

Covariance of Inbred Relatives with Special Reference to Selfing

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ABSTRACT

The covariance of inbred relatives from a population in linkage and identity equilibrium in the presence of dominance and epistasis is formulated using a similar procedure to that which B. S. WEIR and C. C. COCKERHAM used to derive a general expression for the genotypic variance. An alternative model based on the description of a genotype in terms of the homozygotes of its constituent alleles is defined which leads to an equivalent set of 21 quadratic components, but when the relatives are descended from a common ancestor by selfing some confounding occurs and only 12 are necessary. This covariance can be subdivided into components arising among families at different levels of the hierarchy generated by a selfing series, and the component among descendants of distinct members of the base population has a different form from those arising at lower levels of the hierarchy. The 12 quadratic components together with an error variance can be estimated using the 20 statistics provided by analyses of variance and covariance of families generated by four generations of selfing.

A general expression for the genotypic variance of a population arising from two loci with no restrictions on genotypic structure or gene action was given by WEIR and COCKERHAM (1977). If linkage disequilibrium is excluded, this expression involves 21 quadratic components. The model underlying this derivation describes the genotype in a noninbred format and inbreeding is catered for by allowing nonzero values for the probability of identity by descent of alleles at a locus within a genotype. The quadratic components familiar from the description of a noninbred population are used in the company of others which allow for the effects of inbreeding. A similar method is used here to derive an expression for the covariance of inbred relatives in a population in linkage and identity equilibrium in the presence of dominance and epistasis.

WRIGHT and COCKERHAM (1986) showed that for one locus an alternative but equivalent set of quadratic components can be specified which includes the variance of homozygous genotypes instead of the usual additive genetic variance, and for relatives which are descended from a common ancestor by selfing there is confounding and fewer components are needed. In this paper the homozygote-based model is used explicitly in an extension of the covariance of relatives to include epistasis.

THE CONVENTIONAL GENOTYPIC MODEL

Definitions of effects and descent measures: Using a similar notation to that of WEIR and COCKERHAM (1977), the genotypic values of typical individuals x

and y with genotypes G_{rs}^{ij} and G_{uv}^{kl} , respectively, can be expanded as

$$\begin{aligned} x = G_{rs}^{ij} &= \mu_o + a_i + a_j + b_r + b_s + d_{ij}^a + d_{rs}^b \\ &+ (ab)_{ir} + (ab)_{is} + (ab)_{jr} + (ab)_{js} + (ad^b)_{irs} \\ &+ (ad^b)_{jrs} + (bd^a)_{ijr} + (bd^a)_{ijs} + (d^a d^b)_{ijrs}, \\ y = G_{uv}^{kl} &= \mu_o + a_k + a_l + b_u + b_v + d_{kl}^a + d_{uv}^b \\ &+ (ab)_{ku} + (ab)_{kv} + (ab)_{lu} + (ab)_{lv} + (ad^b)_{kuv} \\ &+ (ad^b)_{luv} + (bd^a)_{klu} + (bd^a)_{klv} + (d^a d^b)_{kluv}. \end{aligned}$$

Here i, j, k and l are alleles at locus A and r, s, u and v those at locus B . The term μ_o is the mean of the noninbred population, the a 's are the additive effects of alleles at locus A , the b 's those at locus B , and d^a and d^b are the dominance effects at the two loci. Also included are the epistatic terms ab, ad^b, bd^a , and $d^a d^b$, which are, respectively, the additive by additive, additive by dominance, dominance by additive and dominance by dominance interactions of the two loci. All effects are indexed in sequence according to the alleles involved. The terms are defined so as to have the usual summation properties in the noninbred reference population:

$$\begin{aligned} \sum_i p_i a_i &= \sum_i p_i p_j d_{ij} = \sum_j p_j d_{ij} = \sum_i p_i q_r (ab)_{ir} = \sum_r p_r q_s (ab)_{rs} \\ &= \sum_i p_i q_r q_s (ad^b)_{irs} = \sum_r p_r q_s q_t (ad^b)_{rst} = \sum_s p_s q_r q_t (ad^b)_{rst} \\ &= \sum_i p_i p_j q_r (bd^a)_{ijr} = \sum_j p_j p_i q_r (bd^a)_{ijr} = \sum_r p_r p_i p_j q_r (bd^a)_{ijr} \\ &= \sum_i p_i p_j q_r q_s (d^a d^b)_{ijrs} = \sum_j p_j p_i q_r q_s (d^a d^b)_{ijrs} \\ &= \sum_r p_r p_i p_j q_r q_s (d^a d^b)_{ijrs} = \sum_s p_s p_i p_j q_r q_s (d^a d^b)_{ijrs} = 0, \end{aligned}$$

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TABLE 1
Identity measures

General term	When $x = y$
$F_x = P(i = j) = P(r = s)$	F
$F_y = P(k = l) = P(u = v)$	F
$4\theta_{xy} = P(i = k) + P(i = l) + P(j = k) + P(j = l)$ $= P(r = u) + P(r = v) + P(s = u) + P(s = v)$	$2(1 + F)$
$4\gamma_{xy} = P(i = j = k) + P(i = j = l) + P(i = k = l) +$ $P(j = k = l)$ $= P(r = s = u) + P(r = s = v) + P(r = u = v) +$ $P(s = u = v)$	$4F$
$2\Delta_{xy} = P(i = k \text{ and } j = l) + P(i = l \text{ and } j = k) -$ $2P(i = j = k = l)$ $= P(r = u \text{ and } s = v) + P(r = v \text{ and } s = u) -$ $2P(r = s = u = v)$	$1 - F$
$\delta_{xy} = P(i = j = k = l) = P(r = s = u = v)$	F
$\alpha_{xy} = P(i = j \text{ and } k = l) = P(r = s \text{ and } u = v)$ $= P(i = j \text{ and } u = v) = P(k = l \text{ and } r = s)$	F

in which p_i is the population frequency of the i th allele at locus A , q_r that of the r th allele at locus B , and $\sum_i p_i = \sum_r q_r = 1$.

The covariance of x and y depends on the probability that two, three or all four genes defined for a locus are descended from a common gamete. Although the effects in the above model are designated as though dependent on nonidentical genes (*nibd*), genes may be identical by descent (*ibd*) when either x or y is inbred. F_x and F_y are the usual coefficients of inbreeding of x and y , and Table 1 gives five other descent measures which were described by COCKERHAM (1971) and are equivalent for either locus. For the sake of simplicity, a general three-gene descent measure γ_{xy} is written for the mean of the two measures which individually specify whether it is x or y which carries two of the three genes involved. With linkage equilibrium and identity equilibrium the genotypic distributions of the two loci are independent and all two-locus probabilities can be expressed as products of single-locus measures.

The covariance of relatives: The covariance is derived in the usual way as the difference between two parts, the expectation of the product of x and y and the product of the expectations:

$$C_{xy} = EG_{rs}^{ij} G_{uv}^{kl} - EG_{rs}^{ij} EG_{uv}^{kl}$$

in which E denotes an expectation taken over the populations of interest which are inbred to an arbitrary degree. The latter term is the most easily found as it depends only on determining which effects do not sum to zero over the population. Using ϵ_0 to denote an expectation taken over effects of a particular type as defined for the noninbred population, the conditions

$$\begin{aligned} \epsilon_0 a_i &= \epsilon_0 b_r = \epsilon_0 d_{ij}^a = \epsilon_0 d_{rs}^b = \epsilon_0 (ab)_{ir} \\ &= \epsilon_0 (ad^b)_{irs} = \epsilon_0 (bd^a)_{ijr} = \epsilon_0 (d^a d^b)_{ijrs} = 0, \end{aligned}$$

are equivalent to those given earlier. In the inbred population derived from the noninbred reference,

$$\begin{aligned} \epsilon_I d_{ii}^a &= \sum_i p_i d_{ii}^a, \quad \epsilon_I d_{rr}^b = \sum_r q_r d_{rr}^b, \quad \text{and} \\ \epsilon_I (d^a d^b)_{iirr} &= \sum_i \sum_r p_i q_r (d^a d^b)_{iirr} \end{aligned}$$

are not necessarily zero. There are also terms whose expectations cannot logically be taken over either the inbred or noninbred populations as they belong to a hypothetical population which is inbred for one locus and noninbred for the other. However, they can be explicitly expressed in terms of allele frequencies and effects. Retaining the expectation notation but without the subscript O or I

$$\epsilon(ad^b)_{irr} = \sum_i \sum_r p_i q_r (ad^b)_{irr} = 0,$$

$$\epsilon(bd^a)_{iir} = \sum_i \sum_r p_i q_r (bd^a)_{iir} = 0,$$

$$\epsilon(d^a d^b)_{iirs} = \sum_i \sum_r \sum_s p_i q_r q_s (d^a d^b)_{iirs} = 0, \quad \text{and}$$

$$\epsilon(d^a d^b)_{ijrr} = \sum_i \sum_j \sum_r p_i p_j q_r (d^a d^b)_{ijrr} = 0.$$

These expectations are zero because at least one unmatched random subscript is involved. Thus, the mean of a population inbred to degree F is

$$\mu_F = \mu_0 + F(\epsilon_I d_{ii}^a + \epsilon_I d_{rr}^b) + F^2 \epsilon_I (d^a d^b)_{iirr}.$$

as shown by WEIR and COCKERHAM (1977).

The next step in the procedure is to determine which quadratic components can contribute to $EG_{rs}^{ij} G_{uv}^{kl}$. All cross products between effects in x and y are involved, but some of these have zero expectations. This is the case for any product in which summation of effects over an unmatched subscript has a zero expectation. This applies to all products of heteroallelic effects and those of the effects of different loci, and also leads to

$$\begin{aligned} \epsilon a_i (bd^a)_{iir} &= \epsilon a_i (d^a d^b)_{iirs} = \epsilon a_i (d^a d^b)_{ijrr} = \epsilon d_{ij}^a d_{ii}^a \\ &= \epsilon d_{ij}^a (bd^a)_{iir} = \epsilon d_{ij}^a (ad^b)_{irr} = \epsilon d_{ij}^a (d^a d^b)_{iirs} \\ &= \epsilon d_{ij}^a (d^a d^b)_{iirr} = \epsilon d_{ii}^a (ab)_{ir} = \epsilon d_{ii}^a (bd^a)_{ijr} \\ &= \epsilon d_{ii}^a (bd^a)_{iir} = \epsilon d_{ii}^a (bd^a)_{irs} = \epsilon d_{ii}^a (d^a d^b)_{ijrs} \\ &= \epsilon d_{ii}^a (d^a d^b)_{iirs} = \epsilon d_{ii}^a (d^a d^b)_{ijrr} = \epsilon (ab)_{ir} (d^a d^b)_{iirs} \\ &= \epsilon (ab)_{ir} (d^a d^b)_{ijrr} = \epsilon (ad^b)_{irs} (ad^b)_{iir} \\ &= \epsilon (ad^a)_{irs} (d^a d^b)_{ijrr} = \epsilon (ad^b)_{irs} (d^a d^b)_{iirr} \\ &= \epsilon (ad^b)_{iirr} (d^a d^b)_{ijrs} = \epsilon (ad^b)_{iirr} (d^a d^b)_{iirs} \\ &= \epsilon (ad^b)_{iirr} (d^a d^b)_{ijrr} = \epsilon (ad^b)_{irs} (bd^a)_{iir} \\ &= \epsilon (ad^b)_{iirr} (bd^a)_{ijr} = \epsilon (d^a d^b)_{iirs} (d^a d^b)_{ijrr} \\ &= \epsilon (d^a d^b)_{iirs} (d^a d^b)_{iirr} \\ &= \epsilon (d^a d^b)_{ijrr} (d^a d^b)_{iirr} = 0 \end{aligned}$$

TABLE 2

Components and coefficients of the covariance of G_{rs}^{ij} and G_{uv}^{kl} in terms of the conventional heterozygote-based model*

Terms	Coefficients	Components	
		Model	Summary
ea_i^2	$4\theta_{xy}$	$\sigma_{A(a)}^2/2$	
eb_i^2	$4\theta_{xy}$	$\sigma_{A(b)}^2/2$	$\sigma_A^2/2$
$e(d^a)_{ij}^2$	$2\Delta_{xy}$	$\sigma_{D(a)}^2$	
$e(d^b)_{rs}^2$	$2\Delta_{xy}$	$\sigma_{D(b)}^2$	σ_D^2
$e(ab)_{ir}^2$	$16\theta_{xy}^2$	$\sigma_{AD}^2/4$	$\sigma_{AD}^2/4$
$e(ad^b)_{ijrs}^2$	$8\theta_{xy}\Delta_{xy}$	$\sigma_{AD(a)}^2/2$	
$e(bd^a)_{ijrs}^2$	$8\theta_{xy}\Delta_{xy}$	$\sigma_{AD(b)}^2/2$	$\sigma_{AD}^2/2$
$e(d^a d^b)_{ijrs}^2$	$4\Delta_{xy}^2$	σ_{DD}^2	σ_{DD}^2
$e(d^a)_{ii}^2 - (ed_{ii}^a)^2$	δ_{xy}	$\sigma_{D^*(a)}^2$	
$e(d^b)_{rr}^2 - (ed_{rr}^b)^2$	δ_{xy}	$\sigma_{D^*(b)}^2$	$\sigma_{D^*}^2$
$(ed_{ii}^a)^2 + (ed_{rr}^b)^2$	$\alpha_{xx} - F_x F_y$		H^*
$e(ad^b)_{iir}^2$	$4\theta_{xy}\delta_{xy}$	$\sigma_{AD^*(a)}^2/2$	
$e(bd^a)_{iir}^2$	$4\theta_{xy}\delta_{xy}$	$\sigma_{AD^*(b)}^2/2$	$\sigma_{AD^*}^2/2$
$e(d^a d^b)_{ijrr}^2$	$2\Delta_{xy}\delta_{xy}$	$\sigma_{DD^*(a)}^2$	
$e(d^a d^b)_{iirv}^2$	$2\Delta_{xy}\delta_{xy}$	$\sigma_{DD^*(b)}^2$	$\sigma_{DD^*}^2$
$e(d^a d^b)_{iirv}^2 - [e(d^a d^b)_{iirr}]^2$	δ_{xy}^2	$\sigma_{DD^{**}}^2$	$\sigma_{DD^{**}}^2$
$[e(d^a d^b)_{iirr}]^2$	$\alpha_{xy}^2 - F_x^2 F_y^2$		L^*
$ea_i d_{ii}^a$	$4\gamma_{xy}$	$\sigma_{A \cdot D^*(a)}$	
$eb_i d_{ii}^b$	$4\gamma_{xy}$	$\sigma_{A \cdot D^*(b)}$	$\sigma_{A \cdot D^*}$
$ea_i (ad^b)_{iir}$	$4(F_x + F_y)\theta_{xy}$	$\sigma_{A \cdot AD^*(a)}^2/2$	
$eb_i (bd^a)_{iir}$	$4(F_x + F_y)\theta_{xy}$	$\sigma_{A \cdot AD^*(b)}^2/2$	$\sigma_{A \cdot AD^*}^2/2$
$ea_i (d^a d^b)_{iirr}$	$2(F_x + F_y)\gamma_{xy}$	$\sigma_{A \cdot DD^{**}(a)}$	
$eb_i (d^a d^b)_{iirr}$	$2(F_x + F_y)\gamma_{xy}$	$\sigma_{A \cdot DD^{**}(b)}$	$\sigma_{A \cdot DD^{**}}$
$ed_{ii}^a (ad^b)_{iir}$	$2(F_x + F_y)\gamma_{xy}$	$\sigma_{D^* \cdot AD^*(a)}$	
$ed_{ii}^b (bd^a)_{iir}$	$2(F_x + F_y)\gamma_{xy}$	$\sigma_{D^* \cdot AD^*(b)}$	$\sigma_{D^* \cdot AD^*}$
$ed_{ij}^a (d^a d^b)_{ijrr}$	$2(F_x + F_y)\Delta_{xy}$	$\sigma_{D \cdot DD^*(a)}$	
$ed_{uv}^b (d^a d^b)_{iirv}$	$2(F_x + F_y)\Delta_{xy}$	$\sigma_{D \cdot DD^*(b)}$	$\sigma_{D \cdot DD^*}$
$ed_{ii}^a (d^a d^b)_{iirv} - ed_{ii}^b (d^a d^b)_{iirv}$	$(F_x + F_y)\delta_{xy}$	$\sigma_{D^* \cdot DD^{**}(a)}$	
$ed_{ii}^a (d^a d^b)_{iirr} - ed_{ii}^b (d^a d^b)_{iirr}$	$(F_x + F_y)\delta_{xy}$	$\sigma_{D^* \cdot DD^{**}(b)}$	$\sigma_{D^* \cdot DD^{**}}$
$(ed_{ii}^a + ed_{ii}^b)[e(d^a d^b)_{iirr}]$	$(\alpha_{xy} - F_x F_y)(F_x + F_y)$		J^*
$e(ab)_{ir} (ad^b)_{iir}$	$16\theta_{xy}\gamma_{xy}$	$\sigma_{AA \cdot AD^*(a)}^2/2$	
$e(ab)_{ir} (bd^a)_{iir}$	$16\theta_{xy}\gamma_{xy}$	$\sigma_{AA \cdot AD^*(b)}^2/2$	$\sigma_{AA \cdot AD^*}^2/2$
$e(ab)_{ir} (d^a d^b)_{iirr}$	$8\gamma_{xy}^2$	$\sigma_{AA \cdot DD^{**}(a)}$	
$e(ad^b)_{iir} (bd^a)_{iir}$	$8\gamma_{xy}^2$	$\sigma_{AD^* \cdot DA^*(b)}$	$\sigma_{AD^* \cdot DA^*}$
$e(ad^b)_{iir} (d^a d^b)_{iirv}$	$8\gamma_{xy}\Delta_{xy}$	$\sigma_{AD \cdot DD^*(a)}$	
$e(bd^a)_{iir} (d^a d^b)_{ijrr}$	$8\gamma_{xy}\Delta_{xy}$	$\sigma_{AD \cdot DD^*(b)}$	$\sigma_{AD \cdot DD^*}$
$e(ad^b)_{iir} (d^a d^b)_{iirr}$	$4\gamma_{xy}\delta_{xy}$	$\sigma_{AD^* \cdot DD^{**}(a)}$	
$e(bd^a)_{iir} (d^a d^b)_{iirr}$	$4\gamma_{xy}\delta_{xy}$	$\sigma_{AD^* \cdot DD^{**}(b)}$	$\sigma_{AD^* \cdot DD^{**}}$

* By convention, definitions are halved for every occurrence of θ_{xy} in probability arguments.

with obvious reflections between loci where necessary. These expectations are defined for products of terms which may be drawn from different populations; inbred, noninbred or the hypothetical type described earlier. However, they can always be written in expanded form by noting that summation is taken over the product of allele frequencies specified by the subscripts carried, but ignoring any repeated subscripts in *ibd* effects. For example:

$$e(d^a d^b)_{ijrr}(d^a d^b)_{iirr} = \sum_{ijr} p_i p_j q_r (d^a d^b)_{ijrr}(d^a d^b)_{iirr}.$$

Noting that no terms involving the mean μ_0 can contribute to the covariance, the 38 remaining are

given in Table 2 using the above convention for expectations.

The usual terminology familiar from the description of outbreeding populations is used for additive, dominance and epistatic variance components arising from single alleles or *nibd* combinations. The lower case subscript refers to the locus involved, but then summation is taken over all individual loci for single locus effects and over all pairs for epistatic terms. One or more asterisks added to the subscript of a variance indicates that effects of *ibd* combinations are involved. For example, variances involving $(d^a d^b)$ terms can have none, one, or two asterisks according to whether the interacting dominance effects are due to identical

alleles at neither, one, or both loci. Covariances are written in a similar fashion, the subscripts for the two effects being separated by a dot.

The coefficients for $\sigma_{D^*}^2$ and H^* are obtained together from a single argument. In $EG_{rs}^j G_{uv}^{kl}$ there is a probability α_{xy} that both genotypes have alleles which are identical by descent and this includes the probability δ_{xy} that they are *ibd* for the same allele. The coefficient of $(\epsilon d_{ii}^a \epsilon d_{kk}^a)$ in $EG_{rs}^j EG_{uv}^{kl}$ is $F_x F_y$. Altogether the terms for locus A are

$$\delta_{xy} \epsilon(d_{ii}^a)^2 + (\alpha_{xy} - \delta_{xy} - F_x F_y) \epsilon d_{ii}^a \epsilon d_{kk}^a \\ = \delta_{xy} [\epsilon(d_{ii}^a)^2 - (\epsilon d_{ii}^a)^2] + (\alpha_{xy} - F_x F_y) (\epsilon d_{ii}^a)^2$$

since $\epsilon d_{ii}^a \epsilon d_{kk}^a = (\epsilon d_{ii}^a)^2$. There are cross products between the two loci $(\epsilon d_{ii}^a \epsilon d_{rr}^b)$ but the contributions from $EG_{rs}^j G_{uv}^{kl}$ and $EG_{rs}^j EG_{uv}^{kl}$ are equal with identity equilibrium and cancel (COCKERHAM and WEIR 1984). The coefficients for $\sigma_{D^*.D^{**}}$ and J^* and for $\sigma_{D^{**}}^2$ and L^* are obtained by similar arguments. Coefficients for other components are given by direct probability arguments in which the probabilities for the two loci are independent.

Of the 23 summary components, nine are variances, 11 are covariances and three arise as products of expectations for *ibd* effects. However, because of the similar coefficients for $\sigma_{A.DD^{**}}$ and $\sigma_{D^*.AD^*}$ and for $\sigma_{AA.DD^{**}}$ and $\sigma_{AD^*.DA^*}$, these are confounded and the original 23 components can be reduced to 21. The covariance can be written in full as

$$C_{xy} = 2\theta_{xy}\sigma_A^2 + 2\Delta_{xy}\sigma_D^2 + 4\theta_{xy}^2\sigma_{AA}^2 + 4\theta_{xy}\Delta_{xy}\sigma_{AD}^2 \\ + 4\Delta_{xy}^2\sigma_{DD}^2 + \delta_{xy}\sigma_{D^*}^2 + 2\theta_{xy}\delta_{xy}\sigma_{AD^*}^2 + 2\Delta_{xy}\delta_{xy}\sigma_{DD^{**}}^2 \\ + \delta_{xy}^2\sigma_{D^{**}}^2 + 4\gamma_{xy}\sigma_{A.D^*} + 2(F_x + F_y)\theta_{xy}\sigma_{A.AD^*} \\ + 2(F_x + F_y)\gamma_{xy}(\sigma_{A.DD^{**}} + \sigma_{D^*.AD^*}) \\ + 2(F_x + F_y)\Delta_{xy}\sigma_{D.DD^{**}} + (F_x + F_y)\delta_{xy}\sigma_{D^*.DD^{**}} \\ + 8\theta_{xy}\gamma_{xy}\sigma_{AA.AD^*} + 8\gamma_{xy}^2(\sigma_{AA.DD^{**}} + \sigma_{AD^*.DA^*}) \\ + 8\gamma_{xy}\Delta_{xy}\sigma_{AD.DD^*} + 4\gamma_{xy}\delta_{xy}\sigma_{AD^*.DD^{**}} \\ + (\alpha_{xy} - F_x F_y)H^* + (\sigma_{xy}^2 - F_x^2 F_y^2)L^* \\ + (\sigma_{xy} - F_x F_y)(F_x + F_y)J^*.$$

When $x = y$, this covariance reduces to the population genotypic variance, and is equivalent to the expression given by WEIR and COCKERHAM (1977) when linkage equilibrium and identity equilibrium are assumed.

AN ALTERNATIVE MODEL BASED ON HOMOZYGOTES

In a paper dealing with the covariance of relatives arising from a single locus, WRIGHT and COCKERHAM (1986) found that in systems of self-pollination an equivalent but smaller set of quadratic components

could be obtained by replacing the variance of additive effects (σ_A^2) and their covariance with the dominance effects of identical alleles ($\sigma_{A.D^*}$) by the variance of homozygotes (σ_M^2) and their covariance with the same dominance effects ($\sigma_{M.H}$). The underlying model was not given explicitly, but for one locus (A) it is

$$G^j = \mu_o + (m_i^a + m_j^a)/2 + d_{ij}^a - (d_{ii}^a + d_{jj}^a)/2.$$

This model contrasts with the conventional one treated above which is heterozygote-based, and will be referred to as a homozygote-based model. Although the overall mean remains that of the non-inbred population, the mean of the effects of the *i*th and *j*th homozygotes, equal to $m_i^a = 2a_i + d_{ii}^a$ and $m_j^a = 2a_j + d_{jj}^a$, is used instead of the additive allelic effects (a_i and a_j), and then the surplus d_{ii}^a and d_{jj}^a terms are subtracted. It can be expanded to include two loci:

$$G_{rs}^j = \mu_o + (m_i^a + m_j^a + m_r^b + m_s^b)/2 \\ + d_{ij}^a - (d_{ii}^a + d_{jj}^a)/2 + d_{rs}^b \\ - (d_{rr}^b + d_{ss}^b)/2 + [(m^a m^b)_{ir} + (m^a m^b)_{is} \\ + (m^a m^b)_{jr} + (m^a m^b)_{js}]/4 \\ + [(m^a d^b)_{irs} + (m^a d^b)_{jrs} + (m^b d^a)_{ijr} \\ + (m^b d^a)_{ijs}]/2 - [(m^a d^b)_{irr} + (m^a d^b)_{iss} \\ + (m^a d^b)_{jrr} + (m^a d^b)_{jss} + (m^b d^a)_{iir} + (m^b d^a)_{iis} \\ + (m^b d^a)_{jir} + (m^b d^a)_{jis}]/4 + (d^a d^b)_{ijrs} \\ - [(d^a d^b)_{ijrr} + (d^a d^b)_{ijss} + (d^a d^b)_{iirs} \\ + (d^a d^b)_{jjrs}]/2 + [(d^a d^b)_{iirr} + (d^a d^b)_{jjrr} \\ + (d^a d^b)_{iiss} + (d^a d^b)_{jjss}]/4.$$

This includes the two-locus interactions of homozygous genotypes ($m^a m^b$ terms) and the various interactions of homozygotes and dominance effects ($m^a d^b$ and $m^b d^a$). As before an effect designated as *nibd* in the noninbred model has a nonzero probability of being *ibd* with inbreeding but those explicitly designated as *ibd* cannot be *nibd*.

The dominance effects and their interactions have the same summation properties as in the earlier model, but effects and interactions involving homozygote terms have properties which depend on those of the effects from which they have been made up. This complicates the detection of zero quadratic components for this model. The following relations hold:

$$m_i^a = 2a_i + d_{ii}^a, \\ (m^a m^b)_{ir} = 4(ab)_{ir} + 2(ad^b)_{irr} + 2(bd^a)_{iir} + (d^a d^b)_{iirr} \\ (m^a d^b)_{irs} = 2(ad^b)_{irs} + (d^a d^b)_{iirs} \text{ and} \\ (m^b d^a)_{ijr} = 2(bd^a)_{ijr} + (d^a d^b)_{ijrr}.$$

TABLE 3

Quadratic components arising from the homozygote-based model and their coefficients in the covariance of inbred relatives

		In general	With selfing	For $t = 0$
σ_M^2	$\varepsilon(m^a)_i^2 + \varepsilon(m^b)_i^2 - H^*$	θ	θ	1/2
σ_{M-MM}	$\varepsilon m_i^a(m^a m^b)_{ir} + \varepsilon m_i^b(m^a m^b)_{ir} - J^*$	2θ	2θ	1
σ_{MM}^2	$\varepsilon(m^a m^b)_{ir}^2 - L^*$	θ^2	θ^2	1/4
σ_D^2	$\varepsilon(d^a)_{ij}^2 + \varepsilon(d^b)_{ij}^2$	2Δ	2Δ	2Δ
σ_{D-DM}	$\varepsilon d_{ij}^a(m^b m^a)_{ijr} + \varepsilon d_{ij}^b(m^a d^b)_{ijr}$	4Δ	4Δ	4Δ
$\sigma_{D^*}^2$	$\varepsilon(d^a)_{ii}^2 + \varepsilon(d^b)_{ii}^2 - H^*$	$(\theta - 2\gamma + \delta)$	Δ	Δ
$\sigma_{D^*-DM^*}$	$\varepsilon d_{ii}^a(m^b d^a)_{iir} + \varepsilon d_{ii}^b(m^a d^b)_{iir} - J^*$	$2(\theta - 2\gamma + \delta)$	2Δ	2Δ
σ_{MD}^2	$\varepsilon(m^a d^b)_{ir}^2 + \varepsilon(m^b d^a)_{ir}^2$	$2\theta\Delta$	$2\theta\Delta$	Δ
$\sigma_{MD^*}^2$	$\varepsilon(m^a d^b)_{iir}^2 + \varepsilon(m^b d^a)_{iir}^2 - 2L^*$	$\theta(\theta - 2\gamma + \delta)$	$\theta\Delta$	$\Delta/2$
σ_{DD}^2	$\varepsilon(d^a d^b)_{ijrs}^2$	$4\Delta^2$	$4\Delta^2$	$4\Delta^2$
$\sigma_{DD^*}^2$	$\varepsilon(d^a d^b)_{iirs}^2 + \varepsilon(d^a d^b)_{iirs}^2$	$2\Delta(\theta - 2\gamma + \delta)$	$2\Delta^2$	$2\Delta^2$
$\sigma_{DD^{**}}^2$	$\varepsilon(d^a d^b)_{iirs}^2 - L^*$	$(\theta - 2\gamma + \delta)^2$	Δ^2	Δ^2
σ_{M-D^*}	$\varepsilon m_i^a d_{ii}^a + \varepsilon m_i^b d_{ii}^b - H^*$	$2(\gamma - \theta)$	$2(\gamma - \theta)$	$2(\gamma - \theta)$
σ_{MM-D^*}	$\varepsilon d_{ii}^a(m^a m^b)_{ir} + \varepsilon d_{ii}^b(m^a m^b)_{ir} - J^*$	$2(\gamma - \theta)$	$2(\gamma - \theta)$	$2(\gamma - \theta)$
σ_{M-DM^*}	$\varepsilon m_i^a(m^b d^a)_{iir} + \varepsilon m_i^b(m^a d^b)_{iir} - J^*$	$2(\gamma - \theta)$	$2(\gamma - \theta)$	$2(\gamma - \theta)$
σ_{M-MD^*}	$\varepsilon m_i^a(m^b d^a)_{iir} + \varepsilon m_i^b(m^a d^b)_{iir} - J^*$	$\theta(F_x + F_y - 2)$	$4\theta(\gamma - \theta)$	$2(\gamma - \theta)$
σ_{MM-MD^*}	$\varepsilon(m^a m^b)_{ir}(m^a d^b)_{iir} + \varepsilon(m^a m^b)_{ir}(m^b d^a)_{iir} - 2L^*$	$2\theta(\gamma - \theta)$	$2\theta(\gamma - \theta)$	$(\gamma - \theta)$
$\sigma_{M-DD^{**}}$	$\varepsilon m_i^a(d^a d^b)_{iirs} + \varepsilon m_i^b(d^a d^b)_{iirs} - J^*$	$(F_x + F_y - 2)(\gamma - \theta)$	$4(\gamma - \theta)^2$	$4(\gamma - \theta)^2$
$\sigma_{D^*-MD^*}$	$\varepsilon d_{ii}^a(m^a d^b)_{iir} + \varepsilon d_{ii}^b(m^b d^a)_{iir} - J^*$	$(F_x + F_y - 2)(\gamma - \theta)$	$4(\gamma - \theta)^2$	$4(\gamma - \theta)^2$
$\sigma_{MM-DD^{**}}$	$\varepsilon(m^a m^b)_{ir}(d^a d^b)_{iirs} - L^*$	$2(\gamma - \theta)^2$	$2(\gamma - \theta)^2$	$2(\gamma - \theta)^2$
$\sigma_{MD^*-DM^*}$	$\varepsilon(m^a d^b)_{iir}(d^a m^b)_{iir} - L^*$	$2(\gamma - \theta)^2$	$2(\gamma - \theta)^2$	$2(\gamma - \theta)^2$
σ_{D-DD^*}	$\varepsilon d_{ij}^a(d^a d^b)_{ijrs} + \varepsilon d_{ij}^b(d^a d^b)_{ijrs}$	$2(F_x + F_y - 2)\Delta$	$8(\gamma - \theta)\Delta$	$8(\gamma - \theta)\Delta$
$\sigma_{D^*-DD^{**}}$	$\varepsilon d_{ii}^a(d^a d^b)_{iirs} + \varepsilon d_{ii}^b(d^a d^b)_{iirs}$	$(F_x + F_y - 2)(\theta - 2\gamma - \delta)$	$4(\gamma - \theta)\Delta$	$4(\gamma - \theta)\Delta$
σ_{MD-DD^*}	$\varepsilon(m^a d^b)_{iir}(d^a d^b)_{iirs} + \varepsilon(m^b d^a)_{iir}(d^a d^b)_{iirs}$	$4(\gamma - \theta)\Delta$	$4(\gamma - \theta)\Delta$	$4(\gamma - \theta)\Delta$
$\sigma_{MD^*-DD^{**}}$	$\varepsilon(m^a d^b)_{iir}(d^a d^b)_{iirs} + \varepsilon(m^b d^a)_{iir}(d^a d^b)_{iirs} - 2L^*$	$2(\gamma - \theta)(\theta - 2\gamma - \delta)$	$2(\gamma - \theta)\Delta$	$2(\gamma - \theta)\Delta$
H^*	$(\varepsilon d_{ii}^a)^2 + (\varepsilon d_{ii}^b)^2$	$\alpha - F_x F_y$	$\alpha - F_x F_y$	0
J^*	$(\varepsilon d_{ii}^a + \varepsilon d_{ii}^b)\varepsilon(d^a d^b)_{iirs}$	$(\alpha - F_x F_y)(F_x + F_y)$	$(\alpha - F_x F_y)(F_x + F_y)$	0
L^*	$[\varepsilon(d^a d^b)_{iirs}]^2$	$\alpha^2 - F_x^2 F_y^2$	$\alpha^2 - F_x^2 F_y^2$	0

The nonzero components and their expectations are given in the first two columns of Table 3, with a similar convention in the use of asterisks in subscripts as before. The coefficients appear quite different from those for the heterozygote-based model, as the occurrence of several dominance terms of the same type leads to coefficients which are often compounds of descent measures, notably $(F_x + F_y - 2)$, $(\gamma_{xy} - \theta_{xy})$, and $(\theta_{xy} - 2\gamma_{xy} + \delta_{xy})$. In addition the divisors of two or four applied to additive and other variances are no longer required and many factors of two disappear from the coefficients as a result of the divisors included in the model.

Because *ibd* terms have been confounded into homozygous effects and interactions, many more quadratic components need to be corrected for the products of nonzero expectations than was the case for the heterozygote-based model. From the above relationships

$$\begin{aligned} \varepsilon m_i^a &= \varepsilon d_{ii}^a, & \text{and} & & \varepsilon(m^a m^b)_{ir} \\ & & & & = \varepsilon(m^a d^b)_{iir} = \varepsilon(m^b d^a)_{iir} = \varepsilon(d^a d^b)_{iirs}. \end{aligned}$$

Contributions from $EG_{rs}^{ij}G_{uv}^{kl}$ to $[(\varepsilon d_{ii}^a)^2 + (\varepsilon d_{ii}^b)^2]$ arise from correction of σ_M^2 , $\sigma_{D^*}^2$ and σ_{M-D^*} , whose coefficients can be summed:

$$\theta_{xy} + (\theta_{xy} - 2\gamma_{xy} + \delta_{xy}) + 2(\gamma_{xy} - \theta_{xy}) = \delta_{xy}.$$

This equals the coefficient for $(\varepsilon d_{ii}^a)^2$ arising from $EG_{rs}^{ij}G_{uv}^{kl}$ in the heterozygote-based model (Table 2). In a similar fashion the summed coefficients for $(\varepsilon d_{ii}^a + \varepsilon d_{ii}^b)(\varepsilon d^a d^b)_{iirs}$ and $(\varepsilon d^a d^b)_{iirs}^2$ are found to be $(F_x + F_y)\delta_{xy}$ and δ_{xy}^2 respectively, again matching those from the heterozygote-based model. This procedure serves as a check that the two models are in fact equivalent, and shows that the residual terms in H^* , J^* and L^* have the same coefficients in each case. In the interests of simplicity, the *xy* subscript is dropped from the coefficients which are given in the third column of Table 3. The coefficients have the property that all are positive except those of covariances which involve an odd number of homoallelic effects, denoted by an odd number of asterisks, as these include the negative term $(\gamma - \theta)$ unsquared.

GENOTYPES RELATED UNDER SYSTEMS OF
SELFING

Confounding of quadratic components: As it stands, the model based on homozygote values fulfills the same function as the one used earlier, and uses the same number of parameters to express the covariance of relatives with arbitrary inbreeding and epistasis. However, it has particular properties under selfing. When x and y are relatives produced after one or more cycles of selfing, then only three different genotypes can arise from the two alleles carried by their common ancestor. If x and y both have the heterozygous genotype, the quantities Δ_{xy} and $(\theta_{xy} - 2\gamma_{xy} + \delta_{xy})$ both equal $1/2$, otherwise they are zero. This is also true if x is the ancestor of y . Thus, under selfing the equality

$$\Delta_{xy} = \theta_{xy} - 2\gamma_{xy} + \delta_{xy}$$

always holds.

COCKERHAM (1983) defined the covariance between individuals in the g th and g' th generation of selfing (the noninbred source being generation zero) whose last common ancestor occurred in the t th generation as $C_{tgg'}$, and the various identity measures in an analogous manner. With selfing the identity measures can be expressed as powers of $1/2$, and using results from COCKERHAM (1983) and WRIGHT and COCKERHAM (1986):

$$F_x = F_g = 1 - (1/2)^g$$

$$F_y = F_{g'} = 1 - (1/2)^{g'}$$

$$\theta_{xy} = \theta_{tgg'} = 1 - (1/2)^{t+1}$$

$$\gamma_{xy} = \gamma_{tgg'} = 1 - (1/2)^{g+2} - (1/2)^{g'+2} - (1/2)^{t+1}$$

$$\Delta_{xy} = \Delta_{tgg'} = (1/2)^{g+g'-t+1}$$

$$\delta_{xy} = \delta_{tgg'} = 1 - (1/2)^{t+1} - (1/2)^{g+1} - (1/2)^{g'+1} \\ + (1/2)^{g+g'-t+1}$$

$$\text{and } \alpha_{xy} = \alpha_{tgg'} = 1 - (1/2)^g - (1/2)^{g'} + (1/2)^{g+g'-t}$$

This again demonstrates the equality $\Delta_{xy} = \theta_{xy} - 2\gamma_{xy} + \delta_{xy}$, and also shows that $4(\theta_{xy} - \gamma_{xy}) = (2 - F_x - F_y)$. These two substitutions lead to considerable simplification as now some quadratic components are completely confounded and only 12 independent parameters remain. The new coefficients in the covariance are given in the fourth column of Table 3. In particular, the contributions of *ibd* and *nibd* effects can be pooled in the variances due to single locus dominance, homozygous by dominance, and dominance by dominance interactions. This phenomenon in the case of the single locus dominance terms was previously noted by WRIGHT and COCKERHAM (1986). There is similar pooling among the covariance terms and the following definitions can be made:

$$\sigma_H^2 = 2\sigma_D^2 + \sigma_{D^*}^2 + 4\sigma_{D \cdot DM} + 2\sigma_{D^* \cdot DM^*},$$

$$\sigma_{MH}^2 = 2\sigma_{MD} + \sigma_{MD^*},$$

$$\sigma_{HH}^2 = 4\sigma_{DD}^2 + 2\sigma_{DD^*}^2 + \sigma_{DD^{**}}^2,$$

$$\sigma_{M \cdot H} = \sigma_{M \cdot D^*} + \sigma_{MM \cdot D^*} + \sigma_{M \cdot DM^*},$$

$$\sigma_{M \cdot MH} = 2\sigma_{M \cdot MD^*} + \sigma_{MM \cdot MD^*},$$

$$\sigma_{M \cdot HH} = 2(\sigma_{M \cdot DD^{**}} + \sigma_{D^* \cdot MD^*}) + \sigma_{MM \cdot DD^{**}} + \sigma_{MD^* \cdot DM^*},$$

and

$$\sigma_{H \cdot HH} = 4\sigma_{D \cdot DD^*} + 2(\sigma_{D^* \cdot DD^{**}} + \sigma_{MD \cdot DD^*}) + \sigma_{MD^* \cdot DD^{**}}.$$

Then

$$C_{tgg'} = \theta(\sigma_M^2 + 2\sigma_{M \cdot MM}) + \theta^2\sigma_{MM}^2 + \Delta\sigma_H^2 + \theta\Delta\sigma_{MH}^2 \\ + \Delta^2\sigma_{HH}^2 + 2(\gamma - \theta)\sigma_{M \cdot H} \\ + 2\theta(\gamma - \theta)\sigma_{M \cdot MH} + 2(\gamma - \theta)^2\sigma_{M \cdot HH} \\ + 2\Delta(\gamma - \theta)\sigma_{H \cdot HH} + (\alpha - F_g F_{g'})H^* \\ + (\alpha - F_g F_{g'})(F_g + F_{g'})J^* \\ + [\alpha^2 - (F_g F_{g'})^2]L^*$$

from which the subscripts (tgg') have been omitted.

It may be noted here that some further simplification occurs when there are only two alleles at a locus. Although the single locus equality $H^* = \sigma_D^2$ generally fails in the presence of epistasis, there is a new relationship $L^* = \sigma_{DD}^2$. With equally frequent alleles, H^* , J^* , and L^* are confounded with σ_H^2 , $\sigma_{H \cdot HH}$ and σ_{HH}^2 , respectively, $\sigma_{M \cdot H}$ and $\sigma_{M \cdot HH}$ are zero, and just seven components remain. This case corresponds to the descendants of a single F_1 , for which MATHER and JINKS (1982, pp. 172–173) also recognized seven components (their d^2 , h^2 , i^2 , j^2 , l^2 , dj and hl).

Components of covariance in the selfing series: Following HORNER (1952), the total covariance $C_{tgg'}$ was subdivided by WRIGHT and COCKERHAM (1986) into the components arising at each level of the hierarchy of families. The component arising among families in the g th and g' th generations with a common ancestor in generation zero is given directly as $C_{0gg'}$, but for $t > 0$ the component for families with a common ancestor in the t th but belonging to a subpopulation descended from a common ancestor in the k th is written as $C_{ktgg'}$. This covariance can be found by difference as

$$C_{ktgg'} = C_{tgg'} - C_{kgg'}$$

where $t > k \geq 0$. Along with $C_{0gg'}$ it leads to a complete specification of the components of covariance in the hierarchical analysis of covariance when $k = t - 1$, as $C_{t-1gg'}$ is the component arising between families in the t th generation within families in the $(t-1)$ th.

In the case of $t = 0$, $\theta_{0gg'} = 1/2$ and $\alpha_{0gg'} = 2\delta_{0gg'} = F_g F_{g'}$, so that the covariance $C_{0gg'}$ contains no contributions from H^* , J^* or L^* and it involves only eight

parameters (Table 3, final column). For $C_{kigg'}$, the above relation among covariances holds for the descent measures which define the components of covariance, and they can be obtained by subtraction in a similar way. Then $\theta_{kigg'} = \gamma_{kigg'}$ and $\sigma_{M \cdot H}$ and $\sigma_{M \cdot HH}$ both vanish. In addition,

$$\alpha_{igg'} - F_g F_{g'} - (\alpha_{kigg'} - F_g F_{g'}) - \alpha_{kigg'} = 2\Delta_{kigg'},$$

and H^* is confounded with $\sigma_{H^*}^2$. Again there are eight distinct parameters, but a different set from those necessary with $C_{0gg'}$. It should be noted that the coefficients of epistatic components in $C_{kigg'}$ involve the difference between products of descent measures for generations t and k and not the product of the differences.

If covariance components for $t = 0$ and $t > 0$ are used jointly for the estimation of all parameters, then no further contraction is possible as the defined set of parameters needs to be common to both types of covariance. However, when a new set is defined uniquely for $C_{0gg'}$ without reference to $C_{kigg'}$ further confounding occurs and only six separate terms remain, their coefficients being multiples of $(1/2)$, Δ , Δ^2 , $(\gamma - \theta)$, $(\gamma - \theta)^2$ and $(\gamma - \theta)\Delta$.

DISCUSSION

It has been seen that confounding of quadratic components in the homozygote-based model takes place as a result of three successive restrictions. The assumption of selfing reduces the number of unique parameters from 21 to 12, and the two characteristic types of covariance component which arise at the first and later levels of the selfing hierarchy each require eight. Whether these reductions are to be regarded as advantageous or not depends on the purpose to which the analysis is to be put. Because of confounding, the parameters estimated under selfing are insufficient for the prediction of the covariances of relatives under other inbreeding schemes, and in any case estimates of σ_M^2 and related parameters are then probably of less value than the conventional set. The usual use of estimates of quadratic components from observed covariances is the prediction of other covariances which cannot themselves be easily measured. For example, such estimates are necessary for the prediction of response to selection of different types, for which the covariances $C_{igg'}$ and $C_{kigg'}$ with high values of g and g' are generally appropriate (WRIGHT and COCKERHAM, 1986).

The confounding leads to much simpler expressions than with the conventional model, particularly as inbreeding advances. The variance of all homozygous lines descended from the base population is simply

$$C_{\infty\infty} = \sigma_M^2 + 2\sigma_{M \cdot MM} + \sigma_{MM}^2,$$

which conceals the complexity

$$\sigma_M^2 = 2\sigma_A^2 + 4\sigma_{A \cdot D^*} + \sigma_{D^*}^2,$$

$$\sigma_{M \cdot MM} = 2\sigma_{A \cdot AD^*} + 2\sigma_{A \cdot DD^{**}} + 2\sigma_{D^* \cdot AD^*} + \sigma_{D^* \cdot DD^{**}}$$

and

$$\begin{aligned} \sigma_{MM}^2 = & 4\sigma_{AA}^2 + 8\sigma_{AA \cdot AD^*} + 2\sigma_{AD^*}^2 + 8\sigma_{AD^* \cdot DA^*} \\ & + 8\sigma_{AA \cdot DD^{**}} + 4\sigma_{AD^* \cdot DD^{**}} + \sigma_{DD^{**}}^2. \end{aligned}$$

The presence of the covariance $\sigma_{M \cdot MM}$ is an unexpected anomaly. It arises because the conventional definition of effects in relation to the noninbred population used for the heterozygote-based model was retained for the homozygote-based model. Although all extra correction terms necessitated by the use of the noninbred mean were explicitly allowed for, the array of homozygote by homozygote interactions, unlike the parallel array of additive by additive effects, is not constrained to have zero marginal mean values, and orthogonality with the single locus effects cannot be assumed. It is therefore apparent that this model is distinct from the one which would naturally be used to describe a fully inbred population by including homozygous effects and interactions which are defined to be orthogonal. This was the model assumed by WRIGHT and COCKERHAM (1986) when discussing the inclusion of epistasis into their expression for the variance of homozygous lines.

In principle the parameters under selfing can be estimated from the twenty statistics which can be computed from analyses of variance of any four generations and analyses of covariance of the six pairs of generations. Absence of selection is necessary in the development of these generations, and this assumption may be more difficult to fulfill under selfing than other systems as some homozygotes may be lethal. In some species twenty statistics may be estimated from measurements on noninbreds in generation zero and individuals in generations one to three, but for annuals and most important traits in perennials the retention of parents for evaluation alongside their offspring is not feasible. This means that statistics for which $t = g$ are unavailable, and only twelve remain. In practice therefore, remnant seed from generations one to four has to be used, and if all plots are arranged in a single randomized design only one error variance needs to be estimated with the 12 genetic parameters. This estimation can be achieved using either weighted or unweighted regression as described by MATHER and JINKS (1982) and there are seven degrees of freedom for testing the overall goodness of fit and to provide estimates of standard errors. Some parameters are strongly correlated, notably the set σ_H^2 , σ_{MH}^2 , σ_{HH}^2 , $\sigma_{M \cdot H}$, $\sigma_{M \cdot MH}$, $\sigma_{M \cdot HH}$ and $\sigma_{H \cdot HH}$, and also H^* , J^* and L^* , and consequently estimates derived from experiment will often have large standard errors. This

is a feature of selfing systems which arises from the rapid reduction of the contributions of dominance and dominance related epistasis as selfing proceeds. MATHER and JINKS (1982) show the value of including statistics derived from additional generations such as backcrosses and biparental progenies for the estimation of components in the descendants of an F_1 , but their use has not been considered for this more general population. The fit of the full epistatic model can be compared with the simpler model which includes just the four parameters arising from the summed effects of single loci.

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