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On a method of estimating the genetic correlation between characters measured in different experimental units

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Summary. Yamada's method of estimating genetic covariances between traits measured in different experimental units is discussed. It is shown that if the data are unbalanced, this method gives biased estimates of genetic covariances unless the traits have identical genetic and residual variances. An alternative unbiased procedure is suggested.

Key words: Genetic covariance – Genetic correlation – Genetic parameters

Introduction

Estimates of genetic covariances are used to predict correlated responses to selection and to rank prospective parents on the basis of multivariate data. Methods used to estimate components of variance can also be used to estimate covariance components for two traits described by the same linear model. However, when this is not possible, e.g., two traits measured in different sexes, other methods are needed.

Schaeffer et al. (1978) introduced simultaneous variance and covariance component estimation by restricted maximum likelihood for traits described by different mixed models. In situations where the mixed model does not include interactions between random and fixed factors or random factors nested within fixed classifications, genetic covariances can be estimated from functions of least-squares solutions (Wiggans et al. 1980).

Another approach to estimate genetic covariance between characters measured in different experimental units is to regard the two traits as realizations of a single variable (Yamada 1962). The model includes a fixed factor representing the mean of the trait under different conditions (e.g., ovulation rate in females and testes weight in males), a random classification representing genotype (e.g., sire group), and the "trait" by genotype interaction as a random effect. The relationship between analysis of variance (ANOVA) estimates of variance components from this model and the genetic correlation (Robertson 1959; Dickerson 1962; Yamada 1962) is then used to estimate the latter.

The objective of this paper is to show that this relationship does not hold in general and, in particular, when the data are unbalanced. A procedure leading to an unbiased estimator of genetic covariance between traits measured in different experimental units is suggested.

Yamada's method

Falconer (1952) used the concept of genetic correlation between traits to evaluate response to selection in an environment different from the one in which breeding of parents took place, regarding as different the same character expressed in two environments. Robertson (1959) and Dickerson (1962) further developed the underlying theory. Yamada (1962) suggested analyzing the two traits with a univariate linear model including a fixed factor (environment or trait), a random factor (genotype or genetic group), and their interaction; the method would also be applicable to entirely different traits. When the variance among genetic groups is the same in both environments, the genetic correlation (r) can be estimated as

$$\hat{r} = \frac{\hat{\sigma}^2_G}{\hat{\sigma}^2_G + \hat{\sigma}^2_I}, \quad (1)$$

where $\hat{\sigma}^2_G$ and $\hat{\sigma}^2_I$ are ANOVA estimators of the genetic-group and the genotype x environment interaction variance components, respectively, obtained from balanced data. Yamada (1962) showed that with balanced data, the estimate obtained with (1) is identical to the one that would result from a one-way analysis of covari-

ance with genetic group as the classification variable. The relationships are

$$\hat{\sigma}_G^2 = \hat{\sigma}_{12} \tag{2a}$$

$$\hat{\sigma}_G^2 + \hat{\sigma}_I^2 = \tfrac{1}{2}(\hat{\sigma}_1^2 + \hat{\sigma}_2^2) \tag{2b}$$

where $\hat{\sigma}_{12}$ is the estimator of genetic covariance, and $\hat{\sigma}_I^2$ and $\hat{\sigma}_2^2$ are the estimators of genetic variance for traits 1 and 2, respectively. When $\sigma_1^2 = \sigma_2^2$, the expression $\frac{1}{2}(\hat{\sigma}_1^2 + \hat{\sigma}_2^2)$ yields an unbiased estimator of $\sigma_1\,\sigma_2$. When $\sigma_1^2 \neq \sigma_2^2$, Yamada (1962) suggested using

$$\hat{\sigma}_G^2 + \hat{\sigma}_I^2 - \tfrac{1}{2}(\hat{\sigma}_1^2 + \hat{\sigma}_2^2) + \hat{\sigma}_1\,\hat{\sigma}_2 \tag{3}$$

as the denominator in (1). However, in view of (2b), this is tantamount to using $\hat{\sigma}_1\,\hat{\sigma}_2$ as denominator in (1).

Relationships between estimators do not necessarily imply parametric relationships. It can be shown, in completely general terms, that the one-way analysis of covariance and the two-way analysis of variance models used by Yamada (1962) are not equivalent unless the two traits have identical heritabilities and residual variances. Two models are defined to be equivalent if the first and second moments of the variable being analyzed are the same under both models. Consider first the one-way analysis of covariance model (Model A):

$$\mathbf{y} = \begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{l}_1\,\mu_1\\ \mathbf{l}_2\,\mu_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \tag{4}$$

where $\mathbf{y}_i$ is the $n_i \times 1$ vector of data for trait i, $i = 1, 2$, and n_i is the number of observations for trait i; μ_i is the expected value of trait i and $\mathbf{l}_i$ is an $n_i \times 1$ vector of ones; $\mathbf{u}_i$ is a vector of genetic-group effects for trait i with the order of $\mathbf{u}_1$ equal to the order of $\mathbf{u}_2$; $\mathbf{Z}_i$ is a known matrix relating $\mathbf{u}_i$ to $\mathbf{y}_i$, and $\mathbf{e}_i$ is the $n_i \times 1$ vector of residuals for trait i. Location assumptions for Model A are

$$\mathrm{E}(\mathbf{y}_i) = \mathbf{l}_i\,\mu_i, \quad \mathrm{E}(\mathbf{u}_i) = \mathbf{0}, \quad \mathrm{E}(\mathbf{e}_i) = \mathbf{0}. \tag{5}$$

Dispersion matrices are

$$\mathrm{Var}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} = \begin{bmatrix}\mathbf{I}\,\sigma_1^2 & \mathbf{I}\,\sigma_{12}\\ \mathbf{I}\,\sigma_{12} & \mathbf{I}\,\sigma_2^2\end{bmatrix}, \quad \mathrm{Var}\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} = \begin{bmatrix}\mathbf{I}_1\,\sigma_{e_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\,\sigma_{e_2}^2\end{bmatrix} \tag{6}$$

where $\mathbf{I}$, $\mathbf{I}_1$ and $\mathbf{I}_2$ are identity matrices of appropriate order. If residuals are uncorrelated with genetic group effects, then

$$\mathrm{Var}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{Z}_1\,\mathbf{Z}_1'\,\sigma_1^2 & \mathbf{Z}_1\,\mathbf{Z}_2'\,\sigma_{12}\\ \mathbf{Z}_2\,\mathbf{Z}_1'\,\sigma_{12} & \mathbf{Z}_2\,\mathbf{Z}_2'\,\sigma_2^2\end{bmatrix} + \begin{bmatrix}\mathbf{I}\,\sigma_{e_1}^2 & 0\\ 0 & \mathbf{I}\,\sigma_{e_2}^2\end{bmatrix}. \tag{7}$$

Next, describe the data with the two-way analysis of variance model (Model B):

$$\mathbf{y} = \begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{l}_1\,\mu_1\\ \mathbf{l}_2\,\mu_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1\\ \mathbf{Z}_2\end{bmatrix}\mathbf{u}_G + \begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\mathbf{u}_I + \mathbf{e} \tag{8}$$

where $\mathbf{y}_i$, μ_i, $\mathbf{l}_i$ and $\mathbf{Z}_i$ are as defined earlier; $\mathbf{u}_G$ is a vector of genetic-group effects averaged over environments; $\mathbf{u}_I$ is a vector of genotype × environment interaction effects, and $\mathbf{e}_i$ is a vector of residual effects. Expectations and covariance matrices of random variables in Model B are assumed to be

$$\mathrm{E}(\mathbf{y}_i) = \mathbf{l}_i\,\mu_i, \quad \mathrm{E}(\mathbf{u}_G) = \mathbf{0}, \quad \mathrm{E}(\mathbf{u}_I) = \mathbf{0}, \quad \mathrm{E}(\mathbf{e}) = \mathbf{0} \tag{9}$$

and

$$\mathrm{Var}(\mathbf{u}_G) = \mathbf{I}\,\sigma_G^2, \quad \mathrm{Var}(\mathbf{u}_I) = \mathbf{I}\,\sigma_I^2, \quad \mathrm{Var}(\mathbf{e}) = \mathbf{I}\,\sigma_e^2.$$

With $\mathbf{u}_G$, $\mathbf{u}_I$ and $\mathbf{e}$ pairwise independent,

$$\mathrm{Var}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{Z}_1\,\mathbf{Z}_1' & \mathbf{Z}_1\,\mathbf{Z}_2'\\ \mathbf{Z}_2\,\mathbf{Z}_1' & \mathbf{Z}_2\,\mathbf{Z}_2'\end{bmatrix}\sigma_G^2 + \begin{bmatrix}\mathbf{Z}_1\,\mathbf{Z}_1' & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\,\mathbf{Z}_2'\end{bmatrix}\sigma_I^2 + \begin{bmatrix}\mathbf{I}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\end{bmatrix}\sigma_e^2 \tag{10}$$

The variables analyzed have the same expectation under Models A and B. The following relationships should hold for these models to be equivalent:

	Parameter	Model A	Model B
i)	Variance of trait 1	$\sigma_1^2 + \sigma_{e_1}^2$	$\sigma_G^2 + \sigma_I^2 + \sigma_e^2$
ii)	Variance of trait 2	$\sigma_2^2 + \sigma_{e_2}^2$	$\sigma_G^2 + \sigma_I^2 + \sigma_e^2$
iii)	Covariance between individuals in same genetic group, trait 1	σ_I^2	$\sigma_G^2 + \sigma_I^2$
iv)	Covariance between individuals in same genetic group, trait 2	σ_2^2	$\sigma_G^2 + \sigma_I^2$
v)	Covariance between traits 1 and 2 measured in different individuals of same genetic group.	σ_{12}	σ_G^2

The above indicate that Models A and B are equivalent only when $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$. When $\sigma_1^2 \neq \sigma_2^2$ or $\sigma_{e_1}^2 \neq \sigma_{e_2}^2$, no meaningful relationships exist between the parameters of the two models. Hence, the method of Yamada (1962) should not be used in a general setting.

As pointed out, the estimate of genetic correlation obtained with the two models is the same when the data are balanced. However, if the layout is unbalanced, Yamada's (1962) procedure would lead to an unbiased estimator of σ_{12} only if $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$. Yamada's (1962) method, however, has been used in more general situations (Hohenboken and Brinks 1971; Tewolde 1981). To illustrate, consider data from 2 random genetic groups and 2 fixed environments. The number of observations per genetic-group × environment subclass is assumed to be the following

	Genetic group 1	Genetic group 2
Environment 1	5	1
Environment 2	2	1

Because the layout is unbalanced and the model describing the records is mixed, ANOVA estimators of components of variance are biased (Searle 1971). One possibility would be to use Henderson's Method 3 (Henderson 1953) to estimate the genetic-group (σ^2_G), genotype × environment interaction (σ^2_I) and residual (σ^2_e) variance components of Model B. For this two-way mixed model with interaction, and with the subclass numbers given above, Model B can be written as

$$\mathbf{y} = \mathbf{X}_1 \boldsymbol{\beta} + \mathbf{X}_2 \mathbf{u}_G + \mathbf{X}_3 \mathbf{u}_I + \mathbf{e}$$

where

$$\mathbf{y}' = [\mathbf{y}_1', \mathbf{y}_2'], \quad \boldsymbol{\beta}' = [\mu_1, \mu_2],$$

$$\mathbf{X}_1 = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \end{bmatrix}, \quad \mathbf{X}_2 = \begin{bmatrix} \mathbf{Z}_1 \\ \mathbf{Z}_2 \end{bmatrix}, \quad \mathbf{X}_3 = \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix}$$

$$\mathbf{Z}_1 = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}, \text{ and } \mathbf{Z}_2 = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}.$$

Obtaining Method 3 estimates involves equating the quadratic functions $R(\boldsymbol{\beta})$, $R(\boldsymbol{\beta}, \mathbf{u}_G)$, $R(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I)$ and $\mathbf{y}'\mathbf{y}$ to their expectations; $\mathbf{y}'\mathbf{y}$ is the total sum of squares and $R(\cdot)$ indicates a reduction in sums of squares as in Searle (1971). Let $\mathbf{W}_1 = \mathbf{X}_1$, $\mathbf{W}_2 = [\mathbf{X}_1, \mathbf{X}_2]$ and $\mathbf{W}_3 = [\mathbf{X}_1, \mathbf{X}_2, \mathbf{X}_3]$. The reductions in sums of squares can be written as

$$R(\boldsymbol{\beta}) = \mathbf{y}' \mathbf{W}_1 (\mathbf{W}_1' \mathbf{W}_1)^- \mathbf{W}_1' \mathbf{y},$$

$$R(\boldsymbol{\beta}, \mathbf{u}_G) = \mathbf{y}' \mathbf{W}_2 (\mathbf{W}_2' \mathbf{W}_2)^- \mathbf{W}_2' \mathbf{y},$$

and

$$R(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I) = \mathbf{y}' \mathbf{W}_3 (\mathbf{W}_3' \mathbf{W}_3)^- \mathbf{W}_3' \mathbf{y},$$

where $(\mathbf{W}_i' \mathbf{W}_i)^-$ is a generalized inverse of $\mathbf{W}_i' \mathbf{W}_i$, $i = 1, \ldots, 3$. Because $R(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I) = R(\boldsymbol{\beta}, \mathbf{u}_I)$, this can be more easily obtained as $\mathbf{y}' \mathbf{W}_4 (\mathbf{W}_4' \mathbf{W}_4)^- \mathbf{W}_4' \mathbf{y}$, where $\mathbf{W}_4 = [\mathbf{X}_1, \mathbf{X}_3]$. The expected values of the above quadratics are calculated as

$$E(\mathbf{y}' \mathbf{Q}_i \mathbf{y}) = \text{tr}[\mathbf{Q}_i \text{Var}(\mathbf{y})] + E(\mathbf{y}') \mathbf{Q}_i E(\mathbf{y}), \tag{11}$$

where $\mathbf{Q}_i = \mathbf{W}_i (\mathbf{W}_i' \mathbf{W}_i)^- \mathbf{W}_i'$ (Searle 1971). The expected value of the total sum of squares can be obtained with (11) using $\mathbf{Q}_i = \mathbf{I}_{n_1+n_2}$. The expected value of $\mathbf{y}' \mathbf{Q}_i \mathbf{y}$ can be evaluated under Models A and B by replacing Var (y) in (11) by (7) and (10). These expectations include a linear combination of the unknown variance components and $\boldsymbol{\beta}' \mathbf{X}_1' (\mathbf{X}_1' \mathbf{X}_1)^- \mathbf{X}_1' \boldsymbol{\beta}$ in all four of them. This term can be eliminated, thus reducing the system to be solved to one of three equations. The system of equations on σ^2_G, σ^2_I and σ^2_e (Model B) can be written as

$$E(\mathbf{b}) = \mathbf{B} \boldsymbol{\theta}_B, \tag{12}$$

where $\mathbf{b}' = [R(\boldsymbol{\beta}, \mathbf{u}_G) - \mathbf{R}(\boldsymbol{\beta}), \quad R(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I) - R(\boldsymbol{\beta}), \quad \mathbf{y}'\mathbf{y} - R(\boldsymbol{\beta})]$, $\mathbf{B}$ is a 3×3 matrix usually of full rank, and $\boldsymbol{\theta}_B' = [\sigma^2_G, \sigma^2_I, \sigma^2_e]$. The Method 3 estimator of $\boldsymbol{\theta}_B$ is

$$\hat{\boldsymbol{\theta}}_B = \mathbf{B}^{-1} \mathbf{b}. \tag{13}$$

and

$$E(\hat{\boldsymbol{\theta}}_B) = \mathbf{B}^{-1} E(\mathbf{b}) = \boldsymbol{\theta}_B \tag{14}$$

so $\hat{\boldsymbol{\theta}}_B$ is an unbiased estimator of $\boldsymbol{\theta}_B$.

The expected value of $\hat{\boldsymbol{\theta}}_B$ can also be evaluated in terms of

$$\boldsymbol{\theta}_A' = [\sigma^2_I, \sigma_{I2}, \sigma^2_2, \sigma^2_{e_1}, \sigma^2_{e_2}], \tag{15}$$

a vector containing the parameters of Model A. Hence,

$$E(\hat{\boldsymbol{\theta}}_B) = \mathbf{B}^{-1} \mathbf{E}(\mathbf{b}) = \mathbf{B}^{-1} \mathbf{A} \boldsymbol{\theta}_A \tag{16}$$

where $\mathbf{A}\boldsymbol{\theta}_A$ is the expected value of $\mathbf{b}$ under Model A, and $\mathbf{A}$ is a 3×5 matrix, the elements of which are obtained from (11) by using (7) for Var (y).

For the data in the example,

$$\mathbf{A} = \begin{bmatrix} .93 & 1.48 & .59 & .56 & .44 \\ 1.67 & 0 & 1.33 & 1.00 & 1.00 \\ 1.67 & 0 & 1.33 & 5.00 & 2.00 \end{bmatrix},$$

$$\mathbf{B} = \begin{bmatrix} 3 & 1.52 & 1 \\ 3 & 3 & 2 \\ 3 & 3 & 7 \end{bmatrix},$$

and

$$\mathbf{B}^{-1} \mathbf{A} = \begin{bmatrix} .057 & 1 & -.057 & .043 & -.043 \\ .5 & -1 & .5 & -.243 & .243 \\ 0 & 0 & 0 & .8 & .2 \end{bmatrix}.$$

Thus, the relationship between the parameters of Model B and those of Model A is

$$E(\hat{\sigma}^2_G) = .057\,\sigma^2_I + \sigma_{I2} - .057\,\sigma^2_2 + .043\,\sigma^2_{e_1} - .043\,\sigma^2_{e_2}$$

$$E(\hat{\sigma}^2_I) = .5\,\sigma^2_I - \sigma_{I2} + .5\,\sigma^2_2 - .243\,\sigma^2_{e_1} + .243\,\sigma^2_{e_2}$$

and

$$E(\hat{\sigma}^2_e) = .8\,\sigma^2_{e_1} + .2\,\sigma^2_{e_2}.$$

If the genetic correlation between the two traits is calculated as suggested by Yamada (1962), the numer-

ator in equation (1) would be a biased estimator of σ_{12} unless $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$. When the assumption $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$ can be justified, the expected value of the denominator in equation (1) is

$$E(\hat{\sigma}_G^2 + \hat{\sigma}_I^2) = .5(\sigma_1^2 + \sigma_2^2) = \sigma_1 \sigma_2.$$

However, when $\sigma_1^2 \neq \sigma_2^2$ or $\sigma_{e_1}^2 \neq \sigma_{e_2}^2$, the expected value of the "adjusted" (Yamada 1962) denominator is

$$E[\hat{\sigma}_G^2 + \hat{\sigma}_I^2 - (\hat{\sigma}_1 - \hat{\sigma}_2)^2/2] = \\ = .057\,\sigma_1^2 - .057\,\sigma_2^2 - .2\,\sigma_{e_1}^2 + .2\,\sigma_{e_2}^2 + E(\hat{\sigma}_1 \hat{\sigma}_2).$$

Now

$$E(\hat{\sigma}_1 \hat{\sigma}_2) = \mathrm{Cov}(\hat{\sigma}_1, \hat{\sigma}_2) + E(\hat{\sigma}_1)\,E(\hat{\sigma}_2)$$

and because the records for traits 1 and 2 are correlated through common genetic groups, it follows that $\mathrm{Cov}(\hat{\sigma}_1, \hat{\sigma}_2) \neq 0$. Further, $E(\hat{\sigma}_i) \neq \sigma_i$. Therefore even, if $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$, the "adjusted" denominator yields a biased estimator of $\sigma_1 \sigma_2$.

In conclusion, Yamada's (1962) method is not well defined, except when $\sigma_1^2 = \sigma_2^2$ and $\sigma_{e_1}^2 = \sigma_{e_2}^2$, and should not be used with unbalanced data. These are very restrictive conditions which preclude utilization of the procedure in general settings, particularly in animal breeding.

Alternative procedure

Schaeffer et al. (1978) presented a general solution to the problem of estimating correlations between traits observed in different experimental units. However, computations are formidable and require iteration. Convergence may be slow or may not occur in some instances. The procedure suggested by Wiggans et al. (1980) cannot be used with some models commonly encountered in animal breeding practice.

It is possible to obtain unbiased estimators of genetic covariance from statistics arising in Henderson's Method 3. Using the example of the previous section, observe in $E(\hat{\boldsymbol{\theta}}_B) = \mathbf{B}^{-1}\mathbf{A}\,\boldsymbol{\theta}_A$, that there are 2 equations involving σ_{12}. From these, two unbiased estimators of σ_{12} can be obtained as

$$\hat{\sigma}_{12}^{*} = \hat{\sigma}_G^2 - .057\,\hat{\sigma}_1^2 + .057\,\hat{\sigma}_2^2 - .043\,\hat{\sigma}_{e_1}^2 + .043\,\hat{\sigma}_{e_2}^2 \qquad (17)$$

and

$$\hat{\sigma}_{12}^{**} = .5(\hat{\sigma}_1^2 + \hat{\sigma}_2^2) + .243(\hat{\sigma}_{e_2}^2 - \hat{\sigma}_{e_1}^2) - \hat{\sigma}_I^2 \qquad (18)$$

provided that the estimators in the right-hand sides of (17) and (18) are unbiased for their respective parameters. The two estimators may be combined as

$$\hat{\sigma}_{12} = w\,\hat{\sigma}_{12}^{*} + (1 - w)\,\hat{\sigma}_{12}^{**} \qquad (19)$$

where w is a real number usually taken in the interval (0, 1). The method is arbitrary in that the combined estimator depends on the choice of w. It would be theoretically possible to find the value of w minimizing the sampling variance of such a pooled estimator (Eisen 1967; Gianola 1979; Grossman and Norton 1981; Ollivier 1982). However, as pointed out by Thompson (1977), calculations can be intractable in the general case. Maximum likelihood, or variations thereof as in Schaeffer et al. (1978), automatically take into account all information available (Thompson 1977).

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