

Generalised Heritability and its Estimation

Prem Narain and Lal Chand*

Indian Agricultural Research Institute, New Delhi

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SUMMARY

Heritability has been found to play a very important role in developing plans for the improvement of individual economic characters in plant and animal breeding. For more than one character, however, the concept of heritability has not been so widely exploited, though it can be generalised, using multivariate methods. There could then be several measures of generalised heritability. In this paper, the concept of standard generalised variance (SGV) which is the k th root of the determinant of a matrix has been used to give a measure of generalised heritability. Its method of estimation by half-sib analysis has also been discussed and illustrated with the help of data on poultry for three characters.

Keywords : Generalised heritability, multivariate methods, half-sib analysis for correlated traits, poultry.

Introduction

In genetics, coefficient of heritability plays a very important role in developing suitable breeding plans for the improvement of economic characteristics in domesticated plants and animals. In the univariate case, this coefficient is the square of the correlation between the breeding value and the phenotypic value of the character and therefore expresses the reliability of the phenotypic value as a guide to the breeding value. When there are several characters determining economic merit of the population, the method of selection index, given by Hazel and Lush [5], is normally adopted. The procedure uses the concept of linear discriminant function given by Fisher [4]. The weights to be attached to the phenotypic values of the character are chosen in such a manner that the correlation between the compounded phenotypic values and the corresponding compounded breeding values is maximum. The latter is a linear function of the unobservable breeding values of the characters with known relative economic weights to be attached to them. Since, the relative economic values of the characters vary over time due to changes in price structure and shifts in demand, the selection index needs periodical revision. This difficulty can be overcome if we adopt instead the principle of canonical correlation between the two sets of breeding and phenotypic values of the

* Indian Agricultural Statistics Research Institute, New Delhi

characters as shown in Narain [8] [9] and Lal Chand & Narain [7]. This approach leads to the concept of generalised heritability which is the multivariate analogue of heritability and is taken as the largest eigen-root of a matrix \mathbf{H} given in Narain [9]. On the other hand, Vondracek [10] used the method of Principal Components to develop similar concepts. He gave generalised components of heritability and interpreted them by means of an interpretation character. The components of heritability are genetically uncorrelated and the first of them has the maximum heritability.

When we numerically studied the behaviour of the generalised heritability for two characters in terms of the largest eigen-root of \mathbf{H} with variation in the set of four genetic parameters viz. the heritabilities of the two characters, the genetic and phenotypic correlations between them, we encountered some difficulty in its interpretation. There could be situations where the largest eigen-root of \mathbf{H} is greater than one which is not admissible for the concept of heritability. It seemed desirable, therefore, to seek for other measures of the generalised heritability. Recently Zhivotovsky [11] introduced a *standard generalised variance* (SGV) of a matrix for the analysis of k correlated quantitative characters in terms of the k -th root of the determinant of the matrix. Such a measure has several desirable statistical properties. It seems if we adopt this definition we have a measure of generalised heritability which might be more meaningful for interpretation. We therefore examine in this paper the generalised heritability through this measure. We also discuss the method of its estimation from half-sib analysis and illustrate the theory by analysing a given set of data in poultry for three characters.

2. Generalised Heritability

Let the phenotypic measurements $[P(x_1), P(x_2), \dots, P(x_k)]$ of an individual in respect of k quantitative characters be expressed in the form of $k \times 1$ column vector \mathbf{p} whereas the corresponding breeding values of the individual $[A(x_1), A(x_2), \dots, A(x_k)]$ be expressed as a $k \times 1$ column vector \mathbf{g} . The non-additive and environmental effects taken together and represented by $[E(x_1), E(x_2), \dots, E(x_k)]$ may be expressed in terms of column vector \mathbf{e} .

Then we have

$$\mathbf{p} = \mathbf{g} + \mathbf{e} \quad (1)$$

where the variables are expressed as deviations from the means and standardised to have variances as unity and covariances as equal to correlations so that the correlation matrix of order $k \times k$ of the variables \mathbf{p} is

$$\Sigma_{\mathbf{p}} = ((\rho_{ij})) \text{ with } \rho_{ii} = 1 \text{ and } \rho_{ij} = \rho_{ji}$$

Further let the variance-covariance matrices each of order $k \times k$ of the vector variables g and e be respectively.

$\Sigma_A = ((h_{ij}))$ and $\Sigma_E = ((e_{ij}))$ with $h_{ij} = h_{ji}$ and $e_{ij} = e_{ji}$ for $i, j = 1, 2, \dots, k$. The h_{ii} 's are heritabilities of the characters and h_{ij} 's are the covariances of the breeding values between the characters. If the genetic correlation between the i -th and the j -th character is denoted by r_{ij} , then h_{ij} can be expressed as $r_{ij} h_{ii} h_{jj}$. Also in view of (1)

$$\text{cov}(g, p) = E(gp^T) = \Sigma_A \quad (2)$$

since $\text{Cov}(A_i, P_j) = \text{Cov}(P_i, A_j) = \text{Cov}(A_i, A_j) = h_{ij}$ and

$$\text{Cov}(A_i, P_i) = \text{Var}(A_i) = h_{ii} \quad (i, j = 1, 2, \dots, k)$$

The matrices Σ_p , Σ_A and Σ_E are assumed to be positive definite and hence non-singular.

If we set up linear functions of the characters with the same coefficients $a^T = (a_1, a_2, \dots, a_k)$ for g and p , the optimum values of these coefficients are found (Narain [9]) by the determinantal equation given by

$$|H - h^2(a) I| = 0 \quad (3)$$

where $H = \Sigma_A \Sigma_p^{-1}$ (4)

and $h(a) = \left[\frac{(a^T \Sigma_A a)}{(a^T \Sigma_p a)} \right]^{1/2}$ (5)

is the correlation between A and P

This means that the desired coefficients are the eigen-roots of the matrix H . But the roots are the squares of the set of canonical correlations between the multiple correlated breeding and phenotypic vectors of the corresponding set of characters. Since the co-efficients of the corresponding canonical variates are chosen such that for the compounded character, the correlation between the breeding and phenotypic values of the compounded character is maximum, it is the square of the largest canonical correlation which was taken as a measure of *generalised heritability* (Narain [8]). For the compounded character, the heritability $h^2(a)$ should be less than 1. This implies, from (5), that

$$a^T \Sigma_A a < a^T \Sigma_p a$$

i.e. $a^T (\Sigma_A - \Sigma_p) a < 0$ (6)

Since $\Sigma_A - \Sigma_p = -\Sigma_E$ and Σ_E is positive definite and hence non-singular, the condition (6) is always satisfied. This means $(H-I)$ would always be negative definite and therefore all the roots $h^2(a_i)$, $i = 1, 2, \dots, k$ would be less than

unity. This, in the univariate case, is self-evident. Taking $h^2 = \sigma_A^2 / \sigma_P^2 = \sigma_P^{-2} \sigma_A^2$, the equation becomes

$$\sigma_A^2 - \lambda \sigma_P^2 = 0 \quad (7)$$

and the solution for λ is necessarily less than unity as $(\sigma_A^2 - \sigma_P^2)$ or $(\sigma_P^{-2} \sigma_A^2 - 1)$ is negative. The analogy between the univariate and multivariate cases is therefore apparent but in the latter case, we have k roots which are candidates for the heritability status. The largest root (LR) is thus one measure for the heritability of the compounded character. But there is no reason why any other measure depending on the k roots cannot be adopted for this purpose.

Zhivotovsky [11] introduced a scalar multivariate analogue of the variance, which possesses some desirable statistical properties. Let \mathbf{x} be a k -variate vector having the variance-covariance matrix Σ and let a scalar function $V(\mathbf{x})$ be some variability measure for this vector based on Σ . Assume that $V(\mathbf{x})$ has the following properties equivalent to properties of the univariate variance

- (i) $V(\mathbf{x}) \geq 0$
- (ii) $V(\mathbf{x}) = 1$ if all the components of the corresponding vector \mathbf{x} are independently distributed with variance 1.
- (iii) $V(k\mathbf{x}) = k^2 V(\mathbf{x})$ for any real k
- (iv) $V(\mathbf{x}_1) = V(\mathbf{x}_2)$ implies that $V(A\mathbf{x}_1) = V(A\mathbf{x}_2)$

where \mathbf{x}_1 and \mathbf{x}_2 are two random vectors each having its own distribution with its own variance-covariance matrix, and A is any arbitrary non-singular matrix. This means that equality or inequality of variability measures in the two populations is invariant to a linear transformation of variables. It can be shown that the only function satisfying all the above properties is

$$V(\mathbf{x}) = |\det \Sigma|^{1/k} \quad (8)$$

which is termed as *Standard Generalised Variance* (SGV).

When we apply the SGV measure for the generalised heritability represented by the matrix H , we have to consider two matrices of variance-covariances viz. Σ_A and Σ_P . Let ϕ_1 and ϕ_2 be the SGV's for the two matrices respectively i.e.

$$\begin{aligned} \phi_1 &= |\Sigma_A|^{1/k} \\ \phi_2 &= |\Sigma_P|^{1/k} \end{aligned} \quad (9)$$

$$\begin{aligned}
 \text{Then } \phi_1 \phi_2^{-1} &= \frac{|\Sigma_A|^{1/k}}{|\Sigma_P|^{1/k}} \\
 &= |\Sigma_A \Sigma_P^{-1}|^{1/k} \\
 &= |\mathbf{H}|^{1/k} \\
 &= \phi_k, \text{ say}
 \end{aligned} \tag{10}$$

is a new measure of generalised heritability.

But

$$|\mathbf{H}|^{1/k} = [h(a_1) h(a_2) \dots h(a_k)]^{2/k} \tag{11}$$

In other words, we consider all the roots by taking their product, extract k -th root of the same and designate it as generalised heritability.

3. Estimation of Generalised Heritability

For estimating heritability in the univariate case, we normally adopt the method of half-sib analysis. A set of n sires are randomly chosen and r_t half-sibs from t -th sire, $t = 1, 2, \dots, n$ are scored for the character under study. In the multivariate case, we have the same design but now k characters on each of the half-sibs of a given sire are scored. Following Dahm *et al.* [3], the linear vectorial model for the analysis is given by

$$y_{ts} = \mu + \eta_t + \delta_{ts}, \quad s = 1, 2, \dots, r_t \quad t = 1, 2, \dots, n \tag{12}$$

where y_{ts} is $k \times 1$ vector of observations on the s th half-sib of the t -th sire, μ is $k \times 1$ vector of the overall means, η_t is the $k \times 1$ vector of sire effects for the t -th sire and δ_{ts} is the $k \times 1$ vector of half-sib effects for the s -th half-sib of the t -th sire. We assume that η_t and δ_{ts} are independently and identically distributed in a multivariate normal form with zero mean vectors and dispersion matrices as Σ_η and Σ_δ respectively whereas y_{ts} is multivariate normal with mean vector as μ and dispersion matrix as Σ_P . While Σ_P and Σ_δ are assumed positive definite, Σ_η could be positive semi-definite. We note that Σ_η is also the matrix of variance-covariances between half-sibs for the set of k characters. This can be seen from

$$\begin{aligned}
 \text{Cov}(y_{ts}, y_{tj}) &= \text{Cov}(\eta_t + \delta_{ts}, \eta_t + \delta_{tj}) \\
 &= \text{Cov}(\eta_t, \eta_t) \\
 &= \Sigma_\eta
 \end{aligned} \tag{13}$$

Also, $\Sigma_{\eta} = (1/4) (\Sigma_A)$ since Cov (HS) equals one-fourth of the additive genetic variance for each character and one fourth of the additive genetic covariance between pairs of characters.

If S_B and S_W denote the matrices of mean sums of squares and products (MSP) for the k -characters for *between sires and within sires* respectively, we have the MANOVA.

MANOVA			
	d.f.	MSP	E(MSP)
Between sires	$n - 1$	S_B	$\Sigma_{\delta} + r \Sigma_{\eta}$
Within sires	$\Sigma_t (r_t - 1)$	S_W	Σ_{δ}

In this table r is given by

$$r = (n - 1)^{-1} [\Sigma r_t - (\Sigma r_t)^{-1} (\Sigma r_t^2)] \tag{14}$$

The matrices of sum of squares and products have independent central Wishart distributions i.e.

$$\begin{aligned} (n - 1) S_B &\sim W_k [(n - 1), \Sigma_{\delta} + r \Sigma_{\eta}] \\ \Sigma (r_t - 1) S_W &\sim W_k [\Sigma (r_t - 1), \Sigma_{\delta}] \end{aligned} \tag{15}$$

We now reduce the multivariate analysis to the univariate case by introducing the compounded character as a linear combination of the set of characters for the observed data, the coefficients of the function being so chosen as to maximise the correlation between half-sibs (HS) for the compounded character. With a_i 's as coefficients.

$$\begin{aligned} X_{ts} &= \Sigma a_i y_{tsi} = \mathbf{a}^T \mathbf{y}_{ts} \\ m &= \Sigma a_i \mu_i = \mathbf{a}^T \boldsymbol{\mu} \\ \eta_t &= \Sigma a_i \eta_{tsi} = \mathbf{a}^T \boldsymbol{\eta}_{ts} \\ d_{ts} &= \Sigma a_i \delta_{tsi} = \mathbf{a}^T \boldsymbol{\delta}_{ts} \end{aligned} \tag{16}$$

Then the linear model for the single compounded character is

$$X_{ts} = m + \eta_t + d_{ts} \tag{17}$$

Then

$$\begin{aligned}\text{Cov (HS)} &= (\mathbf{a}^T \mathbf{y}_{ts}, \mathbf{a}^T \mathbf{y}_{tj}) \\ &= (\mathbf{a}^T \mathbf{y}_{ts} \mathbf{y}_{tj} \mathbf{a}) \\ &= \mathbf{a}^T \Sigma_{\eta} \mathbf{a}\end{aligned}\quad (18)$$

$$\text{Var}(\mathbf{a}^T \mathbf{y}_{ts}) = \mathbf{a}^T \Sigma_{\rho} \mathbf{a} \quad (19)$$

The correlation between HS is then

$$r_{\text{HS}} = \frac{(\mathbf{a}^T \Sigma_{\eta} \mathbf{a})}{(\mathbf{a}^T \Sigma_{\rho} \mathbf{a})} = \frac{(1/4) (\mathbf{a}^T \Sigma_A \mathbf{a})}{(\mathbf{a}^T \Sigma_{\rho} \mathbf{a})} \quad (20)$$

Its maximisation leads to the determinantal equation

$$|(1/4) \Sigma_A - \lambda \Sigma_{\rho}| = 0 \quad \text{or} \quad |(1/4) \mathbf{H} - \lambda \mathbf{I}| = 0 \quad (21)$$

This shows that the eigen-roots of this determinantal equation are

$$(1/4) h^2(a_i), \quad i = 1, 2, \dots, k.$$

From the MANOVA we have the estimates of Σ_{η} & Σ_{ρ} as

$$\begin{aligned}\hat{\Sigma}_{\eta} &= \frac{(\mathbf{S}_B - \mathbf{S}_W)}{r} = (1/4) \hat{\Sigma}_A \\ \hat{\Sigma}_{\delta} &= \mathbf{S}_W \\ \hat{\Sigma}_{\rho} &= \hat{\Sigma}_{\eta} + \hat{\Sigma}_{\delta} \\ &= \frac{[\mathbf{S}_B + (r-1) \mathbf{S}_W]}{r}\end{aligned}\quad (22)$$

Substituting in the determinantal equation, we get

$$|\mathbf{S}_B - \lambda^* \mathbf{S}_W| = 0 \quad (23)$$

where

$$\lambda^* = \frac{[1 + (1/4) h^2(a) (r-1)]}{[1 - (1/4) h^2(a)]} \quad (24)$$

If $\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_k$ denote the corresponding eigen-vectors, we have

$$\mathbf{S}_W = \sum_{i=1}^k \mathbf{v}_i \mathbf{v}_i^T, \quad \mathbf{S}_B = \sum_{i=1}^k \lambda_i^* \mathbf{v}_i \mathbf{v}_i^T \quad (25)$$

From the observed data, we estimate the eigen-roots λ_i^* of the matrix $(S_B S_W^{-1})$ provided S_W is positive definite and hence non-singular. Using these eigen-roots, we obtain $h^2(a_i)$ as

$$\hat{h}^2(a_i) = 4 \left[1 + \frac{r}{(\lambda_i^* - 1)} \right]^{-1}, \quad i = 1, 2, \dots, k \tag{26}$$

The estimate of generalised heritability is then given by

$$\begin{aligned} \hat{\phi}_k &= [\hat{h}^2(a_1) \hat{h}^2(a_2) \dots \hat{h}^2(a_k)]^{1/k} \\ \hat{\phi}_k &= [\hat{h}(a_1) \hat{h}(a_2) \dots \hat{h}(a_k)]^{2/k} \end{aligned} \tag{27}$$

Let the sampling variances of the estimated values $\hat{h}^2(a_i) = Z_i$ say, be denoted by $\sigma_{z_i}^2$, $i = 1, 2, \dots, k$. Then

Since
$$\hat{\phi}_k = [Z_1 Z_2 \dots Z_k]^{1/k} \tag{28}$$

$$\log \phi_k = (1/k) \Sigma \log Z_i, \tag{29}$$

$$\text{Var}(\hat{\phi}_k) = \left(\frac{\hat{\phi}_k}{k} \right)^2 \Sigma \left(\frac{\sigma_{z_i}^2}{Z_i^2} \right), \tag{30}$$

as $\text{Cov}(Z_i, Z_j) = 0$, λ_i^* and λ_j^* being uncorrelated.

The standard error of generalised heritability can, therefore, be estimated as

$$\text{SE}(\hat{\phi}_k) = \left(\frac{\hat{\phi}_k}{k} \right) \left[\Sigma \left(\frac{\sigma_{z_i}^2}{Z_i^2} \right) \right]^{1/2} \tag{31}$$

The standard error of Z_i or $h^2(a_i)$ can be obtained in two ways. Firstly from (26)

$$\sigma_{z_i}^2 = \left[\frac{16 r^2}{(\lambda_i^* - 1 + r)^4} \right] \text{Var}(\lambda_i^*) \tag{32}$$

The asymptotic variance of λ_i^* is $\frac{2\lambda_i^{*2}}{n}$ in view of Konishi & Rao [6] and Anderson [2].

Then

$$\text{S.E. } (Z_i) = \left[\frac{4r\lambda_i^*}{(\lambda_i^* - 1 + r)^2} \right] \left(\frac{2}{n} \right)^{1/2} \quad (33)$$

Secondly, for each root of the matrix $(S_B S_W^{-1})$ estimated from MANOVA, we have the compounded character as a linear function of the k - variates with the estimated coefficients. This single compounded character can be subject to usual half-sib analysis to obtain an estimate of the heritability which would be same as $\hat{h}^2(a_i)$, $i = 1, 2, \dots k$ as well as the estimates of the standard errors of the estimated heritabilities.

4. Illustration with Data on Poultry

The breeding data of pure female line of the parent lines ILI-80 developed by CARI, Izatnagar maintained at Poultry Breeding Farm, Bhopal (M.P.) for the year 1990-91 were utilised for illustration of the above procedure. The data are on three characters viz. age at maturity (y_1), 280 day egg production (y_2) and egg weight (y_3) measured on each progeny of the 39 sires. The records on these characters were adjusted for non-genetic hatch effect (fixed) by using least squares constants technique and the univariate heritabilities were estimated by half-sib method. These estimates for the characters with their S.E.'s were found to be 0.1946 ± 0.0963 , 0.1127 ± 0.0845 and 0.4633 ± 0.1456 respectively.

As defined in Section 3, the matrices of mean sum of squares and products \hat{S}_B and \hat{S}_W for *Between sires* and *within sires* respectively are presented in Table 1.

Table 1. Between Sires (\hat{S}_B) and within sires (\hat{S}_W) variance-covariance matrices for the three characters.

Character	Covariance					
	\hat{S}_B			\hat{S}_W		
Age at maturity (y_1)	204.58	-129.01	12.25	120.47	-54.86	0.14
280 day Egg production (y_2)		329.72	-13.90		228.45	-1.95
Egg weight (y_3)			42.69			14.21

The roots of the determinantal equation

$$|\hat{S}_B - \lambda \hat{S}_W| = 0$$

are found to be

$(\lambda_1, \lambda_2, \lambda_3) = (3.068, 1.723, 1.155)$. $(\hat{S}_B - \hat{S}_W)$ being positive definite, the roots are all greater than one. As per procedure given in Section 3, the estimates of $h^2(a_i)$ are

$$\hat{h}^2(a_i) = 4 \left[\frac{1+r}{(\lambda_i - 1)} \right]^{-1}, \quad i = 1, 2, 3$$

where r is found to be 15.294. Substituting the values of r and $\hat{\lambda}_i$, the values of $\hat{h}^2(a_i)$ are (0.4765, 0.1804, 0.0405).

The estimate of the generalised heritability is then

$$\begin{aligned} \hat{\phi} &= [\hat{h}^2(a_1) \hat{h}^2(a_2) \hat{h}^2(a_3)]^{1/3} \\ &= (.4765 \times .1804 \times .0405)^{1/3} \\ &= 0.1510 \end{aligned}$$

Taking the estimates of the asymptotic variance of λ_i 's, the standard errors of $\hat{h}^2(a_i)$ using (33), are found to be (0.1406, 0.0929, 0.0671). The standard error of the generalised heritability ($\hat{\phi}$) is then, from (31); 0.0885.

The other way to obtain the estimate of the standard error of the generalised heritability is to obtain the three linear discriminant functions by maximising the variation *Between sires* relative to that *Within sires* corresponding to each root of the determinantal equation $(S_B - \lambda S_W) = 0$. The estimated linear functions are found as

$$X_1 = y_1 - 0.28 y_2 + 15.57 y_3$$

$$X_2 = y_1 - 0.41 y_2 - 0.90 y_3$$

$$X_3 = y_1 + y_2 - 0.04 y_3$$

Using the half-sib correlation method for estimating the heritability for each compounded character X_1, X_2, X_3 the estimates of the heritabilities of these compounded characters viz. $\hat{h}^2(x_1), \hat{h}^2(x_2), \hat{h}^2(x_3)$ are, along with S.E.'s, found to be $(0.4765 \pm 0.1476, 0.1804 \pm 0.0974, 0.0405 \pm 0.0703)$. While the estimates are, as expected, exactly the same as those of $h^2(a_i)$, $i = 1, 2, 3$ respectively, their standard errors are also found to be quite close to the estimates obtained by the first method. Using (31), the standard error of the generalised heritability ($\hat{\phi}$) is now estimated as 0.0928 which is quite near to 0.0885 obtained by the first method.

5. Discussion

It is apparent from the theory and illustration presented in the previous sections that the measure of the generalised heritability based on the concept of the SGV can be helpful for genetic studies with multivariate data. However, when estimated from half-sib analysis, we may encounter situations where the difference between S_B and S_W is not non-negative definite, although both the matrices are positive definite. The MANOVA estimator Σ_η is then outside the parameter space, and one or more roots of $S_B \cdot S_W^{-1}$ happen to be less than one. Amemiya [1] has discussed this problem and indicated a way out. Suppose m be the number of λ_i such that $\lambda_i \geq 1$ and $(k - m)$ be the number of λ_j such that $\lambda_j < 1$ then $(S_B - S_W)$ can be expressed as the sum $(S_B - S_W)_+ + (S_B - S_W)_-$. The former $(S_B - S_W)_+$ being non-negative definite, can be considered to be the closest matrix to $(S_B - S_W)$ among all the non-negative definite matrices that have the same characteristic vectors in the metric of S_W as those of $(S_B - S_W)$. Then the MANOVA estimators of Σ_η and Σ_δ are respectively $\left[r^{-1} (S_B - S_W)_+ \right]$ and $\left[S_B - (S_B - S_W)_+ \right]$. However, often the estimators in such a case are not in a readily computable form because the expression involves characteristic roots and vectors of S_B in the metric of S_W . The MATRIX PROCEDURE OF SAS software package can be used in such a case. For details, reference may be made to Amemiya [1] who has illustrated the procedure by using a part of the data presented in Dahm *et al* [3].

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