetic parameter, useful to plant and animal breeders. Precise estimation of this parameter is vital for deciding the breeding strategy for improving the characteristics of the population. In this paper, an expression for the approximate variance of heritability estimate based simultaneously on sire and dam components ( $h_{S+D}^2$ ) of full-sib analysis is derived. The estimates obtained from this expression under different family structures are compared with those obtained from bootstrap method. A comparison is also made between sire component estimate ( $h_S^2$ ) and  $h_{S+D}^2$  for their variances. In the light of the results the bootstrap method is recommended for computing the variances  $h_S^2$  and  $h_{S+D}^2$ . It is also shown that  $h_{S+D}^2$  is more precise than  $h_S^2$  when the trait is highly heritable.

*Key words:* Heritability, Mating design, Bootstrap procedure.

### **1. INTRODUCTION**

The characters of economic importance, in plants and animals, which are generally controlled by polygenes, show continuous variation in the phenotypic values of the individuals in the population. The heritability ( $h^2$ ), in the narrow sense, measures the fraction of phenotypic variance that can be attributed to the additive genetic effects of genes controlling such characters. Knowledge of this parameter is of vital importance to the breeders because it is through the manipulation of the additive genetic variability the characteristics of the population are improved. Mainly there are two approaches available for the estimation of  $h^2$ : one based on the intra-sire regression of offspring on parent and the other based on half-sib correlation (Falconer 1989). The estimate in the former case is generally obtained by pooling the regression within sire groups in a weighted average and in the latter, by making use of intra-class correlation between paternal and maternal half-sibs. Under full-sib mating design, the estimate heritability is a function of either or both of the two components (i) intra-class correlation between paternal half-sibs, and (ii) intra-class

correlation between maternal half-sibs. The estimates of  $h^2$  obtained from these components are popularly known as sire component heritability, dam component heritability and sire-plus-dam components heritability (when both components are used), denoted by  $h_S^2$ ,  $h_D^2$  and  $h_{S+D}^2$  respectively.

Fisher (1950) gives the formula for the standard error of intra-class correlation coefficient for large samples size. Osborne and Patterson (1952) derive the formula for standard errors, both with single and double classifications. Sastry (1956) has given the expression for approximate variance of  $h_{S+D}^2$  while Robertson (1959) obtained closer approximations to the variances of estimates of both paternal and maternal half-sib intra-class correlations, assuming additive gene action. The expressions given by these workers are quite complicated and not amenable for easy computation of variance of  $h^2$  and are also restrictive because of the assumption of additive model, which may not be the case. Thus, there is a case for the development of a computer intensive procedure to work out the variances with a satisfactory level of accuracy and precision.

Aastveit (1990) suggests the use of bootstrap technique for the estimation of the standard deviation of variance and covariance components. Following this approach, Ansari *et al.* (1999) obtained approximate variances of  $h^2$  estimates under several full-sib family structures and utilized these in deciding the best mating design for heritability estimation. This investigation focused on the determination of optimum sample size, and structure for half-sib and full-sib mating designs. The design giving least variances of the character under study under optimum structures (i.e. for the number of offspring per sire is around  $4/h^2$ ) was adjudged superior to other designs.

It can be noted that the sampling variance of heritability estimates and the probability of inadmissible estimates (i.e., those falling outside the prescribed limits, 0 and 1) are inter-linked, as a larger variance, will increase the chance of obtaining inadmissible estimates of heritability. Prabhakaran and Jain (1988) discussed the merits of various mating designs from the point of view of the probability of obtaining inadmissible estimates. They observed that under full-sib mating design  $h_s^2$  is more precise than  $h_{s+D}^2$  if the population value of heritability is  $< 0.25$  and vice-versa; at  $h^2 = 0.25$  both being equally precise. An explanation for this is as follows. Since,  $h_{s+D}^2$  is the simple average of  $h_s^2$  and  $h_D^2$ , in view of the Cauchy-Schwartz inequality, it can be concluded that  $h_{s+D}^2$  will either lie between the two direct estimates or assume a value less than  $h_s^2$ . The possibility of  $h_{s+D}^2$  (also called the combined estimate) taking a smaller value relative to  $h_s^2$  is understandable because after all the variance expressions depend on, the sire, dam and progeny numbers as well as population heritability and there could be some combinations of these parameters for which,  $h_{s+D}^2 < h_s^2$ .

The above discussion clearly shows the importance of  $h_{s+D}^2$  and its variance in relation to highly heritable traits ( $h^2 > 0.25$ ), for which  $h_s^2$  is not quite reliable. However, no reliable expression of variance of the combined estimate has been reported in the literature. The suitability of bootstrap procedure for computing the approximate variance of the combined estimate has to

be decided based on its performance vis-a-vis a standard technique. Hence, the main objectives of this paper are (i) to derive the expression for the variance of the combined estimate, and having obtained this, (ii) to compare variances of heritability estimates obtained from bootstrap procedure with those based on a standard procedure, called the delta technique explained below, and (iii) to compare  $h_s^2$  and  $h_{s+D}^2$  for their precision under various sample sizes and family structures.

## 2. THE DELTA TECHNIQUE

Suppose  $X_1, X_2, \dots, X_k$  be a set of random variables with known variances and covariances

$$E(X_i) = \xi_i$$

$$V(X_i) = V_{ii}$$

$$\text{Cov}(X_i, X_j) = V_{ij}$$

We wish to find an approximate expression for the variance of some function of the  $X_i$ 's, say,  $Y = f(X)$ . To do this we expand  $f(X)$  in Tailor series about,  $X = \xi$ .

$$Y = f(\xi) + \sum_{i=1}^k (X_i - \xi_i) \frac{\partial f}{\partial X_i} \Big|_{X=\xi} + \text{higher terms}$$

Here,  $E(Y) \cong f(\xi)$  and

$$V(Y) = E[Y - E(Y)]^2 \cong \sum_{i,j=1}^k V_{ij} \frac{\partial f}{\partial X_i} \frac{\partial f}{\partial X_j} \Big|_{X=\xi}$$

This approximate expression for  $V(Y)$  is useful in many contexts. It can be generalized in an obvious way for finding the covariance of two functions of the  $X_i$ 's namely  $Y_1 = f_1(X)$  and  $Y_2 = f_2(X)$  as

$$\text{Cov}(Y_1, Y_2) = \sum_{i,j} V_{ij} \frac{\partial f_1}{\partial X_i} \cdot \frac{\partial f_2}{\partial X_j}$$

## 3. METHOD OF COMPUTATION OF $h^2$ FROM FULL-SIB ANALYSIS

There are quite a few species such as poultry, where the data confirm to a two-way nested structure. Here, each of a set of sires is mated to a set of dams chosen at random from the female population and each mating produces several progeny, which are measured to

generate data. The model for the measurement  $y_{ijk}$ , on  $k^{\text{th}}$  progeny of  $j^{\text{th}}$  dam mated to the  $i^{\text{th}}$  sire can be written as

$$y_{ijk} = \mu + s_i + d_{ij} + e_{ijk} \tag{1}$$

where  $\mu$  is the general mean,  $s_i$  the effect of  $i^{\text{th}}$  sire ( $i = 1, 2, \dots, s$ ),  $d_{ij}$  the effect of the  $j^{\text{th}}$  dam ( $j = 1, 2, \dots, d$ ) mated to the  $i^{\text{th}}$  sire, and  $e_{ijk}$  the error ( $k = 1, 2, \dots, n$ ). Let us further assume that all the effects are randomly and independently distributed with the expectations

$$E(s_i) = E(d_{ij}) = E(e_{ijk}) = 0$$

and variances

$$E(s_i^2) = \sigma_s^2, E(d_{ij}^2) = \sigma_d^2 \text{ and } E(e_{ijk}^2) = \sigma_w^2$$

Under these assumptions, the analysis of variance, as per the linear model of Eq. (1) is as shown in Table 1. The expectations of mean squares given in the table are based on the additive genetic model, which implies that the paternal ( $t_1$ ) and maternal ( $t_2$ ) intra-class correlations are equal ( $t$ ), i.e.,  $t_1 = t_2 = t$ . The analysis of variance (ANOVA) estimates of the observational components of the total phenotypic variance ( $\sigma_p^2$ ), namely  $\sigma_s^2$ ,  $\sigma_d^2$ ,  $\sigma_w^2$  denoted by,  $\hat{\sigma}_s^2$ ,  $\hat{\sigma}_d^2$ ,  $\hat{\sigma}_w^2$  respectively can be obtained by equating the mean square components with their corresponding expectations. Using these, the estimate of the intra-class correlation between paternal half-sibs is given by Ansari (1999) as

$$t_1 = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_d^2 + \hat{\sigma}_w^2} = \frac{M_1 - M_2}{M_1 + (d-1)M_2 + d(n-1)M_3} \tag{2}$$

and, for maternal half-sibs, it is

$$t_2 = \frac{\hat{\sigma}_d^2}{\hat{\sigma}_s^2 + \hat{\sigma}_d^2 + \hat{\sigma}_w^2} = \frac{d(M_2 - M_3)}{M_1 + (d-1)M_2 + d(n-1)M_3} \tag{3}$$

**Table 1.** Analysis of Variance for full-sib data

Source	d.f.	MS	E(MS)
Between sires	$(s-1)$	$M_1$	$[1 + (nd + n - 2)t]\sigma_p^2$
Between dams/sires	$s(d-1)$	$M_2$	$[1 + (n-2)t]\sigma_p^2$
Between progenies/dams /sires	$sd(n-1)$	$M_3$	$[1 - 2t]\sigma_p^2$

Using  $t_1$  and  $t_2$ , three estimates of heritability can be obtained as

$$\begin{aligned} h_S^2 &= 4t_1 \\ h_D^2 &= 4t_2 \\ h_{S+D}^2 &= 2(t_1 + t_2) \end{aligned} \tag{4}$$

Expressions for variances of  $h_S^2$  and  $h_D^2$  as given by Robertson (1959) are as under

$$V(h_S^2) = 32\{(1-t)^2X + [1 + (d-1)t]^2Y + (n-1)^2t^2Z\} \tag{5}$$

$$V(h_D^2) = 32\{t^2X + [d - (d-1)t]^2Y + [1 + (n-1)t]^2Z\} \tag{6}$$

where

$$X = [1 + (nd + n - 2)t]^2[n^2d^2(s-1)]^{-1}$$

$$Y = [1 + (n-2)t]^2[n^2d^2s(d-1)]^{-1}$$

$$Z = [1 - 2t]^2[n^2sd(n-1)]^{-1}$$

#### 4. DERIVATION OF THE VARIANCE OF $h_{S+D}^2$

The sire and dam combined estimate of  $h^2$ , using Eqs. (2) and (3), can be written as

$$h_{S+D}^2 = \frac{2[(M_1 + (d-1)M_2 - dM_3)]}{M_1 + (d-1)M_2 + d(n-1)M_3} \tag{7}$$

The variance of  $h_{S+D}^2$ , using delta-technique, is

$$\begin{aligned} V(h_{S+D}^2) &= \left(\frac{\partial h_{S+D}^2}{\partial M_1}\right)_{M_1=E(M_1)}^2 \sigma_{M_1}^2 + \left(\frac{\partial h_{S+D}^2}{\partial M_2}\right)_{M_2=E(M_2)}^2 \sigma_{M_2}^2 \\ &+ \left(\frac{\partial h_{S+D}^2}{\partial M_3}\right)_{M_3=E(M_3)}^2 \sigma_{M_3}^2 \end{aligned} \tag{8}$$

where  $\sigma_{M_1}^2$ ,  $\sigma_{M_2}^2$  and  $\sigma_{M_3}^2$  are the variances of  $M_1$ ,  $M_2$  and  $M_3$  respectively. This gives

$$V(h_{S+D}^2) = \frac{4n^2d^2}{G^4} \left[ M_3^2\sigma_{M_1}^2 + (d-1)^2M_3^2\sigma_{M_2}^2 + (M_1 + d - 1M_2)^2\sigma_{M_3}^2 \right] \tag{9}$$

in which  $G = M_1 + (d-1)M_2 + (n-1)dM_3$  and  $M_1$ ,  $M_2$  and  $M_3$  are to be replaced by their expectations.

Noting that

$$(s - 1)M_1 \sim \chi_{s-1}^2 \cdot [1 + (nd + n - 2)t] \sigma_p^2$$

$$s(d - 1)M_2 \sim \chi_{s(d-1)}^2 \cdot [1 + (n - 2)t] \sigma_p^2$$

$$sd(n - 1)M_3 \sim \chi_{sd(n-1)}^2 \cdot (1 - 2t) \sigma_p^2$$

we find

$$\sigma_{M_1}^2 = 2[1 + (nd + n - 2)t]^2 \sigma_p^4 / (s - 1)$$

$$\sigma_{M_2}^2 = 2[1 + (n - 2)t]^2 \sigma_p^4 / s(d - 1)$$

$$\sigma_{M_3}^2 = 2(1 - 2t)^2 \sigma_p^4 / sd(n - 1)$$

Accordingly, Eq. (9), reduces to

$$V(h_{S+D}^2) = 8 [ (1 - 2t)^2 X + [(1 - 2t)]^2 (d - 1)^2 Y + \{1 + 2(n - 1)t\}^2 Z ] \quad (10)$$

where X, Y, Z are as defined earlier

Replacing t by  $h^2 / 4$  and simplifying, the variance can be expressed as

$$V(h_{S+D}^2) = 2 [ (2 - h^2)^2 X + (2 - h^2)^2 (d - 1)^2 Y + \{2 + (n - 1)h^2\}^2 Z ] \quad (11)$$

where

$$X = [4 + (nd + n - 2)h^2]^2 [16n^2 d^2 (s - 1)]^{-1}$$

$$Y = [4 + (n - 2)h^2]^2 [16n^2 d^2 s(d - 1)]^{-1}$$

$$Z = [2 - h^2]^2 [4n^2 sd(n - 1)]^{-1}$$

and this is an expression of variance of  $h_{S+D}^2$  in terms of  $h^2$ .

### 5. BOOTSTRAP PROCEDURE FOR THE ESTIMATION OF VARIANCE OF HERITABILITY

The bootstrapping, as explained at the end of this section, is executed on simulated data (master samples). Since the variances are to be estimated for different full-sib family structures and population heritability levels, master samples with these attributes are generated. The simulation procedure (Ronningen 1974) followed for the full-sib case is based on the model

$$y_{ij} = \mu + \sigma_s s'_i + \sigma_d d'_{ij} + \sigma_e e'_{ij} \quad (12)$$

where  $s'_i$ ,  $d'_{ij}$  and  $e'_{ij}$  are the standard normal variates obtained from the Box-Muller transformation (Kennedy and Gentle 1980). The values of  $\sigma_s$ ,  $\sigma_d$  and  $\sigma_e$  are so chosen and substituted in (12) as to generate data, for different sire(s) and dam(d) numbers, and three different levels of population heritability (0.10, 0.25 and 0.50), assuming additive gene action ( $\sigma_s^2 = \sigma_d^2$ ). Further, we assume n progenies are resulting from a mating of a sire and a dam.

For a particular level of population  $h^2$ , consider a full-sib mating design with s sires, d dams and suppose that each mating produces n offspring. Bootstrapping is applied both at sire and dam levels. First s sires are selected at random from s sires by Simple Random Sampling With Replacement by a sequence of random numbers by giving a 'seed' value and then the d dams mated to the selected ith sire are sampled from the d dams in the same fashion. Then all the progenies attached to the (i, j)th sire-dam combination are considered for estimation of heritability. An estimate of heritability from thus selected sdn observations forms one bootstrap replication (sample). Repeating this method of sire and dam resampling, a total of N (100, 200, 500) bootstrap samples are drawn. The generation of bootstrap samples was carried out for several combinations of s (= 4, 8, 10, 16, 20, 25, 40, 50), d (= 10, 20, 25), n (= 2) and true  $h^2$  (0.10, 0.25, 0.50). The computation of estimate of variance of bootstrap heritability estimate was carried out as follows.

For any specified ( $h^2$ , s, d and n) combination, let  $\hat{h}^2$  be the estimate of  $h^2$  from the corresponding master sample and  $\hat{h}^{2*}(1)$ ,  $\hat{h}^{2*}(2)$ , ...,  $\hat{h}^{2*}(N)$  be the estimates from N bootstrap samples. A bootstrap estimator of  $h^2$  is then defined as

$$\hat{h}^{2*}(\cdot) = \left[ \sum_{i=1}^N \hat{h}^{2*}(i) \right] / N \text{ with bias, } \hat{\beta}_{\hat{h}^2} = \hat{h}^{2*}(\cdot) - \hat{h}^2.$$

From these, the bootstrap estimate of sample variance is determined as

$$\hat{V}_{h^2}^*(\text{BOOT}) = \frac{1}{N-1} \sum_{i=1}^N [\hat{h}^{2*}(i) - \hat{h}^{2*}(\cdot)]^2 \quad (13)$$

## 6. PERFORMANCE OF THE BOOTSTRAP METHOD VIS-A-VIS DELTA TECHNIQUE

The variance estimates for  $h_S^2$  and  $h_{S+D}^2$  obtained by adopting bootstrap and delta techniques under different sample sizes and family structures, for different population heritability levels are given in Table 2. These values also help in knowing the behaviour of the estimates, when the number of bootstrap replications increases from 100 to 500. The most encouraging result emerging from the present study is that the bootstrap estimates of  $h^2$  are very close to the approximate theoretical variance determined from the delta technique and this trend is all the more visible when the trait is highly heritable ( $h^2 > 0.25$ ). This shows that the bootstrap technique can be safely and advantageously used in the computation of approximate variance of  $h_S^2$  and  $h_{S+D}^2$ .

The results have also provided sufficient evidence to resolve the conjecture,  $h_{S+D}^2$  is more precise than  $h_S^2$  when the trait involved is highly heritable. From Table 2 it can be seen that, when the variances are much lower for the estimate simultaneously based on sire and dam components as compared to the sire component estimate. When  $h^2 = 0.25$ , both the estimates showed approximately the same precision. These findings consolidate the findings of Prabhakaran and Jain (1988) and Prabhakaran and Sharma (1995), where they have drawn similar conclusions based on the probability of inadmissible estimates under different full-sib family structures. In the present study we have not considered the case of dam component heritability because past studies (e.g. Prabhakaran and Jain 1988) revealed that the dam component estimates are much less precise and much less reliable in comparison with the sire component and sire + dam components.

In our investigation, we have proceeded with the notion that a full-sib mating design is optimum when its group-size (i.e. the number of offspring per sire) is around

$4/h^2$ . It is seen that the variance values are higher when the group-size is below the optimum than when it is above. Therefore, in the estimation of heritability of lowly heritable traits it is desirable that the design has family size in the range of 30-40. For a size of 10 will suffice for reliable estimation. A similar view has been expressed also by Prabhakaran and Sharma (1995).

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**Table 2.** Variances of heritability estimates ( $h^2_s$  and  $h^2_{s+d}$ ) based on delta technique and bootstrap method for different levels of  $h^2$  under different sample sizes ( $T = s d n$ ) and family structures where  $s =$  sire,  $d =$  dam, and  $n =$  offspring

Population heritability = 0.10									
T	(s, d, n)	Var( $h^2_s$ )				Var( $h^2_{s+d}$ )			
replications		Delta	Bootstrap replications			technique	Delta	Bootstrap	
		technique	100	200	500		technique	100	200
200	10,10,2	0.02039	0.03166	0.02910	0.02900	0.04066	0.06801	0.06260	0.06130
	5,20,2	0.01952	0.02220	0.01942	0.01932	0.04156	0.05920	0.05390	0.05240
	4,25,2	0.02092	0.02640	0.02532	0.02469	0.04210	0.06278	0.05530	0.05496
400	20,10,2	0.00970	0.01733	0.01440	0.04193	0.02021	0.03790	0.03116	0.03103
	10,20,2	0.00870	0.01340	0.01149	0.01147	0.02053	0.03419	0.02873	0.02680
	8,25,2	0.00899	0.01597	0.01271	0.01235	0.02070	0.03503	0.03071	0.02807
800	40,10,2	0.00473	0.01139	0.00937	0.00935	0.01008	0.02147	0.01831	0.01790
	20,20,2	0.00413	0.00862	0.00760	0.00744	0.01021	0.01833	0.01679	0.01658
	16,25,2	0.00420	0.00997	0.00853	0.00828	0.01028	0.01943	0.01759	0.01718
1000	50,10,2	0.00377	0.10800	0.00875	0.00874	0.00806	0.01862	0.01558	0.01532
	25,20,2	0.00327	0.00768	0.00688	0.00664	0.00816	0.01349	0.01149	0.01059
	20,25,2	0.00332	0.00807	0.00750	0.00728	0.00822	0.01548	0.01273	0.01224
Population heritability = 0.25									
T	(s, d, n)	Var( $h^2_s$ )				Var( $h^2_{s+d}$ )			
		Delta	Bootstrap replications			technique	Delta	Bootstrap replications	
		technique	100	200	500		technique	100	200
Around 200	20,5,2	0.04558	0.06066	0.05643	0.05424	0.04014	0.06480	0.06270	0.06120
	12,8,2	0.04327	0.05207	0.04722	0.04659	0.04284	0.05728	0.05340	0.05317
	10,10,2	0.04196	0.05562	0.05104	0.04920	0.04177	0.05968	0.05677	0.05544
400	40,5,2	0.02229	0.03580	0.03394	0.03233	0.01996	0.03634	0.03285	0.03118
	25,8,2	0.01991	0.03142	0.02782	0.02646	0.02038	0.03282	0.02993	0.02838
	20,10,2	0.01994	0.03370	0.03069	0.02950	0.02066	0.03384	0.03034	0.02952
800	80,5,2	0.01102	0.01779	0.01675	0.01654	0.00995	0.01598	0.01568	0.01554
	50,8,2	0.00977	0.01595	0.01473	0.01437	0.01015	0.01481	0.01418	0.01385
	40,10,2	0.00973	0.01654	0.01523	0.01508	0.01028	0.01507	0.01461	0.01445
Around 1000	96,5,2	0.00917	0.01622	0.01548	0.01540	0.00829	0.01521	0.01474	0.01451
	60,8,2	0.00811	0.01491	0.01319	0.01314	0.00845	0.01361	0.01326	0.01304
	48,10,2	0.00808	0.01530	0.01394	0.01388	0.00856	0.01421	0.01375	0.01339
Population heritability = 0.50									
T	(s, d, n)	Var( $h^2_s$ )				Var( $h^2_{s+d}$ )			
		Delta	Bootstrap replications			technique	Delta	Bootstrap replications	
		technique	100	200	500		technique	100	200
200	50,2,2	0.12164	0.09436	0.08893	0.08524	0.03612	0.04922	0.04510	0.04447
	25,4,2	0.07711	0.08558	0.08227	0.08113	0.03773	0.04545	0.04236	0.04060
	20,5,2	0.07498	0.08885	0.08481	0.08328	0.03857	0.04155	0.04091	0.03810
400	100,2,2	0.06047	0.05266	0.04727	0.04637	0.01799	0.02972	0.02468	0.02275
	50,4,2	0.03790	0.04470	0.04121	0.03941	0.01875	0.02717	0.02222	0.02200
	40,5,2	0.03665	0.04656	0.04400	0.04344	0.01913	0.02804	0.02276	0.00225
800	200,2,2	0.03015	0.03506	0.03021	0.02910	0.00898	0.01452	0.01399	0.01367
	100,4,2	0.01879	0.02589	0.02263	0.02223	0.00934	0.01334	0.01286	0.01267
	80,5,2	0.01813	0.02846	0.02607	0.02562	0.00953	0.01369	0.01320	0.01282
Around 1000	240,2,2	0.02511	0.02908	0.02570	0.02512	0.00748	0.01286	0.01233	0.01218
	120,4,2	0.01564	0.02006	0.01769	0.01766	0.00778	0.01171	0.01120	0.01106
	96,5,2	0.01508	0.02295	0.02038	0.01991	0.00794	0.01233	0.01189	0.01152