

SOLUTIONS TO EXERCISES FOR CHAPTER 10

Exercise 10.1.

a. The primary meaning of the subtitle “Mating Designs with Unrelated Mates” is that the measured individuals X and Y are noninbred when the mates are unrelated. A secondary meaning of the subtitle might also be the implication that individual parents within a set of parents are independent of each other, i.e., chosen at random.

b. Cockerham uses the subtitle so that he can interpret or translate the covariances of relatives into genic variances by the general formula [see equation (9.144)]

$$\text{Cov}(X, Y) = 2\theta_{XY}\sigma_A^2 + \delta_{dXY}\sigma_D^2 + (2\theta_{XY})^2\sigma_{AA}^2 + \dots$$

Exercise 10.2.

Examples of a one-factor mating design are half-sib families, full-sib families, or identical genotypes (pairs of identical twins).

An analysis of variance table for a one-factor mating design consisting of half-sib families is:

Source	df	Expected mean square
Among half-sib families	f - 1	$\sigma_W^2 + n\sigma_F^2 = [\text{Cov}(Y, Y) - \text{Cov}(H.S.)] - n\text{Cov}(H.S.)$
Individuals within half-sib families	f(n - 1)	$\sigma_W^2 = [\text{Cov}(Y, Y) - \text{Cov}(H.S.)]$

The one-factor mating design containing half-sib families is probably the most useful because the single genetic design variance component is composed primarily of additive genetic variance and contains no dominance variance.

Exercise 10.3.

It is advantageous to use inbred parents in estimating genetic variance components, because the components have larger coefficients and, hence, have smaller error variances. The components are estimated more precisely. By using parents with different levels of inbreeding, variation in the coefficients is introduced and thereby permits one to estimate a greater number of covariances of relatives.

Exercise 10.4.

a. An open-pollinated family from a single individual female plant in an open-pollinated variety of maize is formally a maternal half-sib family, i.e., every individual in the family is assumed to have had a different male parent from the population so every individual in the family is truly a half sib to every other individual in the family.

b. This implies that adjacent plants surrounding the harvested female plant did not contribute any more pollen grains or gametes than plants much further removed. This is probably a false assumption. In reality, the family is a mixture of half sibs and a few full sibs. The full sibs result from a single male parent contributing more than one effective pollen grain per female parent. There may also be a small proportion of selfed individuals in the family because maize does not have a self-incompatibility system.

c. The family variance component is generally set equal to the following fractions of additive types of variances in the population $\frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{1}{64}\sigma_{AAA}^2 + \dots$.

d. The assumptions are that we truly have a half-sib family and no maternal effects. There are also many additional assumptions which could be enumerated, namely, regular disomic inheritance, no environmental covariance between relatives, parents of relatives are unrelated so relatives are noninbred, Hardy-Weinberg equilibrium, linkage equilibrium, and no genetic linkage between loci.

Exercise 10.5.

a. $\sigma_g^2 = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AAA}^2 + \dots$ and

$\sigma_s^2 = \sigma_D^2 + \frac{1}{2}\sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \frac{3}{4}\sigma_{AAA}^2 + \sigma_{AAD}^2 + \sigma_{ADD}^2 + \sigma_{DDD}^2 + \dots$ exists when all the parents of a diallel cross are fully inbred ($F = 1$). From Table 10.2, p. 10.11, the design variance components are expressed in terms of covariances of relatives. Then each covariance of relatives can be expressed in terms of genetic variance components for any level of inbreeding of the parents by use of equation (9.144) and $2\theta_{XY}$ in terms of F for different kinds of relatives given in Table 9.5, p. 9.52. Assuming $F = 1$ we have for σ_g^2 :

$$\begin{aligned}\sigma_g^2 &= \frac{C_{ps} + C_{ms} + 2C_{rs}}{4} \\ &= \frac{1}{4} \left\{ \left[\left(\frac{1+F_A}{4} \right) \sigma_A^2 + \left(\frac{1+F_A}{4} \right)^2 \sigma_{AA}^2 + \dots \right] + \left[\left(\frac{1+F_A}{4} \right) \sigma_A^2 + \left(\frac{1+F_A}{4} \right)^2 \sigma_{AA}^2 + \dots \right] + 2 \left[\left(\frac{1+F_A}{4} \right) \sigma_A^2 + \left(\frac{1+F_A}{4} \right)^2 \sigma_{AA}^2 + \dots \right] \right\} \\ &= \frac{1}{4} \left\{ \left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right] + \left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right] + 2 \left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right] \right\} \\ &= \frac{4}{4} \left(\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right) \\ &= \frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots\end{aligned}$$

In like manner for σ_s^2 where we use $2\theta_{XY} = \frac{2+F_A+F_B}{4} = \frac{2+1+1}{4} = 1$ and $\delta_{dXY} = \frac{(1+F_A)(1+F_B)}{4} = \frac{(1+1)(1+1)}{4} = 1$:

$$\begin{aligned}\sigma_s^2 &= \frac{C_f + C_{rf}}{2} - \left[\frac{C_{ps} + C_{ms}}{2} + C_{rs} \right] \\ &= \frac{1}{2} \left\{ \left[\sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAA}^2 + \dots \right] + \left[\sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAA}^2 + \dots \right] \right\} \\ &\quad - \left\{ \frac{\left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right] + \left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right]}{2} + \left[\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right] \right\} \\ &= \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAA}^2 + \dots - \left[\left(\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right) + \left(\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right) \right] \\ &= \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAA}^2 + \sigma_{AAD}^2 + \sigma_{ADD}^2 + \sigma_{AAA}^2 + \dots - \left[\sigma_A^2 + \frac{1}{2} \sigma_{AA}^2 + \frac{1}{4} \sigma_{AAA}^2 + \dots \right] \\ &= \sigma_D^2 + \frac{1}{2} \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \frac{3}{4} \sigma_{AAA}^2 + \sigma_{AAD}^2 + \sigma_{ADD}^2 + \sigma_{DDD}^2 + \dots\end{aligned}$$

b. No. As a minimum assumption, one would have to assume that σ_g^2 contained only σ_A^2 , i.e., all additive-by-additive types of epistatic variance components were equal to zero. In that case, an unbiased estimate

of the additive variance would be two times $\hat{\sigma}_g^2$. In this case,

$\sigma_s^2 = \sigma_D^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \sigma_{AAD}^2 + \sigma_{ADD}^2 + \sigma_{DDD}^2 + \dots$ and σ_s^2 would contain dominance, additive-by-dominance types, and dominance-by-dominance types of variances.

c. Yes, because with $\sigma_s^2 = 0$, σ_D^2 and all epistatic components are equal to zero which means that σ_g^2 contains only $\frac{1}{2}\sigma_A^2$.

Exercise 10.6.

To derive the covariance between any two relatives, X and Y , for any mating design, we write the model for the phenotypic value for individual X and then we write the model again for the phenotypic value for individual Y , putting primes on all of the subscripts. For the diallel model for individual X we have

$$Y_{ijk} = \mu + g_i + g_j + m_i - m_j + s_{ij} + r_{ij} + \varepsilon_{ijk},$$

where the first subscript position on Y occupied by i denotes the male parent and j denotes the female parent of X . Then writing the same model for individual Y with primes on all subscripts, we have

$$Y_{i'j'k'} = \mu + g_{i'} + g_{j'} + m_{i'} - m_{j'} + s_{i'j'} + r_{i'j'} + \varepsilon_{i'j'k'}$$

where again that first position on $Y_{i'j'k'}$ occupied by i' denotes the male parent and j' denotes the female parent of Y . If X and Y are related to each other as reciprocal full sibs, then that relation of the reciprocal full-sib cross can be denoted by $i' = j$ and $j' = i$ with $k' \neq k$ because X and Y are two different individuals. Then

$$Y_{i'j'k'} = Y_{jik} = \mu + g_j + g_i + m_j - m_i + s_{ji} + r_{ji} + \varepsilon_{jik'}$$

Therefore the covariance of reciprocal full sibs is

$$\begin{aligned} C_{rf} &= \text{Cov}(Y_{ijk}, Y_{i'j'k'}) = \text{Cov}(Y_{ijk}, Y_{jik'}) \\ &= E\left[(Y_{ijk} - \mu)(Y_{jik'} - \mu)\right] \\ &= E\left[(\mu + g_i + g_j + m_i - m_j + s_{ij} + r_{ij} + \varepsilon_{ijk} - \mu)(\mu + g_j + g_i + m_j - m_i + s_{ji} + r_{ji} + \varepsilon_{jik'} - \mu)\right] \\ &= E\left[(g_i + g_j + m_i - m_j + s_{ij} + r_{ij} + \varepsilon_{ijk})(g_j + g_i + m_j - m_i + s_{ji} + r_{ji} + \varepsilon_{jik'})\right] \end{aligned}$$

When we multiply the first expression by the second expression, we obtain 49 individual product terms and must consider the expectation of each of the 49 terms. Only those products involving the same terms in the model and have the same subscript contribute a variance component to the covariance. The nonzero terms are

$$\begin{aligned} C_{rf} &= E(g_i)^2 + E(g_j)^2 - E(m_i)^2 - E(m_j)^2 + E(s_{ij}s_{ji}) - E(r_{ij}r_{ji}) + 41 \text{ other products equal zero} \\ &= \sigma_g^2 + \sigma_g^2 - \sigma_m^2 - \sigma_m^2 + \sigma_s^2 - \sigma_r^2 \quad \text{because } s_{ji} = s_{ij} \text{ and } r_{ji} = -r_{ij} \\ &= 2\sigma_g^2 - 2\sigma_m^2 + \sigma_s^2 - \sigma_r^2 \end{aligned}$$

Exercise 10.7.

a. We assume no maternal or reciprocal effects.

$$\sigma_M^2 = C_{ps}, \text{ then since } 2\theta_{XY} = \frac{1}{4}(1 + F_A) = \frac{1}{4}(1 + 1) = \frac{2}{4} = \frac{1}{2}, \text{ and } \delta_{d_{XY}} = 0$$

$$\therefore \sigma_M^2 = C_{ps} = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AAA}^2 + \dots$$

$$\begin{aligned}
\sigma_{F/M}^2 &= C_f - C_{ps} = \left(\frac{2 + F_A + F_B}{4} \right) \sigma_A^2 + \frac{(1 + F_A)(1 + F_B)}{4} \sigma_D^2 + \left(\frac{2 + F_A + F_B}{4} \right)^2 \sigma_{AA}^2 - C_{ps} \\
&= \frac{3}{4} \sigma_A^2 + \frac{1}{2} \sigma_D^2 + \left(\frac{3}{4} \right)^2 \sigma_{AA}^2 + \frac{3}{8} \sigma_{AD}^2 + \frac{1}{4} \sigma_{DD}^2 + \frac{27}{64} \sigma_{AAA}^2 - \left(\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \frac{1}{8} \sigma_{AAA}^2 + \dots \right) \\
&= \frac{1}{4} \sigma_A^2 + \frac{1}{2} \sigma_D^2 + \frac{5}{16} \sigma_{AA}^2 + \frac{3}{8} \sigma_{AD}^2 + \frac{1}{4} \sigma_{DD}^2 + \frac{19}{64} \sigma_{AAA}^2 + \dots
\end{aligned}$$

b. It is certain that the σ_M^2 variance component would be biased upward if the males represent selected individuals or selected inbred lines in the two tails. It is also certain that the covariance among full-sib families would be increased. What I am uncertain about is the effect of the use of selected males on the variance component $\sigma_{F/M}^2$ per se since it is difference between the covariance between full sibs and σ_M^2 , both of which are increased. Nyquist is uncertain.

Exercise 10.8.

Part I.

I.a. The expected variance of family means in terms of genetic effects is obtained by substituting the genetic deviation of each family mean from the grand mean, squaring the deviation, and weighting that expression by the frequency of each of the three corresponding genotypes in the population, as shown in equation (9.15) and in the derivation after equation (3) in Box 9.2, namely,

$$\begin{aligned}
E \left[\frac{\sum_{i=1}^{200} (\bar{Y}_i - \bar{Y})^2}{199} \right] &= E(\bar{Y}_\infty - \mu)^2 = E(\bar{G}_i - G_{..})^2 = p_1^2 \alpha_1^2 + 2p_1 p_2 \left[\frac{1}{2} (\alpha_1 + \alpha_2) \right]^2 + p_2^2 \alpha_2^2 \\
&= \frac{1}{2} \sigma_\alpha^2 \\
&= \frac{1}{4} \sigma_A^2
\end{aligned}$$

where \bar{Y}_∞ denotes the family mean for an infinitely large family size.

I.b. The relationship between two random individuals in any family is half-sibs.

The expected variance among true family means is equal to $\frac{1}{4} \sigma_A^2 = \text{cov}(H.S.)$.

Yes, the value of $\frac{1}{4} \sigma_A^2$ is in agreement with other reported results.

I.c. The expected variance of individuals within families is equal to the deviation of an individual from the family mean squared, weighted by the frequency of the individual in the family. Then these expressions for each of the three kinds of families corresponding to the genotypes, $A_1 A_1$, $A_1 A_2$, and $A_2 A_2$, are weighted by the frequencies of the common parent in the population. The frequencies of the individuals within each family are given in Table 9.1 (p. 9.7) under the conditional probabilities enumerated for the parent-offspring covariance. The frequency of each of the three kinds of families is also given in column 2 of that same table. The deviations of the means of the three kinds of half-sib families are α_1 , $(\alpha_1 + \alpha_2)/2$, and α_2 , one-half of the breeding values of the parent, $A_1 A_1$, $A_1 A_2$, and $A_2 A_2$, respectively, given in the last line of Box 9.1 (p. 9.9). The genotypic values

for individuals, A_1A_1 , A_1A_2 , and A_2A_2 , are $2\alpha_1 + \delta_{11}$, $\alpha_1 + \alpha_2 + \delta_{12}$, and $2\alpha_2 + \delta_{22}$. The expected variance of individuals within families is

$$\begin{aligned}
\sigma_W^2 &= p_1^2 \left\{ p_1 [(2\alpha_1 + \delta_{11}) - \alpha_1]^2 + p_2 [(\alpha_1 + \alpha_2 + \delta_{12}) - \alpha_1]^2 \right\} \\
&\quad + 2p_1p_2 \left\{ \frac{1}{2} p_1 [(2\alpha_1 + \delta_{11}) - \frac{1}{2}(\alpha_1 + \alpha_2)]^2 + \frac{1}{2} [(\alpha_1 + \alpha_2 + \delta_{12}) - \frac{1}{2}(\alpha_1 + \alpha_2)]^2 \right\} \\
&\quad + 2p_1p_2 \left\{ \frac{1}{2} p_2 [(2\alpha_2 + \delta_{22}) - \frac{1}{2}(\alpha_1 + \alpha_2)]^2 \right\} \\
&\quad + p_2^2 \left\{ p_1 [(\alpha_1 + \alpha_2 + \delta_{12}) - \alpha_2]^2 + p_2 [(2\alpha_2 + \delta_{22}) - \alpha_2]^2 \right\} \\
&= p_1^2 \left[p_1 (\alpha_1 + \delta_{11})^2 + p_2 (\alpha_2 + \delta_{12})^2 \right] \\
&\quad + 2p_1p_2 \left[\frac{1}{2} p_1 \left(\frac{3}{2}\alpha_1 - \frac{1}{2}\alpha_2 + \delta_{11} \right)^2 + \frac{1}{2} \left(\frac{1}{2}\alpha_1 + \frac{1}{2}\alpha_2 + \delta_{12} \right)^2 + \frac{1}{2} p_2 \left(-\frac{1}{2}\alpha_1 + \frac{3}{2}\alpha_2 + \delta_{22} \right)^2 \right] \\
&\quad + p_2^2 \left[p_1 (\alpha_1 + \delta_{12})^2 + p_2 (\alpha_2 + \delta_{22})^2 \right] \quad (\text{algebra omitted}) \\
&= \frac{3}{2}\sigma_\alpha^2 + \sigma_\delta^2 \\
&= \frac{3}{4}\sigma_A^2 + \sigma_D^2
\end{aligned}$$

I.d. The variance of individuals within families in terms of covariances of relatives is equal to

$$\begin{aligned}
\sigma_W^2 &= \text{Cov}(Y, Y) - \text{Cov}(H.S.) \quad \text{where } \text{Cov}(Y, Y) = \text{covariance of an individual with itself} \\
&= \sigma_A^2 + \sigma_D^2 - \frac{1}{4}\sigma_A^2 \\
&= \frac{3}{4}\sigma_A^2 + \sigma_D^2 \quad \text{which agrees with that obtained in (c) above.}
\end{aligned}$$

I.e.

Source	df	Expected mean square
Among families	199	$\sigma_W^2 + n\sigma_F^2 = [\text{Cov}(Y, Y) - \text{Cov}(H.S.)] - n\text{Cov}(H.S.)$
Individuals within families	$200(n-1)$	$\sigma_W^2 = [\text{Cov}(Y, Y) - \text{Cov}(H.S.)]$

$$\begin{aligned}
\sigma_W^2 &= [\text{Cov}(Y, Y) - \text{Cov}(H.S.)] = \frac{3}{2}\sigma_\alpha^2 + \sigma_\delta^2 = \frac{3}{4}\sigma_A^2 + \sigma_D^2 \\
\sigma_F^2 &= \text{Cov}(H.S.) = \frac{1}{2}\sigma_\alpha^2 = \frac{1}{4}\sigma_A^2
\end{aligned}$$

To show that the expected mean square among families is equal to that in (a) above, we must divide the expected mean square among families by n and take the limit as $n \rightarrow \infty$ because we assumed that the family size above was a “very large number” (say, infinite), i.e.,

$$\lim_{n \rightarrow \infty} \frac{\sigma_W^2 + n\sigma_F^2}{n} = \lim_{n \rightarrow \infty} \left(\frac{\sigma_W^2}{n} + \sigma_F^2 \right) = \sigma_F^2 = \frac{1}{4}\sigma_A^2$$

which is equal to that in (a) above.

To show that this is also true in terms of the definition mean square, we first write the expectation of the definition mean square for among families as

$$E(\text{Def. } M.S.) = E \left[\frac{n \sum_{i=1}^{200} (\bar{Y}_i - \bar{Y}_{..})^2}{199} \right]$$

Then we divide the expected mean square by n , and let n approach infinity as follows:

$$\lim_{n \rightarrow \infty} \frac{E(\text{Def. } M.S.)}{n} = \lim_{n \rightarrow \infty} E \left[\frac{n \sum_{i=1}^{200} (\bar{Y}_i - \bar{Y}_{..})^2}{199n} \right] = E(\bar{Y}_{\infty} - \mu)^2 = E(\bar{G} - \mu)^2$$

which is equal to that in (a) above. (Note that \bar{Y}_i and $\bar{Y}_{..}$ are functions of n and become \bar{Y}_{∞} and μ as $n \rightarrow \infty$).

I.f. Yes, the expected variance of the family means is different. It is increased because we have an additional sampling variance due to genetic sampling of only 100 individuals within each family. There is a different sample of 100 individuals in every family and that introduces the additional variance among families. The variance of the means in terms of design components and additive and dominance variances is equal to

$$E(\bar{Y}_i - \mu)^2 = \frac{\sigma_W^2}{100} + \sigma_F^2 = \frac{\frac{3}{4}\sigma_A^2 + \sigma_D^2}{100} + \frac{1}{4}\sigma_A^2 = \frac{103}{400}\sigma_A^2 + \frac{1}{100}\sigma_D^2$$

Part II.

II.a. Full sibs,
Half sibs

II.b.

Source	df	Expected mean square
Among groups (G)	199	$\sigma_W^2 + n\sigma_{C/G}^2 + (15)n\sigma_G^2 = [C(Y,Y) - C(F.S.)] + n[C(F.S.) - C(H.S.)] + 15nC(H.S.)$
Among crosses/ groups (C/G)	200(15 - 1)	$\sigma_W^2 + n\sigma_{C/G}^2 = [C(Y,Y) - C(F.S.)] + n[C(F.S.) - C(H.S.)]$
Individuals within crosses (I/C)	3,000(n - 1)	$\sigma_W^2 = [C(Y,Y) - C(F.S.)]$

$$\sigma_W^2 = [Cov(Y,Y) - Cov(F.S.)] = (\sigma_A^2 + \sigma_D^2) - \left(\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2\right) = \frac{1}{2}\sigma_A^2 + \frac{3}{4}\sigma_D^2 = \sigma_\alpha^2 + \frac{3}{4}\sigma_\delta^2$$

$$\sigma_{C/G}^2 = [Cov(F.S.) - Cov(H.S.)] = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 - \frac{1}{4}\sigma_A^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2 = \frac{1}{2}\sigma_\alpha^2 + \frac{1}{4}\sigma_\delta^2$$

$$\sigma_G^2 = [Cov(H.S.)] = \frac{1}{4}\sigma_A^2 = \frac{1}{2}\sigma_\alpha^2$$

The expected variance of the 200 group means, averaged over the progenies of the 15 crosses within each of the 200 groups, is equal to

$$E \left[\frac{\sum_{i=1}^{200} (\bar{Y}_i - \bar{Y}_{..})^2}{199} \right] = \lim_{n \rightarrow \infty} \left(\frac{\sigma_W^2}{15n} + \frac{\sigma_{C/G}^2}{15} + \sigma_G^2 \right)$$

$$= \frac{\sigma_{C/G}^2}{15} + \sigma_G^2$$

It has increased variance because of the sampling variation due to crossing unto only 15 individuals instead of no sampling variation in Part I, (a) to (d).

II.c. The expression for f , the number of individuals crossed unto by each of the 200 parental individuals, is derived as follows:

$$1 + E = \frac{\frac{\sigma_{C/G}^2}{f} + \sigma_G^2}{\sigma_G^2}$$

$$E = \frac{\frac{\sigma_{C/G}^2}{f}}{\sigma_G^2} = \frac{\frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2}{f\left(\frac{1}{4}\sigma_A^2\right)}$$

$$f = \frac{\sigma_A^2 + \sigma_D^2}{E\sigma_A^2}$$

II.d.

$$f = \frac{\sigma_A^2 + \sigma_D^2}{E\sigma_A^2} = \frac{100 + 20}{100(0.05)} = \frac{120}{5} = 24$$

One would need to cross each of the 200 individuals unto 24 or more random individuals to avoid increasing the variance among group means by more than 5%, in contrast to testing 200 half-sib families.

II.e. Yes

The expected variance of the group means with 100 individuals tested in each of the 3,000 crosses is increased from that of a very large number of individuals, say infinite, because of the genetic sampling within each cross. The expected variance of the group means in terms of design variance components is

$$E \left[\frac{\sum_{i=1}^{200} (\bar{Y}_{i..} - \bar{Y}_{...})^2}{199} \right] = \frac{\sigma_W^2 + n\sigma_{C/G}^2 + 15n\sigma_G^2}{15n} = \frac{\sigma_W^2}{15n} + \frac{\sigma_{C/G}^2}{15} + \sigma_G^2$$

$$= \frac{\sigma_W^2}{1,500} + \frac{\sigma_{C/G}^2}{15} + \sigma_G^2$$

The expected variance of group means is increased by $\sigma_W^2/1,500$ compared to an infinitely large number of individuals within each of the 3,000 crosses.

The expected variance of the group means in terms of additive and dominance variances is

$$E \left[\frac{\sum_{i=1}^{200} (\bar{Y}_{i..} - \bar{Y}_{...})^2}{199} \right] = \frac{\frac{1}{2}\sigma_A^2 + \frac{3}{4}\sigma_D^2}{1,500} + \frac{\frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2}{15} + \frac{1}{4}\sigma_A^2 = \left(\frac{1}{3,000} + \frac{1}{60} + \frac{1}{4} \right) \sigma_A^2 + \left(\frac{103}{6,000} \right) \sigma_D^2$$

$$= \frac{801}{3,000} \sigma_A^2 + \frac{103}{6,000} \sigma_D^2$$

Exercise 10.9.

a. When the amount of inbreeding for each of the three sets of parents is different in this three-factor factorial mating design, there are seven distinct covariances of relatives, namely, $2^3 - 1 = 7$. There are seven covariances because the mating design is a three-factor mating design and there are seven terms or effects in the linear model for a three-factor factorial model, $X_{ijkl} = \mu + A_i + B_j + AB_{ij} + C_l + AC_{il} + BC_{jl} + ABC_{ijl} + \varepsilon_{ijkl}$.

To describe the two additional kinds of relatives and the corresponding designation for the covariance beyond the five given by Cockerham as listed in part (a) of Exercise 10.9, we consider the above model for individual X and the same model for individual Y with primes on each of the subscripts. We consider all of the eight combinations when each of the three subscripts, i for the A parent, j for the B parent, and l for the C parent, are equal or not equal in the X and Y models. We deduce the covariance designation from the following analysis and the pedigrees given in part (a) of Exercise 10.9 for the mating pattern.

- | | |
|---|---|
| 1) $i = i', j = j', l = l', k \neq k'$ all three subscripts alike | $C_{fA(BC)}$ (1,1), (2,2), (3,3), (4,4), (5,5), (6,6), (7,7), (8,8) * |
| | Full sibs, parent from mating BC and parent A both common |
| 2) $i = i', j = j', l \neq l'$ | only A and B subscripts alike C_{sAcB} (1,3), (2,4), (5,7), (6,8) |
| | Three quarter sibs, both parent A and grandparent B common |
| 3) $i = i', j \neq j', l = l'$ | only A and C subscripts alike C_{sAcC} (1,5), (2,6), (3,7), (4,8) |
| | Three quarter sibs, both parent A and grandparent C common |
| 4) $i = i', j \neq j', l \neq l'$ | only A subscripts alike C_{sA} (1,7), (2,8), (3,5), (4,6) |
| | Half sibs, parent A common |
| 5) $i \neq i', j = j', l = l'$ | only B and C subscripts alike C_{sBC} (1,2), (3,4), (5,6), (7,8) |
| | Half sibs, parent from BC common |
| 6) $i \neq i', j = j', l \neq l'$ | only B subscripts alike C_{cB} (1,4), (2,3), (5,8), (6,7) |
| | Cousins, grandparent B common |
| 7) $i \neq i', j \neq j', l = l'$ | only C subscripts alike C_{cC} (1,6), (2,5), (3,8), (4,7) |
| | Cousins, grandparent C common |
| 8) $i \neq i', j \neq j', l \neq l'$ | no subscripts alike None |

*Each (X, Y) couplet gives the cross number in which individual X occurs and the cross number in which individual Y occurs. The cross numbers are given above in part (a) of Exercise 10.9 below the mating diagram itself.

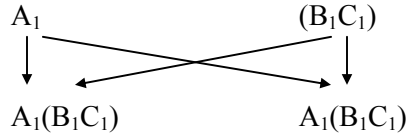
The two additional covariances given above are:

- | | |
|------------|--|
| C_{sAcC} | Three quarter sibs, both parent A and grandparent C common |
| C_{cC} | Cousins, grandparent C common |

b. The expressions for two times the coefficient of coancestry ($2\theta_{XY}$) and the coefficient of dominance coancestry (δ_{dXY}) for each of the seven distinct covariances of relatives are:

1) $C_{fA(BC)}$

When both X and Y come from cross 1 as noted above, the pedigree is



$$\theta_{XY} = \frac{1}{4} \left(\theta_{A_1A_1} + 2\theta_{A_1(B_1C_1)} + \theta_{(B_1C_1)(B_1C_1)} \right) \quad \text{see equations (4.1) and (9.83); Section 9.3.2, pp. 9.42 to 9.52}$$

$$\begin{aligned} &= \frac{1}{4} \left(\frac{1+F_{A_1}}{2} + 2(0) + \frac{1+F_{B_1C_1}}{2} \right) \\ &= \frac{2+F_A+F_{BC}}{8} \\ &= \frac{2+F_A+0}{8} \end{aligned}$$

where $\theta_{mm} = \frac{1+F_A}{2}$

$$\theta_{ff} = \frac{1+F_{BC}}{2} = \frac{1}{2}$$

Note: $F_{BC} = 0$, because B and C sets are unrelated to each other.

Then by taking two times the above expression for θ_{XY} , we obtain

$$2\theta_{XY} = 2 \left(\frac{2+F_A+F_{BC}}{8} \right) = \left(\frac{2+F_A}{4} \right) = \frac{2+F_A}{4} \quad \text{See also full sibs in Table 9.5, p. 9.52.}$$

Or, alternatively, from equation (9.83)

$$2\theta_{XY} = \frac{\theta_{mm} + \theta_{ff}}{2} = \frac{\frac{1+F_A}{2} + \frac{1+F_{BC}}{2}}{2} = \frac{2+F_A+F_{BC}}{4} = \frac{2+F_A}{4}$$

From equation (9.82) the coefficient of dominance coancestry is

$$\delta_{dXY} = \theta_{mm}\theta_{ff} = \left(\frac{1+F_A}{2} \right) \left(\frac{1+F_{BC}}{2} \right) = \frac{1+F_A}{4}$$

2) C_{sAcB} --calculated from equation (9.84)

$$\begin{aligned} 2\theta_{XY} &= 2 \left\{ \frac{1}{4} \left[\left(\frac{1}{2} \right)^1 (1+F_A) + \left(\frac{1}{2} \right)^3 (1+F_B) \right] \right\} \\ &= \left(\frac{1}{2} \right)^2 (1+F_A) + \left(\frac{1}{2} \right)^4 (1+F_B) \\ &= \frac{4+4F_A+1+F_B}{16} \\ &= \frac{5+4F_A+F_B}{16} \end{aligned}$$

δ_{dXY} calculated from equation (9.82) because the A side (male) is independent of the B side (female)

$$\text{Thus, } \theta_{mm} = \frac{1+F_A}{2}$$

$$\theta_{ff} = \left(\frac{1}{2}\right)^3 (1+F_B)$$

$$\begin{aligned} \delta_{dXY} &= \theta_{mm}\theta_{ff} = \frac{1+F_A}{2} \left(\frac{1}{2}\right)^3 (1+F_B) \\ &= \left(\frac{1}{2}\right)^4 (1+F_A)(1+F_B) \\ &= \frac{(1+F_A)(1+F_B)}{16} \end{aligned}$$

3) C_{sAcC} (by analogy with (2) above)

$$2\theta_{XY} = \frac{5+4F_A+F_C}{16}$$

$$\delta_{dXY} = \frac{(1+F_A)(1+F_C)}{16}$$

4) C_{sA}

$$2\theta_{XY} = 2 \left[\left(\frac{1}{2}\right)^3 (1+F_A) \right] = \frac{1+F_A}{4}$$

$$\delta_{dXY} = \theta_{mm}\theta_{ff} = \left(\frac{1}{2}\right)^3 (1+F_A)(0) = 0$$

5) C_{sBC}

$$2\theta_{XY} = 2 \left[\left(\frac{1}{2}\right)^3 (1+F_{BC}) \right] \quad F_{BC} = 0$$

$$= \left(\frac{1}{2}\right)^2$$

$$= \frac{1}{4}$$

$$\delta_{dXY} = \theta_{mm}\theta_{ff} = 0 \left(\frac{1}{2}\right)^3 = 0$$

6) C_{cB}

$$2\theta_{XY} = 2 \left[\left(\frac{1}{2}\right)^5 (1+F_B) \right]$$

$$= \left(\frac{1}{2}\right)^4 (1+F_B)$$

$$= \frac{1+F_B}{16}$$

$$\delta_{dXY} = \theta_{mm}\theta_{ff} = 0 \left(\frac{1}{2}\right)^3 (1+F_B) = 0$$

7) C_{cC} (by analogy with (6) above)

$$2\theta_{XY} = \frac{1+F_C}{16}$$

$$\delta_{dXY} = 0$$

Summary

	$2\theta_{XY}$	δ_{dXY}
1) $C_{fA(BC)}$	$\frac{2+F_A}{4}$	$\frac{1+F_A}{4}$
2) C_{sAcB}	$\frac{5+4F_A+F_B}{16}$	$\frac{(1+F_A)(1+F_B)}{16}$
3) C_{sAcC}	$\frac{5+4F_A+F_C}{16}$	$\frac{(1+F_A)(1+F_C)}{16}$
4) C_{sA}	$\frac{1+F_A}{4}$	0
5) C_{sBC}	$\frac{1}{4}$	0
6) C_{cB}	$\frac{1+F_B}{16}$	0
7) C_{cC}	$\frac{1+F_C}{16}$	0

c.

$$C_{sAcB} = C_{sAcC} \text{ because } 2\theta_{XY} = \frac{5+4F_A+F_B}{16} = \frac{5+4F_A+F_C}{16}$$

$$\text{and } \delta_{XY} = \frac{(1+F_A)(1+F_B)}{16} = \frac{(1+F_A)(1+F_C)}{16}, \text{ if B and C are equally inbred}$$

$$C_{cB} = C_{cC} \text{ because } 2\theta_{XY} = \frac{1+F_B}{16} = \frac{1+F_C}{16}, \text{ if B and C are equally inbred}$$

d. five

e. four In addition to the equivalences of those covariances of relatives given in part (c) above,

$$C_{sA} = C_{sBC} \text{ in that } 2\theta_{XY} \text{ for } C_{sA} = \frac{1+F_A}{4} = \frac{1}{4} \text{ which equals } 2\theta_{XY} \text{ for } C_{sBC} \text{ when } F_A = 0.$$

$$\text{In addition, } C_{cB} = C_{cC} = \frac{1}{16} \text{ when } F_B = F_C = 0.$$

f. To determine what each of the covariances of relatives is equal to in terms of design components, we first write the three-factor factorial model for individual X

$$X_{ijk} = \mu + A_i + B_j + (AB)_{ij} + C_l + (AC)_{il} + (BC)_{jl} + (ABC)_{ijl} + \varepsilon_{(ij)k}$$

and then likewise for individual Y

$$Y_{i'j'l'k'} = \mu + A_{i'} + B_{j'} + (AB)_{i'j'} + C_{l'} + (AC)_{i'l'} + (BC)_{j'l'} + (ABC)_{i'j'l'} + \varepsilon_{(i'j'l')k'}$$

Then we translate each of the covariances of relatives into design components as follows:

1) The covariance between X and Y when $i = i', j = j', l = l', k \neq k'$ is equal to

$$C_{fA(BC)} = C(X, Y) = \sigma_A^2 + \sigma_B^2 + \sigma_{AB}^2 + \sigma_C^2 + \sigma_{AC}^2 + \sigma_{BC}^2 + \sigma_{ABC}^2$$

2) The covariance between X and Y when $i = i', j = j', l \neq l'$ is equal to

$$C_{sAcB} = C(X, Y) = \sigma_A^2 + \sigma_B^2 + \sigma_{AB}^2$$

3) The covariance between X and Y when $i = i', j \neq j', l = l'$ is equal to

$$C_{sAcC} = C(X, Y) = \sigma_A^2 + \sigma_C^2 + \sigma_{AC}^2$$

4) The covariance between X and Y when $i = i', j \neq j', l \neq l'$ is equal to

$$C_{sA} = C(X, Y) = \sigma_A^2$$

5) The covariance between X and Y when $i \neq i', j = j', l = l'$ is equal to

$$C_{sBC} = C(X, Y) = \sigma_B^2 + \sigma_C^2 + \sigma_{BC}^2$$

6) The covariance between X and Y when $i \neq i', j = j', l \neq l'$ is equal to

$$C_{cB} = C(X, Y) = \sigma_B^2$$

7) The covariance between X and Y when $i \neq i', j \neq j', l = l'$ is equal to

$$C_{cC} = C(X, Y) = \sigma_C^2$$

g. To determine what each design variance component is equal to in terms of covariances of relatives, we first write out what each covariance of relative is equal to in terms of design variance components as follows:

$$\sigma_A^2 + \sigma_B^2 + \sigma_C^2 + \sigma_{AB}^2 + \sigma_{AC}^2 + \sigma_{BC}^2 + \sigma_{ABC}^2 = C_{fA(BC)}$$

$$\sigma_A^2 + \sigma_B^2 + \sigma_{AB}^2 = C_{sAcB}$$

$$\sigma_A^2 + \sigma_C^2 + \sigma_{AC}^2 = C_{sAcC}$$

$$\sigma_A^2 = C_{sA}$$

$$\sigma_B^2 + \sigma_C^2 + \sigma_{BC}^2 = C_{sBC}$$

$$\sigma_B^2 = C_{cB}$$

$$\sigma_C^2 = C_{cC}$$

Solving the system of equations for each variance component, we obtain

$$\sigma_A^2 = C_{sA}$$

$$\sigma_B^2 = C_{cB}$$

$$\sigma_C^2 = C_{cC}$$

$$\sigma_{AB}^2 = C_{sAcB} - C_{sA} - C_{cB}$$

$$\sigma_{AC}^2 = C_{sAcC} - C_{sA} - C_{cC}$$

$$\sigma_{BC}^2 = C_{sBC} - C_{cB} - C_{cC}$$

$$\sigma_{ABC}^2 = C_{fA(BC)} - C_{sAcB} - C_{sAcC} - C_{sBC} + C_{sA} + C_{cB} + C_{cC}$$

h. Each design variance component is equal to the following genetic variances:

$$\sigma_A^2 = C_{sA} = \left(\frac{1+F_A}{4}\right)\sigma_A^2 + \left(\frac{1+F_A}{4}\right)^2\sigma_{AA}^2 + \left(\frac{1+F_A}{4}\right)^3\sigma_{AAA}^2$$

$$\sigma_B^2 = C_{cB} = \left(\frac{1+F_B}{16}\right)\sigma_A^2 + \left(\frac{1+F_B}{16}\right)^2\sigma_{AA}^2 + \left(\frac{1+F_B}{16}\right)^3\sigma_{AAA}^2$$

$$\sigma_C^2 = C_{cC} = \left(\frac{1+F_C}{16}\right)\sigma_A^2 + \left(\frac{1+F_C}{16}\right)^2\sigma_{AA}^2 + \left(\frac{1+F_C}{16}\right)^3\sigma_{AAA}^2$$

$$\sigma_{AB}^2 = C_{sAcB} - C_{sA} - C_{cB}$$

$$= \frac{5+4F_A+F_B}{16}\sigma_A^2 + \frac{(1+F_A)(1+F_B)}{16}\sigma_D^2$$

$$+ \left(\frac{5+4F_A+F_B}{16}\right)^2\sigma_{AA}^2 + \left(\frac{5+4F_A+F_B}{16}\right)\frac{(1+F_A)(1+F_B)}{16}\sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_B)}{16}\right)^2\sigma_{DD}^2$$

$$+ \left(\frac{5+4F_A+F_B}{16}\right)^3\sigma_{AAA}^2 + \left(\frac{5+4F_A+F_B}{16}\right)^2\frac{(1+F_A)(1+F_B)}{16}\sigma_{AAD}^2$$

$$- \left[\left(\frac{1+F_A}{4}\right)\sigma_A^2 + \left(\frac{1+F_A}{4}\right)^2\sigma_{AA}^2 + \left(\frac{1+F_A}{4}\right)^3\sigma_{AAA}^2 \right]$$

$$- \left[\left(\frac{1+F_B}{16}\right)\sigma_A^2 + \left(\frac{1+F_B}{16}\right)^2\sigma_{AA}^2 + \left(\frac{1+F_B}{16}\right)^3\sigma_{AAA}^2 \right]$$

$$= \left[\frac{5+4F_A+F_B}{16} - \frac{1+F_A}{4} - \frac{1+F_B}{16} \right]\sigma_A^2 + \frac{(1+F_A)(1+F_B)}{16}\sigma_D^2$$

$$+ \left[\left(\frac{5+4F_A+F_B}{16}\right)^2 - \left(\frac{1+F_A}{4}\right)^2 - \left(\frac{1+F_B}{16}\right)^2 \right]\sigma_{AA}^2$$

$$+ \left(\frac{5+4F_A+F_B}{16}\right)\left(\frac{(1+F_A)(1+F_B)}{16}\right)\sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_B)}{16}\right)^2\sigma_{DD}^2$$

$$+ \left[\left(\frac{5+4F_A+F_B}{16}\right)^3 - \left(\frac{1+F_A}{4}\right)^3 - \left(\frac{1+F_B}{16}\right)^3 \right]\sigma_{AAA}^2 +$$

$$+ \left(\frac{5+4F_A+F_B}{16}\right)^2\left(\frac{(1+F_A)(1+F_B)}{16}\right)\sigma_{AAD}^2$$

$$\begin{aligned}
\sigma_{AC}^2 &= C_{sAcC} - C_{sA} - C_{cC} \\
&= \frac{5+4F_A+F_C}{16} \sigma_A^2 + \frac{(1+F_A)(1+F_C)}{16} \sigma_D^2 \\
&\quad + \left(\frac{5+4F_A+F_C}{16} \right)^2 \sigma_{AA}^2 + \left(\frac{5+4F_A+F_C}{16} \right) \frac{(1+F_A)(1+F_C)}{16} \sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_C)}{16} \right)^2 \sigma_{DD}^2 \\
&\quad + \left(\frac{5+4F_A+F_C}{16} \right)^3 \sigma_{AAA}^2 + \left(\frac{5+4F_A+F_C}{16} \right)^2 \frac{(1+F_A)(1+F_C)}{16} \sigma_{AAD}^2 \\
&\quad - \left[\left(\frac{1+F_A}{4} \right) \sigma_A^2 + \left(\frac{1+F_A}{4} \right)^2 \sigma_{AA}^2 + \left(\frac{1+F_A}{4} \right)^3 \sigma_{AAA}^2 \right] \\
&\quad - \left[\left(\frac{1+F_C}{16} \right) \sigma_A^2 + \left(\frac{1+F_C}{16} \right)^2 \sigma_{AA}^2 + \left(\frac{1+F_C}{16} \right)^3 \sigma_{AAA}^2 \right] \\
&= \left[\frac{5+4F_A+F_C}{16} - \frac{1+F_A}{4} - \frac{1+F_C}{16} \right] \sigma_A^2 + \frac{(1+F_A)(1+F_C)}{16} \sigma_D^2 \\
&\quad + \left[\left(\frac{5+4F_A+F_C}{16} \right)^2 - \left(\frac{1+F_A}{4} \right)^2 - \left(\frac{1+F_C}{16} \right)^2 \right] \sigma_{AA}^2 \\
&\quad + \left(\frac{5+4F_A+F_C}{16} \right) \left(\frac{(1+F_A)(1+F_C)}{16} \right) \sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_C)}{16} \right)^2 \sigma_{DD}^2 \\
&\quad + \left[\left(\frac{5+4F_A+F_C}{16} \right)^3 - \left(\frac{1+F_A}{4} \right)^3 - \left(\frac{1+F_C}{16} \right)^3 \right] \sigma_{AAA}^2 + \\
&\quad + \left(\frac{5+4F_A+F_C}{16} \right)^2 \left(\frac{(1+F_A)(1+F_C)}{16} \right) \sigma_{AAD}^2
\end{aligned}$$

$$\begin{aligned}
\sigma_{BC}^2 &= C_{sBC} - C_{sB} - C_{cC} \\
&= \frac{1}{4} \sigma_A^2 + \left(\frac{1}{4} \right)^2 \sigma_{AA}^2 + \left(\frac{1}{4} \right)^3 \sigma_{AAA}^2 \\
&\quad - \left[\left(\frac{1+F_B}{16} \right) \sigma_A^2 + \left(\frac{1+F_B}{16} \right)^2 \sigma_{AA}^2 + \left(\frac{1+F_B}{16} \right)^3 \sigma_{AAA}^2 \right] \\
&\quad - \left[\left(\frac{1+F_C}{16} \right) \sigma_A^2 + \left(\frac{1+F_C}{16} \right)^2 \sigma_{AA}^2 + \left(\frac{1+F_C}{16} \right)^3 \sigma_{AAA}^2 \right]
\end{aligned}$$

$$\sigma_{ABC}^2 = C_{fA(BC)} - C_{sAcB} - C_{sAcC} - C_{sBC} + C_{sA} + C_{cB} + C_{cC}$$

$$\begin{aligned}
&= \left[\begin{aligned} &\frac{2+F_A}{4}\sigma_A^2 + \frac{(1+F_A)}{4}\sigma_D^2 \\ &+ \left(\frac{2+F_A}{4}\right)^2 \sigma_{AA}^2 + \left(\frac{2+F_A}{4}\right)\frac{(1+F_A)}{4}\sigma_{AD}^2 + \left(\frac{(1+F_A)}{4}\right)^2 \sigma_{DD}^2 \\ &+ \left(\frac{2+F_A}{4}\right)^3 \sigma_{AAA}^2 + \left(\frac{2+F_A}{4}\right)^2 \frac{(1+F_A)}{4}\sigma_{AAD}^2 \end{aligned} \right] \\
&- \left[\begin{aligned} &\frac{5+4F_A+F_B}{16}\sigma_A^2 + \frac{(1+F_A)(1+F_B)}{16}\sigma_D^2 \\ &+ \left(\frac{5+4F_A+F_B}{16}\right)^2 \sigma_{AA}^2 + \left(\frac{5+4F_A+F_B}{16}\right)\frac{(1+F_A)(1+F_B)}{16}\sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_B)}{16}\right)^2 \sigma_{DD}^2 \\ &+ \left(\frac{5+4F_A+F_B}{16}\right)^3 \sigma_{AAA}^2 + \left(\frac{5+4F_A+F_B}{16}\right)^2 \frac{(1+F_A)(1+F_B)}{16}\sigma_{AAD}^2 \end{aligned} \right] \\
&- \left[\begin{aligned} &\frac{5+4F_A+F_C}{16}\sigma_A^2 + \frac{(1+F_A)(1+F_C)}{16}\sigma_D^2 \\ &+ \left(\frac{5+4F_A+F_C}{16}\right)^2 \sigma_{AA}^2 + \left(\frac{5+4F_A+F_C}{16}\right)\frac{(1+F_A)(1+F_C)}{16}\sigma_{AD}^2 + \left(\frac{(1+F_A)(1+F_C)}{16}\right)^2 \sigma_{DD}^2 \\ &+ \left(\frac{5+4F_A+F_C}{16}\right)^3 \sigma_{AAA}^2 + \left(\frac{5+4F_A+F_C}{16}\right)^2 \frac{(1+F_A)(1+F_C)}{16}\sigma_{AAD}^2 \end{aligned} \right] \\
&- \left[\frac{1}{4}\sigma_A^2 + \left(\frac{1}{4}\right)^2 \sigma_{AA}^2 + \left(\frac{1}{4}\right)^3 \sigma_{AAA}^2 \right] \\
&+ \left[\left(\frac{1+F_A}{4}\right)\sigma_A^2 + \left(\frac{1+F_A}{4}\right)^2 \sigma_{AA}^2 + \left(\frac{1+F_A}{4}\right)^3 \sigma_{AAA}^2 \right] \\
&+ \left[\left(\frac{1+F_B}{16}\right)\sigma_A^2 + \left(\frac{1+F_B}{16}\right)^2 \sigma_{AA}^2 + \left(\frac{1+F_B}{16}\right)^3 \sigma_{AAA}^2 \right] \\
&+ \left[\left(\frac{1+F_C}{16}\right)\sigma_A^2 + \left(\frac{1+F_C}{16}\right)^2 \sigma_{AA}^2 + \left(\frac{1+F_C}{16}\right)^3 \sigma_{AAA}^2 \right]
\end{aligned}$$

i. Substituting $F_A = 1, F_B = \frac{1}{2}$, and $F_C = 0$ in (h) above, one obtains (algebra omitted):

$$\sigma_A^2 = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AAA}^2$$

$$\sigma_B^2 = \frac{3}{32}\sigma_A^2 + \frac{9}{1024}\sigma_{AA}^2 + \frac{27}{32,768}\sigma_{AAA}^2$$

$$\sigma_C^2 = \frac{1}{16}\sigma_A^2 + \frac{1}{256}\sigma_{AA}^2 + \frac{1}{4,096}\sigma_{AAA}^2$$

$$\sigma_{AB}^2 = \frac{3}{16}\sigma_D^2 + \frac{3}{32}\sigma_{AA}^2 + \frac{57}{512}\sigma_{AD}^2 + \frac{9}{256}\sigma_{DD}^2 + \frac{171}{2,048}\sigma_{AAA}^2 + \frac{1,083}{16,384}\sigma_{AAD}^2$$

$$\sigma_{AC}^2 = \frac{1}{8}\sigma_D^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{9}{128}\sigma_{AD}^2 + \frac{1}{64}\sigma_{DD}^2 + \frac{27}{512}\sigma_{AAA}^2 + \frac{81}{2,048}\sigma_{AAD}^2$$

$$\sigma_{BC}^2 = \frac{3}{32}\sigma_A^2 + \frac{51}{1024}\sigma_{AA}^2 + \frac{477}{32,768}\sigma_{AAA}^2$$

$$\sigma_{ABC}^2 = \frac{3}{16}\sigma_D^2 + \frac{3}{32}\sigma_{AA}^2 + \frac{99}{512}\sigma_{AD}^2 + \frac{51}{256}\sigma_{DD}^2 + \frac{297}{2,048}\sigma_{AAA}^2 + \frac{2,877}{16,384}\sigma_{AAD}^2$$

An alternative way to obtain the above expressions is to evaluate $2\theta_{XY}$ and δ_{dXY} for each covariance of relative given in part (b) for the above F values and substitute the numerical values in part (g) above. The values for $2\theta_{XY}$ and δ_{dXY} for each covariance of relative are as follows:

	$2\theta_{XY}$	δ_{dXY}
1) $C_{fA(BC)}$	$\frac{2+F_A}{4} = \frac{3}{4}$	$\frac{1+F_A}{4} = \frac{1}{2}$
2) C_{sAcB}	$\frac{5+4F_A+F_B}{16} = \frac{5+4(1)+\frac{1}{2}}{16} = \frac{19}{32}$	$\frac{(1+F_A)(1+F_B)}{16} = \frac{(1+1)(1+\frac{1}{2})}{16} = \frac{3}{16}$
3) C_{sAcC}	$\frac{5+4F_A+F_C}{16} = \frac{5+4(1)+0}{16} = \frac{9}{16}$	$\frac{(1+F_A)(1+F_C)}{16} = \frac{1}{8}$
4) C_{sA}	$\frac{1+F_A}{4} = \frac{1}{2}$	0
5) C_{sBC}	$\frac{1}{4}$	0
6) C_{cB}	$\frac{1+F_B}{16} = \frac{1+\frac{1}{2}}{16} = \frac{3}{32}$	0
7) C_{cC}	$\frac{1+F_C}{16} = \frac{1+0}{16} = \frac{1}{16}$	0

$$C_{fA(BC)} = \frac{3}{4}\sigma_A^2 + \frac{1}{2}\sigma_D^2 + \frac{9}{16}\sigma_{AA}^2 + \frac{3}{8}\sigma_{AD}^2 + \frac{1}{4}\sigma_{DD}^2 + \frac{27}{64}\sigma_{AAA}^2 + \frac{9}{32}\sigma_{AAD}^2$$

$$C_{sAcB} = \frac{19}{32}\sigma_A^2 + \frac{3}{16}\sigma_D^2 + \frac{361}{1,024}\sigma_{AA}^2 + \frac{57}{512}\sigma_{AD}^2 + \frac{9}{256}\sigma_{DD}^2 + \frac{6,859}{32,768}\sigma_{AAA}^2 + \frac{1,083}{16,384}\sigma_{AAD}^2$$

$$C_{sAcC} = \frac{9}{16}\sigma_A^2 + \frac{1}{8}\sigma_D^2 + \frac{81}{256}\sigma_{AA}^2 + \frac{9}{128}\sigma_{AD}^2 + \frac{1}{64}\sigma_{DD}^2 + \frac{729}{4,096}\sigma_{AAA}^2 + \frac{81}{2,048}\sigma_{AAD}^2$$

$$C_{sA} = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AAA}^2$$

$$C_{sBC} = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{1}{64}\sigma_{AAA}^2$$

$$C_{sB} = \frac{3}{32}\sigma_A^2 + \frac{9}{1,024}\sigma_{AA}^2 + \frac{27}{32,768}\sigma_{AAA}^2$$

$$C_{sC} = \frac{1}{16}\sigma_A^2 + \frac{1}{256}\sigma_{AA}^2 + \frac{1}{4,096}\sigma_{AAA}^2$$

$$\sigma_A^2 = C_{sA} = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AAA}^2$$

$$\sigma_B^2 = C_{cB} = \frac{3}{32}\sigma_A^2 + \frac{9}{1,024}\sigma_{AA}^2 + \frac{27}{32,768}\sigma_{AAA}^2$$

$$\sigma_C^2 = C_{cC} = \frac{1}{16}\sigma_A^2 + \frac{1}{256}\sigma_{AA}^2 + \frac{1}{4,096}\sigma_{AAA}^2$$

$$\begin{aligned} \sigma_{AB}^2 &= C_{sAcB} - C_{sA} - C_{cB} \\ &= \left(\frac{19}{32} - \frac{1}{2} - \frac{3}{32}\right)\sigma_A^2 + \frac{3}{16}\sigma_D^2 + \left(\frac{361}{1,024} - \frac{1}{4} - \frac{9}{1,024}\right)\sigma_{AA}^2 + \frac{57}{512}\sigma_{AD}^2 + \frac{9}{256}\sigma_{DD}^2 + \left(\frac{6,859}{32,768} - \frac{1}{8} - \frac{27}{32,768}\right)\sigma_{AAA}^2 \\ &\quad + \frac{1,083}{16,384}\sigma_{AAD}^2 \end{aligned}$$

$$= \frac{3}{16}\sigma_D^2 + \frac{3}{32}\sigma_{AA}^2 + \frac{57}{512}\sigma_{AD}^2 + \frac{9}{256}\sigma_{DD}^2 + \frac{171}{2,048}\sigma_{AAA}^2 + \frac{1,083}{16,384}\sigma_{AAD}^2$$

$$\sigma_{AC}^2 = C_{sAcC} - C_{sA} - C_{cC}$$

$$\begin{aligned} &= \left(\frac{9}{16} - \frac{1}{2} - \frac{1}{16}\right)\sigma_A^2 + \frac{1}{8}\sigma_D^2 + \left(\frac{81}{256} - \frac{1}{4} - \frac{1}{256}\right)\sigma_{AA}^2 + \frac{9}{128}\sigma_{AD}^2 + \frac{1}{64}\sigma_{DD}^2 + \left(\frac{729}{4,096} - \frac{1}{8} - \frac{1}{4,096}\right)\sigma_{AAA}^2 + \frac{81}{2,048}\sigma_{AAD}^2 \\ &= \frac{1}{8}\sigma_D^2 + \frac{1}{16}\sigma_{AA}^2 + \frac{9}{128}\sigma_{AD}^2 + \frac{1}{64}\sigma_{DD}^2 + \frac{27}{512}\sigma_{AAA}^2 + \frac{81}{2,048}\sigma_{AAD}^2 \end{aligned}$$

$$\sigma_{BC}^2 = C_{sBC} - C_{cB} - C_{cC}$$

$$\begin{aligned} &= \left(\frac{1}{4} - \frac{3}{32} - \frac{1}{16}\right)\sigma_A^2 + \left(\frac{1}{16} - \frac{9}{1,024} - \frac{1}{256}\right)\sigma_{AA}^2 + \left(\frac{1}{64} - \frac{27}{32,768} - \frac{1}{4,096}\right)\sigma_{AAA}^2 \\ &= \frac{3}{32}\sigma_A^2 + \frac{51}{1,024}\sigma_{AA}^2 + \frac{477}{32,768}\sigma_{AAA}^2 \end{aligned}$$

$$\sigma_{ABC}^2 = C_{fA(BC)} - C_{sAcB} - C_{sAcC} - C_{sBC} + C_{sA} + C_{cB} + C_{cC}$$

$$\begin{aligned} &= \left(\frac{3}{4} - \frac{19}{32} - \frac{9}{16} - \frac{1}{4} + \frac{1}{2} + \frac{3}{32} + \frac{1}{16}\right)\sigma_A^2 + \left(\frac{1}{2} - \frac{3}{16} - \frac{1}{8}\right)\sigma_D^2 \\ &\quad + \left(\frac{9}{16} - \frac{361}{1,024} - \frac{81}{256} - \frac{1}{16} + \frac{1}{4} + \frac{9}{1,024} + \frac{1}{256}\right)\sigma_{AA}^2 + \left(\frac{3}{8} - \frac{57}{512} - \frac{9}{128}\right)\sigma_{AD}^2 + \left(\frac{1}{4} - \frac{9}{256} - \frac{1}{64}\right)\sigma_{DD}^2 \\ &\quad + \left(\frac{27}{64} - \frac{6,859}{32,768} - \frac{729}{4,096} - \frac{1}{64} + \frac{1}{8} + \frac{27}{32,768} + \frac{1}{4,096}\right)\sigma_{AAA}^2 + \left(\frac{9}{32} - \frac{1,083}{16,384} - \frac{81}{2,048}\right)\sigma_{AAD}^2 \\ &= \frac{3}{16}\sigma_D^2 + \frac{3}{32}\sigma_{AA}^2 + \frac{99}{512}\sigma_{AD}^2 + \frac{51}{256}\sigma_{DD}^2 + \frac{297}{2048}\sigma_{AAA}^2 + \frac{2,877}{16,384}\sigma_{AAD}^2 \end{aligned}$$

Exercise 10.10.

a. The main reason for the regression coefficient being less than one is that the observed heights have an environmental effect, i.e., $P = G + E$. The midparental means above the overall mean tend to have positive environmental effects, i.e., those midparental means are higher on the average than their true genotypic values because of positive environmental effects. Similarly the midparental means below the overall mean tend to have negative environmental effects, i.e., those midparental means are lower on the average than their true genotypic values because of negative environmental effects. That is, the phenotypic variance of the midparental value $\left(\frac{1}{2}\sigma_P^2\right)$ is greater than their genotypic variance $\left(\frac{1}{2}\sigma_G^2\right)$. The variance among the offspring families (being full-sib families) which brings about a departure of the regression coefficient from zero is the additive variance only among those full-sib families, namely, $\frac{1}{2}\sigma_A^2$, i.e., it is the covariance between midparental values and offspring family means. Hence, the regression coefficient is

$$b = \frac{\frac{1}{2}\sigma_A^2}{\frac{1}{2}\sigma_P^2} = \frac{\frac{1}{2}\sigma_A^2}{\frac{1}{2}(\sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \dots + \sigma_E^2)}$$

Thus, the regression coefficient is less than one because of the presence of $\sigma_D^2, \sigma_{AA}^2, \dots$, and σ_E^2 . Assuming that those genetic variance components $(\sigma_D^2, \sigma_{AA}^2, \dots)$ are small compared to σ_E^2 , one would say that the regression coefficient is less than one primarily because of σ_E^2 .

The regression coefficient could be equal to one if only additive genetic variance was present (no dominance or epistatic variance) and no environmental variance existed. In this situation all of the offspring family means would fall on the regression line with a slope of one.

b. The regression coefficient involves genetics in that the numerator of the regression coefficient is equal to the genetic covariance between offspring and midparent. That covariance is equal to

$2\text{Cov}(P, O) = 2\left(\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \dots\right) = \sigma_A^2 + \frac{1}{2}\sigma_{AA}^2 + \dots$. It is a measure of the genetic relation between midparent and offspring. That covariance is the same as that genetic part in the denominator, if all genetic components other than σ_A^2 are equal to zero $(\sigma_D^2 = \sigma_{AA}^2 = \dots = 0)$. In this case, if the environmental variance σ_E^2 were also equal to zero, then b would be one and only genetics would be involved. On the other hand, the regression coefficient would involve only environment if no genetic variation existed. In this case, the regression coefficient would always be equal to zero.

c. Galton would have found b less than one, which in this case is simply due to σ_E^2 . The regression coefficient is $b = \frac{\sigma_{G'}^2}{\sigma_{G'}^2 + \sigma_E^2}$, where $\sigma_{G'}^2$ is the genotypic variance of a fully inbred population.

Exercise 10.11.

a. The main criticism of Model 2 is that no replication or block term was included in the model. Since no replication term was included in the model, then E must include a plot-to-plot effect over the whole experimental area in any location-year combination—not just a plot-to-plot effect within a block. The model with no replication term would be correct for a multiple location-year experiment if a completely randomized design were used in each location-year combination, but a completely randomized design is not commonly used (see my heritability article, *Critical Reviews in Plant Sciences* 10:235-322, 1991, Section VI.A). What is most commonly used is a randomized complete-block design in each location-year combination with many plants per plot or

experimental unit. In that case, since no replication term was included in the model, the replication effect R would have to be present in the error term E , namely,

$$E = R + \varepsilon + \frac{\sum E'}{n}$$

$$\sigma_E^2 = \sigma_R^2 + \sigma_\varepsilon^2 + \frac{\sigma_{E'}^2}{n}$$

where σ_R^2 = block variance

σ_ε^2 = plot-to-plot variance within a block

$\sigma_{E'}^2$ = plant-to-plant environmental variance within a plot

In all of our discussion herein we assume that the plot value observed is the mean of n individual plants.

A better model would be one which includes a replication term R in the model, namely,

$$Y_{ijkl} = \mu + L_i + Y_j + LY_{ij} + R_{(ij)k} + G_l + LG_{il} + YG_{jl} + LYG_{ijl} + E_{(ijkl)}$$

where $E = \varepsilon + \frac{\sum E'}{n}$

$$\sigma_E^2 = \sigma_\varepsilon^2 + \frac{\sigma_{E'}^2}{n}$$

Y_{ijkl} represents the phenotypic value P in that it is the value actually observed, but the total variance of the model is not the phenotypic variance as the term is commonly used in plant quantitative genetics. The phenotypic variance does not include the variances due to the macroenvironmental terms, L , Y , LY , and R , but it does include the interactions of the genotype or family with the macroenvironments. The reader is referred to my heritability article, *Critical Reviews in Plant Sciences* 10:235-322, 1991, particularly Section IV.A for broad-sense heritability and Section IV.B for narrow-sense heritability. In fact, my heritability article (Sections II through VI) discusses and clarifies many topics with respect to models that are not discussed any place in the literature.

If Model 1 were related to Model 2, then E_{ij} in Model 1 would have to contain or absorb many terms in Model 2. With only the G term common to both Models 1 and 2, then the E_{ij} term in Model 1 would have to include or absorb all remaining terms in Model 2. Model 1 with only two terms is a very simple elementary model.

b. If G represents half-sib families instead of homozygous lines, we change all G s to F s in both Models 1 and 2. The main difference now is that E contains some genetic effect present within the plot whereas in part (a) with homozygous lines E contained only pure environmental effects. Again with no replication term specifically given in the model, the replication effect R would have to be hidden or absorbed in the error term. Thus, we have

$$E = R + \varepsilon + \frac{\sum W}{n}$$

$$= R + \varepsilon + \frac{\sum (G^w + G^w L + G^w Y + G^w LY + G^w R + E')}{n}$$

$$\begin{aligned}\sigma_E^2 &= \sigma_R^2 + \sigma_\varepsilon^2 + \frac{\sigma_W^2}{n} \\ &= \sigma_R^2 + \sigma_\varepsilon^2 + \frac{\sigma_{G^w}^2 + \sigma_{G^wL}^2 + \sigma_{G^wY}^2 + \sigma_{G^wLY}^2 + \sigma_{G^wR}^2 + \sigma_{E'}^2}{n}\end{aligned}$$

where σ_R^2 = block variance

σ_ε^2 = plot-to-plot variance within a block

$\sigma_W^2 = \sigma_{G^w}^2 + \sigma_{G^wL}^2 + \sigma_{G^wY}^2 + \sigma_{G^wLY}^2 + \sigma_{G^wR}^2 + \sigma_{E'}^2$ = total plant-to-plant variance within a plot

$\sigma_{G^w}^2 = \frac{3}{4}\sigma_A^2 + \sigma_D^2 + \frac{15}{16}\sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \dots$ = genetic variance within a half-sib family

$\sigma_{G^wL}^2$ = interaction between genetic effects within a half-sib family and locations

$\sigma_{G^wY}^2$ = interaction between genetic effects within a half-sib family and years

$\sigma_{G^wLY}^2$ = interaction between genetic effects within a half-sib family and locations and years

$\sigma_{G^wR}^2$ = interaction between genetic effects within a half-sib family and replications

$\sigma_{E'}^2$ = plant-to-plant environmental variance within a plot

Note that the variation among plants within a plot (σ_W^2) is composed of three major sources: 1) the genetic variation within a half-sib family, 2) the interactions of genetic effects within a family by the macroenvironment terms, locations, years, location-by-years, and replications, and 3) the pure plant-to-plant environment variance with a plot. This is discussed particularly in my 1991 heritability article (see Section VI.C.1.a).

Again a better model would be one which includes a replication term R in the model in which case the E term would have the R effect deleted from the sum of three terms shown above.

c. If genotypes represent different strains within a breed, the model would be most similar to that in (b) above since there would be genetic variation within strains. However, there would usually be no balanced repetition of the whole experiment in different locations and years. In addition, a major distinction between animal experimentation and plant experimentation is that the single pure environmental error effect in animal experimentation is commonly partitioned into two pure environmental sources in plant experimentation: 1) plot-to-plot effect within a block and 2) position-to-position effect within a plot. That is,

$$E = \varepsilon + E^w$$

where E = the pure environmental effect in animal experimentation

ε = plot-to-plot effect within a block or replication in plant experimentation

E^w = plant position-to-plant position within a plot in plant experimentation

This is discussed in my 1991 heritability article in Section VI.B.

Exercise 10.12.

a.i. The model for Set 1 is (see Section 10.1.1, 2, pp. 10.14 to 10.15)

$$G_{ijk} = \mu + A_i^m + B_j^f + \left(A^m B^f \right)_{ij} + W_{(ij)k}$$

where A_i^m = effect of i th individual in set A used as a male parent,

B_j^f = effect of j th individual in set B used as a female parent, and

$W_{(ij)k}$ = genetic effect of k th individual within ij th full-sib family.

a.ii. The derivations of the possible kinds of covariances for Set 1 are given below, showing the details of the derivation for the covariance of an individual with itself.

$i = i', j = j', k = k'$ (individual with itself)

$$\begin{aligned}
C_I &= E(G_{ijk} - \mu)(G_{i'j'k'} - \mu) \\
&= E \left[A_i^m + B_j^f + (A^m B^f)_{ij} + W_{(ij)k} \right] \left[A_{i'}^m + B_{j'}^f + (A^m B^f)_{i'j'} + W_{(i'j')k'} \right] \\
&= E(A_i^m A_{i'}^m) + E(A_i^m B_{j'}^f) + E(A_i^m (A^m B^f)_{i'j'}) + E(A_i^m W_{(i'j')k'}) \\
&\quad + E(B_j^f A_{i'}^m) + E(B_j^f B_{j'}^f) + E(B_j^f (A^m B^f)_{i'j'}) + E(B_j^f W_{(i'j')k'}) \\
&\quad + E((A^m B^f)_{ij} A_{i'}^m) + E((A^m B^f)_{ij} B_{j'}^f) + E((A^m B^f)_{ij} (A^m B^f)_{i'j'}) + E((A^m B^f)_{ij} W_{(i'j')k'}) \\
&\quad + E(W_{(ij)k} A_{i'}^m) + E(W_{(ij)k} B_{j'}^f) + E(W_{(ij)k} (A^m B^f)_{i'j'}) + E(W_{(ij)k} W_{(i'j')k'}) \\
&= \sigma_{A^m}^2 + 0 + 0 + 0 + 0 + \sigma_{B^f}^2 + 0 + 0 + 0 + 0 + \sigma_{AB}^2 + 0 + 0 + 0 + 0 + \sigma_W^2 \\
&= \sigma_{A^m}^2 + \sigma_{B^f}^2 + \sigma_{A^m B^f}^2 + \sigma_W^2
\end{aligned}$$

$i = i', j = j', k \neq k'$

$$C_{fs} = \sigma_{A^m}^2 + \sigma_{B^f}^2 + \sigma_{A^m B^f}^2$$

$i = i', j \neq j'$

$$C_{ps} = \sigma_{A^m}^2$$

$i \neq i', j = j'$

$$C_{ms} = \sigma_{B^f}^2$$

b.i. The model for Set 2 is

$$G_{ijk} = \mu + B_i^m + A_j^f + (B^m A^f)_{ij} + W_{(ij)k}$$

b.ii. The possible kinds of covariances for Set 2 are

$i = i', j = j', k = k'$ (individual with itself)

$$C_I = \sigma_{B^m}^2 + \sigma_{A^f}^2 + \sigma_{B^m A^f}^2 + \sigma_W^2$$

$$i = i', j = j', k \neq k'$$

$$C_{fs} = \sigma_{B^m}^2 + \sigma_{A^f}^2 + \sigma_{B^m A^f}^2$$

$$i = i', j \neq j'$$

$$C_{ps} = \sigma_{B^m}^2$$

$$i \neq i', j = j'$$

$$C_{ms} = \sigma_{A^f}^2$$

c.i. The model for an individual observation within a plot for Set 1 is

$$Y_{ijkl} = \mu + A_i^m + B_j^f + (A^m B^f)_{ij} + R_k + \varepsilon_{(ijk)} + W_{(ijk)l} + E_{(ijk)l}$$

$$i = 1, \dots, a; \quad j = 1, \dots, b; \quad k = 1, \dots, r; \quad l = 1, \dots, n$$

where $\varepsilon_{(ijk)}$ = random effect of ij th plot or experimental unit in the k th replication, and

$E_{(ijk)l}$ = pure environmental effect of l th individual in ij th full-sib family in the k th replication

c.ii. The analysis of variance for Set 1 is

Source	df	Expected mean square
Blocks	$r - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + abn\sigma_R^2$
Among A parents	$a - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{AB}^2 + brn\sigma_{A^m}^2$
Among B parents	$b - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{AB}^2 + arn\sigma_{B^f}^2$
A x B	$(a - 1)(b - 1)$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{AB}^2$
Experimental error	$(r-1)(ab - 1)$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2$
Individuals/plots	$rab(n - 1)$	$\sigma_E^2 + \sigma_W^2$

c.iii. The composition of each variance component for Set 1 is

$$\sigma_{A^m}^2 = C_{ps}$$

$$\sigma_{B^f}^2 = C_{ms}$$

$$\sigma_{AB}^2 = C_f - \sigma_{A^m}^2 - \sigma_{B^f}^2 = C_f - C_{ps} - C_{ms}$$

$$\sigma_R^2 = \text{no genetic component}$$

$$\sigma_\varepsilon^2 = \text{no genetic component}$$

$$\sigma_W^2 = C_I - C_f$$

$$\sigma_E^2 = \text{no genetic component}$$

d.i. The model for an individual observation within a plot for Set 2 is

$$Y_{ijkl} = \mu + B_i^m + A_j^f + \left(B^m A^f \right)_{ij} + R_k + \varepsilon_{(ijk)} + W_{(ijk)l} + E_{(ijk)l}$$

$$i = 1, \dots, b; \quad j = 1, \dots, a; \quad k = 1, \dots, r; \quad l = 1, \dots, n$$

where $\varepsilon_{(ijk)}$ = random effect of ij th plot or experimental unit in the k th replication, and

$E_{(ijk)l}$ = pure environmental effect of l th individual in ij th full-sib family in the k th replication

d.ii. The analysis of variance for Set 2 is

Source	df	Expected mean square
Blocks	$r - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + abn\sigma_R^2$
Among B parents	$b - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{BA}^2 + arn\sigma_{B^m}^2$
Among A parents	$a - 1$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{BA}^2 + brn\sigma_{A^f}^2$
B x A	$(b - 1)(a - 1)$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2 + rn\sigma_{BA}^2$
Experimental error	$(r-1)(ab - 1)$	$\sigma_E^2 + \sigma_W^2 + n\sigma_\varepsilon^2$
Individuals/plots	$rab(n - 1)$	$\sigma_E^2 + \sigma_W^2$

d.iii. The composition of each variance component for Set 2 is

$$\sigma_{B^m}^2 = C_{ps}$$

$$\sigma_{A^f}^2 = C_{ms}$$

$$\sigma_{BA}^2 = C_f - \sigma_{B^m}^2 - \sigma_{A^f}^2 = C_f - C_{ps} - C_{ms}$$

$$\sigma_R^2 = \text{no genetic component}$$

$$\sigma_\varepsilon^2 = \text{no genetic component}$$

$$\sigma_W^2 = C_I - C_f$$

$$\sigma_E^2 = \text{no genetic component}$$

e.

$$\text{From a.i: } G_{ijk} = \mu + A_i^m + B_j^f + \left(A^m B^f \right)_{ij} + W_{(ij)k} \quad (\text{Set 1} = \text{AB})$$

$$\text{From b.i: } G_{i'j'k'} = \mu + B_{i'}^m + A_{j'}^f + \left(B^m A^f \right)_{i'j'} + W_{(i'j')k'} \quad (\text{Set 2} = \text{BA})$$

$$i = j', j = i'$$

$$C_{rf} = \sigma_{A^m A^f} + \sigma_{B^f B^m} + \sigma_{(A^m A^f)(B^m A^f)}$$

where σ = covariance

$$i = j', j \neq i'$$

$$C_{rh} = \sigma_{A^m A^f}$$

$$i \neq j', j = i'$$

$$C_{rh} = \sigma_{B^f B^m}$$

f. Since cell or plot means are used, the model for Set 1 becomes

$$Y_{ijkl} = \mu + A_i^m + B_j^f + (A^m B^f)_{ij} + R_k + \varepsilon'_{(ijk)}$$

$$i = 1, \dots, a; \quad j = 1, \dots, b; \quad k = 1, \dots, r;$$

and that for Set 2 becomes

$$Y_{i'j'k'l'} = \mu + B_{i'}^m + A_{j'}^f + (B^m A^f)_{i'j'} + R_{k'} + \varepsilon'_{(i'j'k')}$$

$$i' = 1, \dots, b; \quad j' = 1, \dots, a; \quad k' = 1, \dots, r;$$

The analysis of covariance between Set 1 and Set 2 is

Source	df	Expected mean cross product
Blocks	$r - 1$	$\sigma_{\varepsilon'} + ab\sigma_R$
Among A parents	$a - 1$	$\sigma_{\varepsilon'} + r\sigma_{(A^m B^f)}(B^m A^f) + br\sigma_{(A^m A^f)}$
Among B parents	$b - 1$	$\sigma_{\varepsilon'} + r\sigma_{(A^m B^f)}(B^m A^f) + ar\sigma_{(B^f B^m)}$
A x B	$(a - 1)(b - 1)$	$\sigma_{\varepsilon'} + r\sigma_{(A^m B^f)}(B^m A^f)$
Experimental error	$(r - 1)(ab - 1)$	$\sigma_{\varepsilon'}$

where $\sigma_{\varepsilon'} = 0$ (i.e., the covariance between any two random plots equals zero because the $2ab$ entries were randomized within each block and a different set of plants was present in every plot)

g. Each covariance component in (f) is equal to the following covariances between relatives:

$$\sigma_{(A^m A^f)} = C_{rh}$$

$$\sigma_{(B^f B^m)} = C_{rh}$$

$$\begin{aligned} \sigma_{(A^m B^f)}(B^m A^f) &= C_{rf} - \sigma_{A^m A^f} - \sigma_{B^f B^m} \\ &= C_{rf} - C_{rh} - C_{rh} = C_{rf} - 2C_{rh} \end{aligned}$$

Exercise 10.13.

Part I.

I.a.i. The model is

$$Y_{ijk} = \mu + R_i + S_j + C_{(j)k} + \varepsilon_{(ijk)}$$

$$i = 1, \dots, r (= 2); \quad j = 1, \dots, s (= 200); \quad k = 1, 2 (= c)$$

where R_i = effect of i th replication or block,

S_j = effect of j th set composed of two different three-way crosses involving the same three parents,

$C_{(j)k}$ = effect of k th three-way crosses within j th set

I.a.ii and iii.

	df		Expected mean squares	
Blocks	$r - 1$	1		
Entries	$e - 1$	399		
Among sets	$s - 1$	199	M_1	$\sigma_\varepsilon^2 + rc\sigma_S^2$
Between crosses/sets	$s(c - 1)$	200	M_2	$\sigma_\varepsilon^2 + r\sigma_C^2$
Error	$(r - 1)(e - 1)$	399	M_3	σ_ε^2

An assumption made is that $C_{(j)1} = -C_{(j)2}$ for every $j = 1, \dots, 200$, and hence σ_C^2 does not carry up into that among sets.

$$\begin{array}{rcl}
 j & C_{(j)1} & + C_{(j)2} \\
 1 & C_{(1)1} & + C_{(1)2} = 0 \\
 2 & C_{(2)1} & + C_{(2)2} = 0 \\
 3 & C_{(3)1} & + C_{(3)2} = 0 \\
 \vdots & \vdots & \vdots \\
 200 & \vdots & \vdots \\
 & \hline & \hline
 & \neq 0 & \neq 0
 \end{array}$$

The $C_{(j)k}$ sum to zero row-wise but not column-wise. Hence they are like the interaction between a random and a fixed factor. Thus, the variance is written as σ_C^2 and not as a fixed variance. This is similar to the assumption that $r_{ij} = -r_{ji}$ in a combining ability analysis and that σ_r^2 does not carry up into the specific combining ability in a diallel analysis per Griffing (1956).

I.a.iv. The component among sets σ_S^2 is equal to

$$\text{Cov}(X, Y) = 2\theta_{XY}\sigma_A^2 + (2\theta_{XY})^2\sigma_{AA}^2 + \dots = 2 \cdot \frac{5}{32}\sigma_A^2 + \left(2 \cdot \frac{5}{32}\right)^2\sigma_{AA}^2 + \dots$$

Notice that X is a random individual in one three-way cross, and Y is a random individual in the other three-way cross. Hence, the covariance is equal to variance among set means. It is similar to the covariance between X and Y in the half-sib or full-sib family case. In either of the half-sib or full-sib case, X and Y are random individuals within a family, and the covariance between X and Y equals the variance among family means. See equations (10.25) and (10.26).

The estimate of the component is

$$\hat{\sigma}_S^2 = (M_1 - M_3)/rc = (M_1 - M_3)/r2$$

I.b.i. An alternative model is

$$Y_{ijk} = \mu + R_i + S_j + \varepsilon_{(ij)}$$

$$i = 1, \dots, r (= 2); j = 1, \dots, s (= 200)$$

where Y_{ij} = mean of two three-way crosses within the j th set

This model assumes that “each plot or experimental unit consisted of a large number of individuals” so that genetic sampling within a three-way crosses can be ignored. Hopefully the set component in the two models would be equal so that the same quantity is estimated in both models.

I.b.ii and iii.

	df			Expected mean square
Blocks	$r - 1$	1		
Sets	$s - 1$	199	M_1	$\sigma_\varepsilon^2 + r\sigma_S^2$
Error	$(r - 1)(s - 1)$	199	M_2	σ_ε^2

I.b.iv. The component among sets σ_S^2 is equal to

$$2\theta_{XY}\sigma_A^2 + (2\theta_{XY})^2\sigma_{AA}^2 + \dots = 2 \cdot \frac{5}{32}\sigma_A^2 + \left(2 \cdot \frac{5}{32}\right)^2\sigma_{AA}^2 + \dots$$

and is the same as that in Part I(a)iv

The estimate of the component is

$$\hat{\sigma}_S^2 = (M_1 - M_2) / r$$

Part II.

II.a.i. The model is

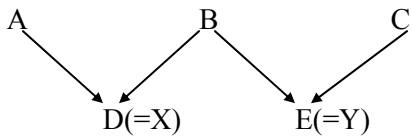
$$Y_{ijk} = \mu + R_i + S_j + C_{(j)k} + \varepsilon_{(ijk)}$$

$$i = 1, \dots, r (= 2); \quad j = 1, \dots, s (= 200); \quad k = 1, 2 (= c)$$

If we assume that individual B in Figure 27A, p. 4.112, was the male parent used in both single crosses, we can rewrite the model as

$$Y_{ijk} = \mu + R_i + M_j + F_{(j)k} + \varepsilon_{(ijk)}$$

$$i = 1, \dots, r (= 2); \quad j = 1, \dots, m (= 200); \quad k = 1, 2 (= f)$$



Notice that D and E are half sibs; D lies in one full-sib family and E lies in another nonindependent full-sib family.

II.a.ii and iii.

	df			Expected mean squares
Blocks	$r - 1$	1		
Entries	$e - 1$	399		
Among males	$m - 1$	199	M_1	$\sigma_\varepsilon^2 + r\sigma_F^2 + rc\sigma_M^2$
Between females/males	$m(f - 1)$	200	M_2	$\sigma_\varepsilon^2 + r\sigma_F^2$
Error	$(r - 1)(e - 1)$	399	M_3	σ_ε^2

It is a nested or B/A or North Carolina Design I. Similar restrictions to those in Part I.a.iii do not apply here for $F_{(j)k}$.

II.a.iv.

$$\sigma_M^2 = \text{Cov}(HS)$$

$$\sigma_F^2 = \text{Cov}(FS) - \text{Cov}(HS)$$

II.b.i. An alternative model is

$$Y_{ijk} = \mu + R_i + M_j + \varepsilon_{(ij)}$$

$$i = 1, \dots, r (= 2); j = 1, \dots, m (= 200)$$

where Y_{ij} is the mean of two full-sib families with the same male parent.

Assuming the same layout and data from Part II.a were used, the model implies that the mean of the two nonindependent full-sib families was calculated within each replication and the analysis performed on the means.

II.b.ii and iii.

	df		Expected mean squares
Blocks	$r - 1$	1	
Males	$m - 1$	199	$M_1 \quad \sigma_\varepsilon^2 + r\sigma_M^2$
Error	$(r - 1)(m - 1)$	199	$M_2 \quad \sigma_\varepsilon^2$

II.b.iv. Although statisticians would often rewrite the model as given in II.b.i and label the treatment component as σ_M^2 , the same as in II.a, it should be understood that the component in II.b does not estimate the same quantity as in II.a. To determine what σ_M^2 estimates in II.b in terms of the model in II.a, we need to multiple the degrees of freedom for males and females within males by the corresponding expected mean squares to obtain the corresponding expected sum of squares, add the two expected sums of squares together, and divide by the sum of the two degrees of freedom to obtain what the male source in II.b.ii and iii is equal to terms of the model in II.a.

Exercise 10.14.

$$a. \quad \sigma_{HS}^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 = \frac{1}{4}\frac{9}{16} + \frac{1}{16}\frac{1}{16} = \frac{37}{256} = 0.1445312$$

$$b. \quad \sigma_{FS}^2 = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \frac{1}{4}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AD}^2 + \frac{1}{16}\sigma_{AA}^2 = \frac{1}{2}\frac{9}{16} + \frac{1}{4}\frac{9}{32} + \frac{1}{4}\frac{1}{16} + \frac{1}{8}\frac{1}{16} + \frac{1}{16}\frac{1}{64} = \frac{385}{1024} = 0.3759766$$

c. Half-sib families:

$$\sigma_{HS}^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{16}(1 + \lambda^2)\sigma_{AA}^2 = \frac{1}{4}\frac{9}{16} + \frac{1}{16}(1 + (0.6)^2)\frac{1}{16} = \frac{1}{4}\frac{9}{16} + \frac{1}{16}(1.36)\frac{1}{16} = \frac{37.36}{256} = 0.1459375$$

Total effect of linkage upon half-sib variance component is

$$\frac{\frac{37.36}{256} - \frac{37.0}{256}}{\frac{37}{256}} = \frac{0.36}{37} = 0.0097297 \text{ or } 0.97297\% \text{ increase. Thus, the total effect of linkage upon the half-sib}$$

covariance component was a little less than 1% increase. Linkage had no effect upon the additive variance component, but increased the coefficient of the σ_{AA}^2 variance component by 36%, namely,

$$\frac{\frac{1+\lambda^2}{16} - \frac{1}{16}}{\frac{1}{16}} = \frac{\frac{1+\lambda^2}{16} - \frac{1}{16}}{\frac{1}{16}} = \lambda^2 = 0.36 \quad \text{or } 36\% \text{ increase.}$$

Full-sib families

$$\begin{aligned}\sigma_{FS}^2 &= \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \frac{1}{4}\left(1 + \frac{1}{2}\lambda^2\right)\sigma_{AA}^2 + \frac{1}{8}\left(1 + \lambda^2\right)\sigma_{AD}^2 + \frac{1}{16}\left(1 + \lambda^2\right)^2\sigma_{DD}^2 \\ &= \frac{1}{2}\frac{9}{16} + \frac{1}{4}\frac{9}{32} + \frac{1}{4}\left(1 + \frac{1}{2}(0.6)^2\right)\frac{1}{16} + \frac{1}{8}\left(1 + (0.6)^2\right)\frac{1}{16} + \frac{1}{16}\left(1 + (0.6)^2\right)^2\frac{1}{64} \\ &= \frac{9}{32} + \frac{9}{128} + \frac{1.18}{64} + \frac{1.36}{128} + \frac{(1.36)^2}{1024} = \frac{391.6096}{1024} = 0.3824312\end{aligned}$$

Total effect of linkage upon full-sib variance component is

$$\frac{\frac{391.6096}{1024} - \frac{385}{1024}}{\frac{385}{1024}} = \frac{6.6096}{385} = 0.0171678 \text{ or } 1.71678\% \text{ increase.}$$

Thus, the total effect of linkage upon the full-sib covariance component was nearly a 2% increase. Linkage had no effect upon the additive and dominance variance components. Linkage affected all of the three epistatic variance components. We compare the above expressions enclosed in parentheses for the full-sib variance component with one itself for no linkage.

Additive-by-additive: $\frac{1 + \frac{1}{2}\lambda^2}{1} = 1 + \frac{1}{2}(0.6)^2 = 1.18$ or 18% increase in the additive-by-additive component

Additive-by-dominance:

$$\frac{1 + \lambda^2}{1} = 1 + (0.6)^2 = 1 + 0.36 \quad \text{or } 36\% \text{ increase in the additive-by-dominance component}$$

Dominance-by-dominance:

$$\frac{(1 + \lambda^2)^2}{1} = (1.36)^2 = 1.8496 \quad \text{or } 85\% \text{ increase in the dominance-by-dominance compound}$$

d. Yes, the F_2 population would be in linkage equilibrium, because independence between loci was assumed [see equations (3.102) and (3.103)].

e. No, the F_2 population would not be in linkage equilibrium, because independence between loci was no longer assumed [see equations (3.102) and (3.103)].