

SOLUTIONS TO EXERCISES FOR CHAPTER 8

Exercise 8.1.

a. Additive effect of an allele: Additive or average effect of an allele is the difference between the mean genotypic value of individuals, which receive that allele from one parent and receive a random one from the population as its second allele, and the mean of the random-mating population. See equations (8.10) and (8.11), and p. 8.10 for a cross population, and equation (8.25) for a single population.

b. Epistasis: The interaction of nonallelic genes. Epistasis exists when genes at different loci combine in a nonadditive manner, i.e., the total genotypic value is different from the sum of the effects of the different loci individually.

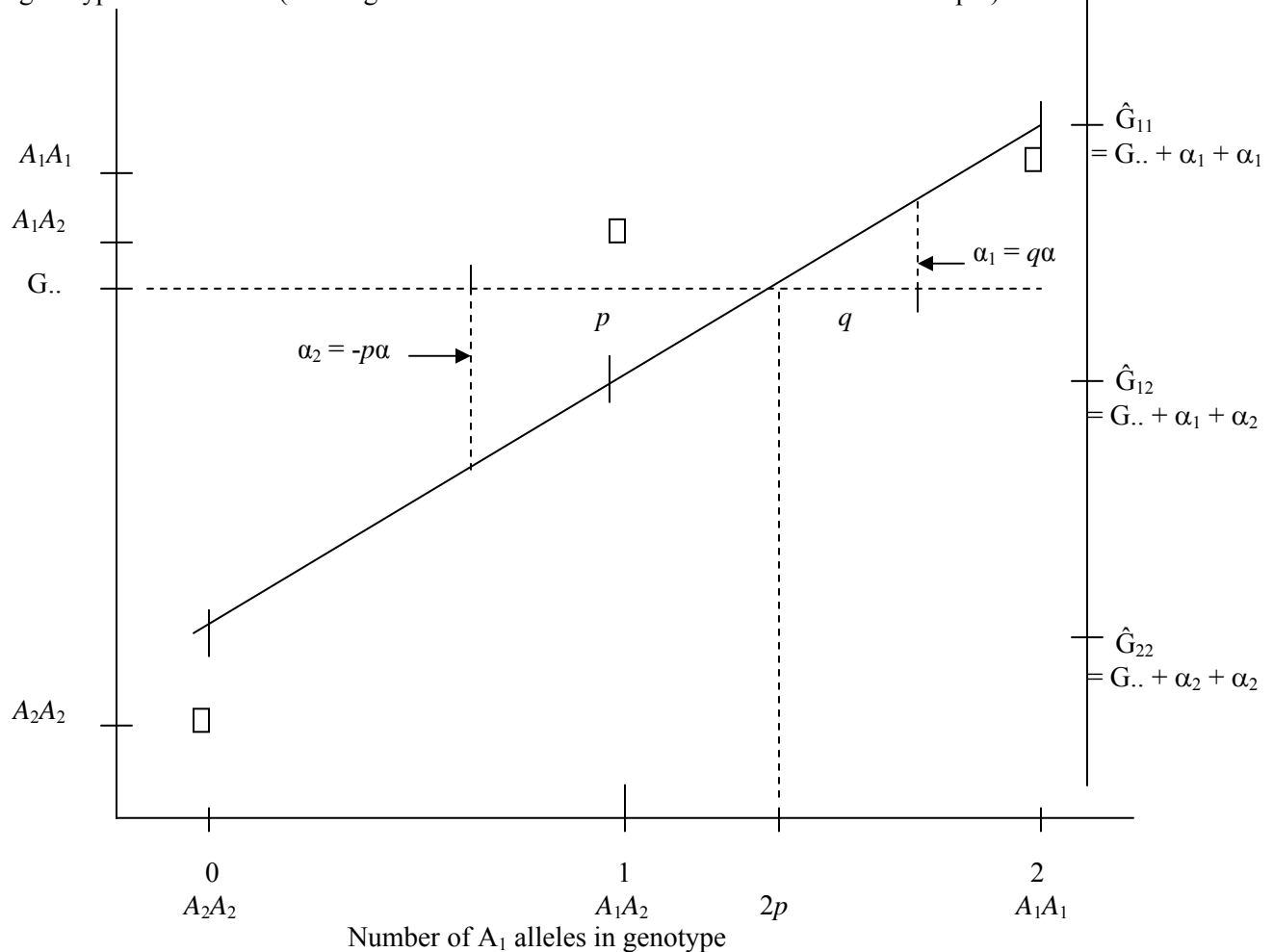
Exercise 8.2.

With n loci there are $2n$ genes in an individual. There are many parallelisms between the genic factorial model and the factorial method of experimentation. Some of the parallelisms are

- 1) Each of the $2n$ genes carried by an individual represents a factor,
- 2) The possible alleles which each of the $2n$ genes may assume are the levels of the factor,
- 3) The average effects of the genes correspond to the main effects in the factorial experiment,
- 4) Dominance effects represent the two-factor interactions between factors at the same locus, and correspond to certain two-factor interactions in a factorial experiment,
- 5) Additive-by-additive effects represent the remaining two-factor interactions and are the interactions between the levels of any two genes at different loci,
- 6) Additive-by-dominance effects represent the three-factor interactions in a factorial experiment,
- 7) Dominance-by-dominance effects represent the four-factor interactions in a factorial experiment, and so on for higher-order interactions.

Exercise 8.3.

a. The schematic diagram for the weighted linear regression of genotypic values on number of A_1 alleles in the genotype is as follows (the diagram was not drawn to scale from a numerical example):



We can label the slope of the least squares regression line, α , as $\alpha = \alpha_1 - \alpha_2$ for the following reason. We know that the regressed values \hat{G}_{22} , \hat{G}_{12} , and \hat{G}_{11} are points on the regression line for 0, 1, and 2. The regressed values are

$$\hat{G}_{11} = G.. + \alpha_1 + \alpha_1$$

$$\hat{G}_{12} = G.. + \alpha_1 + \alpha_2$$

$$\hat{G}_{22} = G.. + \alpha_2 + \alpha_2$$

The difference between $\hat{G}_{11} - \hat{G}_{12}$ or $\hat{G}_{12} - \hat{G}_{22}$ for a change of one unit on the X axis is equal to the slope of the regression line. Thus,

$$\alpha = \hat{G}_{11} - \hat{G}_{12} = G.. + \alpha_1 + \alpha_1 - (G.. + \alpha_1 + \alpha_2)$$

$$= \alpha_1 - \alpha_2$$

Or,

$$\alpha = \hat{G}_{12} - \hat{G}_{22} = G.. + \alpha_1 + \alpha_2 - (G.. + \alpha_2 + \alpha_2)$$

$$= \alpha_1 - \alpha_2$$

To derive α_1 and α_2 as functions of α , we need to note that the regression line goes through the mean $(2p, G..)$. We then note that for the change

$$\begin{aligned}\alpha_1 + \alpha_1 &= (2 - 2p)\alpha \\ 2\alpha_1 &= 2(1 - p)\alpha \\ \alpha_1 &= q\alpha\end{aligned}$$

and

$$\begin{aligned}\alpha_2 + \alpha_2 &= (0 - 2p)\alpha \\ 2\alpha_2 &= -2p\alpha \\ \alpha_2 &= -p\alpha\end{aligned}$$

b. We desire to prove that

$$a_A^2 = 2 \sum_{i=1}^2 p_i (\alpha_i)^2 = 2pq\alpha^2$$

where $p_1 = p$

$$p_2 = q$$

$$\alpha_1 - \alpha_2 = \alpha$$

$$\alpha_1 = p_2\alpha = q\alpha$$

$$\alpha_2 = -p_1\alpha = -p\alpha$$

The proof is

$$\begin{aligned}2 \sum_{i=1}^2 p_i (\alpha_i)^2 &= 2 \left[p_1 \alpha_1^2 + p_2 \alpha_2^2 \right] \\ &= 2 \left[p_1 (p_2 \alpha)^2 + p_2 (-p_1 \alpha)^2 \right] \\ &= 2 \left[p_1 p_2^2 \alpha^2 + p_2 p_1^2 \alpha^2 \right] \\ &= 2 p_1 p_2 \alpha^2 [p_2 + p_1] \\ &= 2 p_1 p_2 \alpha^2 \\ &= 2 pq \alpha^2\end{aligned}$$

Exercise 8.4.

a. The additive effects are computed by definition as follows:

		A ₁	A ₂	A ₃		
		0.3	0.2	0.5		
A ₁	0.3	A ₁ A ₁ 0.09 5	A ₁ A ₂ 0.06 3	A ₁ A ₃ 0.15 2	0.3(5) + 0.2(3) + 0.5(2) = 3.1	α ₁ = 3.1 - 1.7 = 1.4
A ₂	0.2	A ₂ A ₁ 0.06 3	A ₂ A ₂ 0.04 1	A ₂ A ₃ 0.10 0	0.3(3) + 0.2(1) + 0.5(0) = 1.1	α ₂ = 1.1 - 1.7 = -0.6
A ₃	0.5	A ₃ A ₁ 0.15 2	A ₃ A ₂ 0.10 0	A ₃ A ₃ 0.25 1	0.3(2) + 0.2(0) + 0.5(1) = 1.1	α ₃ = 1.1 - 1.7 = -0.6
		1.4	-0.6	-0.6		G.. = μ = 1.7

The additive effects per se are $\alpha_1 = 1.4, \alpha_2 = -0.6, \alpha_3 = -0.6$.

The dominance effects by definition are

$$\delta_{ij} = G_{ij} - (\mu + \alpha_i + \alpha_j)$$

$$\delta_{11} = 5 - (1.7 + 1.4 + 1.4) = 0.5$$

$$\delta_{12} = 3 - (1.7 + 1.4 - 0.6) = 0.5$$

$$\delta_{13} = 2 - (1.7 + 1.4 - 0.6) = -0.5$$

$$\delta_{22} = 1 - (1.7 - 0.6 - 0.6) = 0.5$$

$$\delta_{23} = 0 - (1.7 - 0.6 - 0.6) = -0.5$$

$$\delta_{33} = 1 - (1.7 - 0.6 - 0.6) = -0.5$$

The additive variance by definition is

$$\begin{aligned} \sigma_A^2 &= 2\sigma_\alpha^2 = 2\sum_i p_i (\alpha_i)^2 \\ &= 2\left[0.3(1.4)^2 + 0.2(-0.6)^2 + 0.5(-0.6)^2\right] \\ &= 2\left[0.3(1.96) + 0.2(0.36) + 0.5(0.36)\right] \\ &= 2\left[0.588 + 0.072 + 0.180\right] = 2\left[0.84\right] = 1.68 \end{aligned}$$

The dominance variance by definition is

$$\begin{aligned} \sigma_D^2 &= \sum_i \sum_j p_{ij} (\delta_{ij})^2 \\ &= 0.09(0.5)^2 + 0.06(0.5)^2 + \dots + 0.25(-0.5)^2 \\ &= (0.5)^2 [0.09 + 0.06 + \dots + 0.25] = 0.25 \end{aligned}$$

b. The additive variance calculated by the computing formula is

$$\begin{aligned} \sigma_\alpha^2 &= \sum_i p_i G_i^2 - \mu^2 = 0.3[0.3(5) + 0.2(3) + 0.5(2)]^2 \\ &\quad + 0.2[0.3(3) + 0.2(1) + 0.5(0)]^2 \\ &\quad + 0.5[0.3(2) + 0.2(0) + 0.5(1)]^2 - (1.7)^2 \\ &= 0.3(3.1)^2 + 0.2(1.1)^2 + 0.5(1.1)^2 - (1.7)^2 \\ &= 0.84 \end{aligned}$$

$$\sigma_A^2 = 2\sigma_\alpha^2 = 2(0.84) = 1.68$$

The dominance variance calculated by the computing formula is

$$\begin{aligned} \sigma_D^2 &= \sigma_G^2 - \sigma_A^2 = \left(\sum_i \sum_j p_{ij} G_{ij}^2 - \mu^2 \right) - \sigma_A^2 \\ &= \left[0.09(5)^2 + 0.06(3)^2 + \dots + 0.25(1)^2 - (1.7)^2 \right] - 1.68 = 1.93 - 1.68 = 0.25 \end{aligned}$$

Exercise 8.5.

a. The additive effects are computed by definition as follows:

		A_1	A_2	A_3		
		0.3	0.2	0.5		
A_1	0.3	A_1A_1 0.09 5	A_1A_2 0.06 5	A_1A_3 0.15 4	$0.3(5) + 0.2(5) + 0.5(4) = 4.5$	$\alpha_1 = 4.5 - 3.75 = 0.75$
A_2	0.2	A_2A_1 0.06 5	A_2A_2 0.04 5	A_2A_3 0.10 4	$0.3(5) + 0.2(5) + 0.5(4) = 4.5$	$\alpha_2 = 4.5 - 3.75 = 0.75$
A_3	0.5	A_3A_1 0.15 4	A_3A_2 0.10 4	A_3A_3 0.25 2	$0.3(4) + 0.2(4) + 0.5(2) = 3.0$	$\alpha_3 = 3.0 - 3.75 = -0.75$
		0.75	0.75	-0.75	$G.. = \mu = 3.75$	

The additive effects per se are $\alpha_1 = 0.75, \alpha_2 = 0.75, \alpha_3 = -0.75$

The dominance effects by definition are

$$\delta_{ij} = G_{ij} - (\mu + \alpha_i + \alpha_j)$$

$$\delta_{11} = 5 - (3.75 + 0.75 + 0.75) = -0.25$$

$$\delta_{12} = 5 - (3.75 + 0.75 + 0.75) = -0.25$$

$$\delta_{13} = 4 - (3.75 + 0.75 - 0.75) = 0.25$$

$$\delta_{22} = 5 - (3.75 + 0.75 + 0.75) = -0.25$$

$$\delta_{23} = 4 - (3.75 + 0.75 - 0.75) = 0.25$$

$$\delta_{33} = 2 - (3.75 - 0.75 - 0.75) = -0.25$$

The additive variance by definition is

$$\begin{aligned} \sigma_A^2 &= 2\sigma_\alpha^2 = 2\sum_i p_i (\alpha_i)^2 \\ &= 2\left[0.3(0.75)^2 + 0.2(0.75)^2 + 0.5(-0.75)^2\right] \\ &= 2\left[0.3(0.5625) + 0.2(0.5625) + 0.5(0.5625)\right] \\ &= 2\left[0.16875 + 0.1125 + 0.28125\right] = 2\left[0.5625\right] = 1.1250 \end{aligned}$$

The dominance variance by definition is

$$\begin{aligned} \sigma_D^2 &= \sum_i \sum_j p_{ij} (\delta_{ij})^2 \\ &= 0.09(-0.25)^2 + 0.06(-0.25)^2 + \dots + 0.25(-0.25)^2 \\ &= (0.25)^2 [0.09 + 0.06 + \dots + 0.25] = 0.0625 \end{aligned}$$

b. The additive variance calculated by the computing formula is

$$\begin{aligned}\sigma_{\alpha}^2 &= \sum_i p_i G_i^2 - \mu^2 = 0.3[0.3(5) + 0.2(5) + 0.5(4)]^2 \\ &\quad + 0.2[0.3(5) + 0.2(5) + 0.5(4)]^2 \\ &\quad + 0.5[0.3(4) + 0.2(4) + 0.5(2)]^2 - (3.75)^2 \\ &= 0.3(4.5)^2 + 0.2(4.5)^2 + 0.5(3.0)^2 - (3.75)^2 \\ &= 0.5625\end{aligned}$$

$$\sigma_A^2 = 2\sigma_{\alpha}^2 = 2(0.5625) = 1.1250$$

The dominance variance calculated by the computing formula is

$$\begin{aligned}\sigma_D^2 &= \sigma_G^2 - \sigma_A^2 = \left(\sum_i \sum_j p_{ij} G_{ij}^2 - \mu^2 \right) - \sigma_A^2 \\ &= \left[0.09(5)^2 + 0.06(5)^2 + \dots + 0.25(2)^2 - (3.75)^2 \right] - 1.1250 = 1.1875 - 1.1250 = 0.0625\end{aligned}$$

Exercise 8.6.

a. The solution to this part of the exercise is presented in my notes in equations (8.80), (8.81), and (8.82) and will not be repeated here.

b. The ratios of the different variances are presented in equations (8.85), (8.86), and (8.87) in terms of the favorable allele p . To obtain expressions in terms of the unfavorable allele q , we simply substitute $1 - q = p$ in those expressions as follows:

$$\frac{\sigma_D^2}{\sigma_A^2} = \frac{p}{2(1-p)} = \frac{1-q}{2[1-(1-q)]} = \frac{1-q}{2q} \quad \text{from equation (8.85)}$$

$$\frac{\sigma_A^2}{\sigma_G^2} = \frac{2(1-p)}{2-p} = \frac{2[1-(1-q)]}{2-(1-q)} = \frac{2q}{1+q} \quad \text{from equation (8.86)}$$

$$\frac{\sigma_D^2}{\sigma_G^2} = \frac{p}{2-p} = \frac{1-q}{2-(1-q)} = \frac{1-q}{1+q} \quad \text{from equation (8.87)}$$

c. Instead of plotting the various ratios as a function of q (which would involve different software), I will simply give the value of the particular ratio for different values of q from 0 to 1 in terms of tenths.

Dominance variance to additive variance:

$q:$	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
σ_D^2 / σ_A^2	∞	4.5	2	1.17	0.75	0.5	0.33	0.214	0.125	0.055	0

Additive variance to genotypic variance:

$q:$	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
σ_A^2 / σ_G^2	0	0.18	0.33	0.46	0.57	0.67	0.75	0.82	0.89	0.95	1

Dominance variance to genotypic variance:

$q:$	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
σ_D^2 / σ_G^2	1	0.82	0.67	0.54	0.43	0.33	0.25	0.18	0.11	0.05	0

d. It is emphasized that in our derivation here we have assumed complete dominance. With that assumption we observe that the ratio of σ_D^2 to σ_A^2 is less than one for the higher values of q (1/3 to 1) or, in terms of the favorable allele, for the lower values of p (0 to 2/3). This would imply that we have a lot of low to intermediate allelic frequencies for the dominant favorable alleles, instead of higher frequencies, as one might

surmise due to selection. Hallauer and Miranda, 1988, Quantitative Genetics in Maize Breeding, second edition, p. 116, reported the ratio of σ_D^2 to σ_A^2 for many traits. They also reviewed the literature for the average level of dominance (see p. 122 in Hallauer and Miranda).

Exercise 8.7.

a. As $p_1 (= p)$ approaches one, the ratio of σ_A^2 / σ_G^2 approaches zero. The frequency of the recessive genotype goes to zero and the slope of the regression line approaches zero. Hence, the additive variance (the variance due to regression) is decreasing. The total genotypic variance is also decreasing, but the additive variance is apparently decreasing faster than the total genotypic variance because the ratio of σ_A^2 / σ_G^2 is going to zero. The fact that the additive variance is decreasing faster than the genotypic variance is not easy to see.

b. As p_1 approaches zero, the ratio σ_A^2 / σ_G^2 approaches one. The frequency of the recessive genotype goes to one, while the frequency of the heterozygote and that for the dominant homozygote go to zero. The slope of the regression line would essentially increase and in so doing the σ_D^2 would approach zero and σ_A^2 would approach σ_G^2 so the ratio σ_A^2 / σ_G^2 approaches one. More specifically the slope of the regression line for complete dominance ($G_{11} = G_{12}$) is [equation (8.63)]

$$\begin{aligned}\alpha &= p_1(G_{11} - G_{12}) + p_2(G_{12} - G_{22}) \\ &= p_1(G_{11} - G_{11}) + p_2(G_{11} - G_{22}) \\ &= p_2(G_{11} - G_{22})\end{aligned}$$

which is equal to $(G_{11} - G_{22})$ as $p_2 (= q) \rightarrow 1$. Thus, the regression line converges on the genotypic values of the heterozygote and the recessive homozygote. The genotypic value G_{11} has weight of zero. The additive and genotypic variances are the same.

c. All variances and their ratios depend very much upon allelic frequencies. Heritability (with no environmental variance) would change from 0 to 1 in the limit as the frequency of the recessive allele goes from 0 to 1.

Exercise 8.8.

a. When the heterozygote lies half the distance between the favorable homozygote G_{11} and the midhomozygote $\frac{G_{11} + G_{22}}{2}$, the heterozygote genotypic value is $G_{12} = G_{22} + \frac{3}{4}(G_{11} - G_{22})$. The level of dominance is $a = \frac{1}{2}$ (Comstock and Robinson's notation, 1952) (see p. 8.67). Then the additive variance from equation (8.51) is

$$\begin{aligned}\sigma_A^2 &= 2p_1p_2 \left[p_1(G_{11} - G_{12}) + p_2(G_{12} - G_{22}) \right]^2 \\ &= 2p_1p_2 \left[p_1 \frac{1}{4}(G_{11} - G_{22}) + p_2 \frac{3}{4}(G_{11} - G_{22}) \right]^2 \\ &= 2p_1p_2 \left[p_1 + 3p_2 \right]^2 \frac{(G_{11} - G_{22})^2}{16} \\ &= \frac{1}{8} p_1p_2 \left[p_1 + 3p_2 \right]^2 (G_{11} - G_{22})^2\end{aligned}$$

The dominance variance from equation (8.52) is

$$\begin{aligned}
\sigma_D^2 &= p_1^2 p_2^2 (2G_{12} - G_{11} - G_{22})^2 \\
&= p_1^2 p_2^2 \left\{ 2 \left[G_{22} + \frac{3}{4} (G_{11} - G_{22}) \right] - G_{11} - G_{22} \right\}^2 \\
&= p_1^2 p_2^2 \left\{ \frac{2}{4} [4G_{22} + 3G_{11} - 3G_{22}] - G_{11} - G_{22} \right\}^2 \\
&= p_1^2 p_2^2 \left\{ \frac{2}{4} [G_{22} + 3G_{11}] - G_{11} - G_{22} \right\}^2 \\
&= p_1^2 p_2^2 \left\{ \frac{1}{2} G_{22} + \frac{3}{2} G_{11} - G_{11} - G_{22} \right\}^2 \\
&= p_1^2 p_2^2 \left\{ \frac{1}{2} (G_{11} - G_{22}) \right\}^2 \\
&= \frac{1}{4} p_1^2 p_2^2 \{G_{11} - G_{22}\}^2
\end{aligned}$$

The genotypic variance is

$$\begin{aligned}
\sigma_G^2 &= \sigma_A^2 + \sigma_D^2 \\
&= \frac{1}{8} p_1 p_2 [p_1 + 3p_2]^2 (G_{11} - G_{22})^2 + \frac{1}{4} p_1^2 p_2^2 \{G_{11} - G_{22}\}^2 \\
&= \frac{1}{8} p_1 p_2 \left[(p_1 + 3p_2)^2 + 2p_1 p_2 \right] (G_{11} - G_{22})^2 \\
&= \frac{1}{8} p_1 p_2 \left[p_1^2 + 6p_1 p_2 + 9p_2^2 + 2p_1 p_2 \right] (G_{11} - G_{22})^2 \\
&= \frac{1}{8} p_1 p_2 \left[p_1^2 + 8p_1 p_2 + 9p_2^2 \right] (G_{11} - G_{22})^2
\end{aligned}$$

Next we consider the ratios of certain variances. The ratio of the dominance variance to additive variance is

$$\begin{aligned}
\frac{\sigma_D^2}{\sigma_A^2} &= \frac{\frac{1}{4} p_1^2 p_2^2 \{G_{11} - G_{22}\}^2}{\frac{1}{8} p_1 p_2 [p_1 + 3p_2]^2 (G_{11} - G_{22})^2} \\
&= \frac{2p_1 p_2}{[p_1 + 3p_2]^2}
\end{aligned}$$

or that ratio in terms of p_1 only is (we express the ratio entirely in terms of p_1 so that we can more simply take the derivative of that ratio with respect to p_1 to determine the value of p_1 when the function is a maximum or minimum)

$$\begin{aligned}
\frac{\sigma_D^2}{\sigma_A^2} &= \frac{2p_1 p_2}{[p_1 + 3p_2]^2} \\
&= \frac{2p_1(1-p_1)}{[p_1 + 3(1-p_1)]^2} \\
&= \frac{2p_1 - 2p_1^2}{[p_1 + 3 - 3p_1]^2} \\
&= \frac{2p_1 - 2p_1^2}{[3 - 2p_1]^2} \\
&= \frac{2p_1 - 2p_1^2}{9 - 12p_1 + 4p_1^2}
\end{aligned}$$

The ratio of the additive genetic variance to the genotypic variance is

$$\begin{aligned}\frac{\sigma_A^2}{\sigma_G^2} &= \frac{\frac{1}{8} p_1 p_2 [p_1 + 3p_2]^2 (G_{11} - G_{22})^2}{\frac{1}{8} p_1 p_2 [p_1^2 + 8p_1 p_2 + 9p_2^2] (G_{11} - G_{22})^2} \\ &= \frac{[p_1 + 3p_2]^2}{p_1^2 + 8p_1 p_2 + 9p_2^2} \\ &= \frac{p_1^2 + 6p_1 p_2 + 9p_2^2}{p_1^2 + 8p_1 p_2 + 9p_2^2}\end{aligned}$$

or that ratio in terms of p_1 only is

$$\begin{aligned}\frac{\sigma_A^2}{\sigma_G^2} &= \frac{p_1^2 + 6p_1 p_2 + 9p_2^2}{p_1^2 + 8p_1 p_2 + 9p_2^2} \\ &= \frac{p_1^2 + 6p_1(1-p_1) + 9(1-p_1)^2}{p_1^2 + 8p_1(1-p_1) + 9(1-p_1)^2} \\ &= \frac{p_1^2 + 6p_1 - 6p_1^2 + 9 - 18p_1 + 9p_1^2}{p_1^2 + 8p_1 - 8p_1^2 + 9 - 18p_1 + 9p_1^2} \\ &= \frac{9 - 12p_1 + 4p_1^2}{9 - 10p_1 + 2p_1^2}\end{aligned}$$

The ratio of the dominance variance to the genotypic variance is

$$\begin{aligned}\frac{\sigma_D^2}{\sigma_G^2} &= \frac{\frac{1}{4} p_1^2 p_2^2 \{G_{11} - G_{22}\}^2}{\frac{1}{8} p_1 p_2 [p_1^2 + 8p_1 p_2 + 9p_2^2] (G_{11} - G_{22})^2} \\ &= \frac{2p_1 p_2}{p_1^2 + 8p_1 p_2 + 9p_2^2}\end{aligned}$$

or that ratio in terms of p_1 only is

$$\begin{aligned}\frac{\sigma_D^2}{\sigma_G^2} &= \frac{2p_1 p_2}{p_1^2 + 8p_1 p_2 + 9p_2^2} \\ &= \frac{2p_1(1-p_1)}{p_1^2 + 8p_1(1-p_1) + 9(1-p_1)^2} \\ &= \frac{2p_1 - 2p_1^2}{p_1^2 + 8p_1 - 8p_1^2 + 9 - 18p_1 + 9p_1^2} \\ &= \frac{2p_1 - 2p_1^2}{9 - 10p_1 + 2p_1^2}\end{aligned}$$

We plot the various ratios by simply tabulating the relative values for the additive, dominance, and total genotypic variances for increasing values of p_1 in one tenth units for the level of dominance of $a = \frac{1}{2}$ as follows:

	(1)	(2)	(3)	2)/(1)	(1)/(3)	(2)/(3)
	σ_A^2	σ_D^2	σ_G^2	σ_D^2/σ_A^2	σ_A^2/σ_G^2	σ_D^2/σ_G^2
p_1	$(p_1+3p_2)^2$	$2p_1p_2$	$(p_1+3p_2)^2+2p_1p_2$			
0.0	9	0	9	0	1	0
0.1	7.84	0.18	8.02	0.023	0.978	0.022
0.2	6.76	0.32	7.08	0.047	0.955	0.045
0.3	5.76	0.42	6.18	0.073	0.932	0.068
0.4	4.84	0.48	5.32	0.099	0.910	0.090
0.5	4.00	0.50	4.50	0.125	0.889	0.111
0.6	3.24	0.48	3.72	0.148	0.871	0.129
0.7	2.56	0.42	2.98	0.164	0.859	0.141
0.8	1.96	0.32	2.28	0.163	0.860	0.140
0.9	1.44	0.18	1.62	0.125	0.889	0.111
1.0	1	0	1	0	1	0

It appears that σ_D^2/σ_A^2 and σ_D^2/σ_G^2 are maximum between 0.7 and 0.8, and σ_A^2/σ_G^2 is minimum between 0.7 and 0.8. First we desire to find the value of p_1 when the ratio of σ_D^2/σ_A^2 is a maximum. We do that by taking the derivative of the ratio with respect to p_1 . The ratio is

$$\frac{\sigma_D^2}{\sigma_A^2} = \frac{2p_1 - 2p_1^2}{9 - 12p_1 + 4p_1^2}$$

From any calculus book we know that

$$\frac{d\left(\frac{u}{v}\right)}{dx} = \frac{v \frac{du}{dx} - u \frac{dv}{dx}}{v^2}$$

$$\frac{d\left(\frac{\sigma_D^2}{\sigma_A^2}\right)}{dp_1} = \frac{(9 - 12p_1 + 4p_1^2)(2 - 4p_1) - (2p_1 - 2p_1^2)(-12 + 8p_1)}{(9 - 12p_1 + 4p_1^2)^2}$$

algebraic simplification omitted

$$\begin{aligned} &= \frac{16p_1^2 - 36p_1 + 18}{(9 - 12p_1 + 4p_1^2)^2} \\ &= \frac{(4p_1 - 3)(4p_1 - 6)}{(9 - 12p_1 + 4p_1^2)^2} = 0 \end{aligned}$$

$$4p_1 - 3 = 0$$

$$p_1 = \frac{3}{4}$$

$$4p_1 - 6 = 0$$

$$p_2 = \frac{3}{2}$$

For finding the values of p_1 when the ratio of σ_A^2/σ_G^2 is a maximum, we proceed in a similar manner. The ratio is

$$\frac{\sigma_A^2}{\sigma_G^2} = \frac{9-12p_1+4p_1^2}{9-10p_1+2p_1^2}$$

$$\frac{d\left(\frac{\sigma_A^2}{\sigma_G^2}\right)}{dp_1} = \frac{(9-10p_1+2p_1^2)(-12+8p_1) - (9-12p_1+4p_1^2)(-10+4p_1)}{(9-10p_1+2p_1^2)^2}$$

algebraic simplification omitted

$$= \frac{-18+36p_1-16p_1^2}{(9-10p_1+2p_1^2)^2}$$

$$= \frac{16p_1^2-36p_1+18}{(9-10p_1+2p_1^2)^2}$$

$$= \frac{(4p_1-3)(4p_1-6)}{(9-10p_1+2p_1^2)^2} = 0$$

$$4p_1-3=0$$

$$p_1 = \frac{3}{4}$$

$$4p_1-6=0$$

$$p_2 = \frac{3}{2}$$

Likewise for the ratio of σ_D^2/σ_G^2 , we have

$$\frac{\sigma_D^2}{\sigma_G^2} = \frac{2p_1-2p_1^2}{9-10p_1+2p_1^2}$$

$$\frac{d\left(\frac{\sigma_D^2}{\sigma_G^2}\right)}{dp_1} = \frac{(9-10p_1+2p_1^2)(2-4p_1) - (2p_1-2p_1^2)(-10+4p_1)}{(9-10p_1+2p_1^2)^2}$$

algebraic simplification omitted

$$= \frac{16p_1^2-36p_1+18}{(9-10p_1+2p_1^2)^2}$$

$$= \frac{(4p_1-3)(4p_1-6)}{(9-10p_1+2p_1^2)^2} = 0$$

$$4p_1-3=0$$

$$p_1 = \frac{3}{4}$$

$$4p_1-6=0$$

$$p_2 = \frac{3}{2}$$

All three ratios have either a maximum or a minimum for $p_1 = 0.75$.

b. The graph for the ratio of σ_D^2 / σ_A^2 for the level of dominance of $a = \frac{1}{2}$ is considerably altered from that presented in the notes on p. 8.54 for complete dominance ($a = 1$). With no dominance ($a = 0$) the ratio of σ_D^2 / σ_A^2 is always zero for all values of p_1 . As the level of dominance increases, the graph for the ratio of σ_D^2 / σ_A^2 becomes positive for intermediate values of p_1 and increases as the level of dominance increases from $a = 0$ to $a = 1$. The value of p_1 for the maximum value of the ratio also increases as the level of dominance increases. From a rough plotting of the ratio of σ_D^2 / σ_A^2 we find that for $a = 0.8$, the maximum value of the ratio is a little less than 1 for p_1 equal to about 0.9. The graph starts at zero for $p_1 = 0$ and returns to zero for $p_1 = 1$, as the graphs for all levels of dominance do except for complete dominance ($a = 1$). For $a = 0.9$ the maximum value of the ratio rises rapidly to over 2 for p_1 equal to about 0.95 and declines precipitously as p_1 approaches 1. Obviously as the level of dominance approaches 1, the maximum values skyrocket to very large values corresponding to increasingly larger values of p_1 as p_1 approaches 1. But in all cases the graphs drops precipitously to 0, except for the case when $a = 1$ in which case the graph does not return to zero for $p_1 = 1$ but continues to infinity.

Yes, the conclusion regarding the frequency of the dominant favorable allele being low is altered. The results for partially dominant alleles ($a = 0.7$ to 0.9) completely alters the conclusion to one consistent with the experimental results of the favorable alleles being partially dominant and having frequencies above intermediate values.

The writer would surmise that a generalization of the above piece-meal approach is presented someplace in the literature, but it is unknown to the writer.

Exercise 8.9.

From equation (8.51) the additive variance equals zero whenever

$$p_1(G_{11} - G_{12}) + p_2(G_{12} - G_{22}) = 0$$

$$\text{or } p_1(G_{11} - G_{12}) = -p_2(G_{12} - G_{22})$$

If $p_1 = p_2 = 1/2$, then from (8.51)

$$\frac{1}{2}(G_{11} - G_{12}) = -\frac{1}{2}(G_{12} - G_{22})$$

$$G_{11} - G_{12} = G_{22} - G_{12}$$

$$G_{11} = G_{22}$$

or, alternatively from equation (8.53) for $p_1 = p_2 = 1/2$

$$\frac{G_{11} - G_{22}}{2} = 0$$

$$G_{11} = G_{22}$$

Exercise 8.10.

	B_1B_1	B_1B_2	B_2B_2	Frequency	Mean
A_1A_1	4	4	2	$\frac{1}{4}$	$\frac{\frac{1}{16}(4) + \frac{1}{8}(4) + \frac{1}{16}(2)}{\frac{1}{4}} = 3.5$
	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{16}$		
A_1A_2	3	3	1	$\frac{1}{2}$	$\frac{\frac{1}{8}(3) + \frac{1}{4}(3) + \frac{1}{8}(1)}{\frac{1}{2}} = 2.5$
	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$		
A_2A_2	2	2	0	$\frac{1}{4}$	$\frac{\frac{1}{16}(2) + \frac{1}{8}(2) + \frac{1}{16}(0)}{\frac{1}{4}} = 1.5$
	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{16}$		
	3	3	1	1	2.5

Applying equations (8.51) and (8.52) for the A and B loci separately

$$\begin{aligned}\sigma_{A_a}^2 &= 2p_1p_2[p_1(G_{11} - G_{12}) + p_2(G_{12} - G_{22})]^2 \\ &= 2\left(\frac{1}{2}\right)\left(\frac{1}{2}\right)\left[\frac{1}{2}(3.5 - 2.5) + \frac{1}{2}(2.5 - 1.5)\right]^2 \\ &= \frac{1}{2}\left[\frac{1}{2} + \frac{1}{2}\right]^2 \\ &= \frac{1}{2}\end{aligned}$$

$$\sigma_{D_a}^2 = 0$$

$$\begin{aligned}\sigma_{A_b}^2 &= 2\left(\frac{1}{2}\right)\left(\frac{1}{2}\right)\left[\frac{1}{2}(3 - 3) + \frac{1}{2}(3 - 1)\right]^2 \\ &= \frac{1}{2}\left[\frac{1}{2}(2)\right]^2 \\ &= \frac{1}{2}\end{aligned}$$

$$\begin{aligned}\sigma_{D_b}^2 &= p_1^2 p_2^2 (2G_{12} - G_{11} - G_{22})^2 \\ &= \left(\frac{1}{2}\right)^2 \left(\frac{1}{2}\right)^2 [2(3) - 3 - 1]^2 \\ &= \frac{1}{16}(6 - 4)^2 \\ &= \frac{1}{4}\end{aligned}$$

$$\sigma_I^2 = 0 \text{ because } e_{11} = e_{12} = e_{21} = e_{22} = 0 \quad [\text{see equation (8.162)}]$$

No, linkage disequilibrium would not affect the mean of this population because there is no epistasis [see (8.171)].

Yes, linkage disequilibrium would affect the variance because even with no epistasis the gametic variance is affected [see equation (8.173)]. But what about other variances?

Exercise 8.11.

There are four additive-by-additive genetic terms in the linear model for every pair of loci. For example, for loci A and B we have the following terms

$$\cdots + (\alpha\alpha)_{a_i^m b_k^m} + (\alpha\alpha)_{a_i^m b_k^f} + (\alpha\alpha)_{a_i^f b_k^m} + (\alpha\alpha)_{a_i^f b_k^f} + \cdots$$

Hereafter we will consider a total of only two loci. Each effect is defined as the residual effect in a two-way table of m_A A alleles and m_B B alleles, namely,

	B ₁	B ₂	...	B _{m_B}
A ₁				
A ₂				
⋮				
A _{m_A}				

For the first term every $(\alpha\alpha)_{a_i^m b_k^m}$ effect is defined as the residual in a cell in the above table where both A and B alleles are present in the same male gamete, namely,

$$(\alpha\alpha)_{a_i^m b_k^m} = G_{i,k} - \mu - \alpha_{a_i}^m - \alpha_{b_k}^m$$

and its variance is defined

$$\sigma_{(\alpha\alpha)^{mm}}^2 = \sum_{i=1}^{m_A} \sum_{k=1}^{m_B} p_{a_i}^m p_{b_k}^m \left[(\alpha\alpha)_{a_i^m b_k^m} \right]^2$$

Each of the four terms is similarly defined and is equal to each other. Each contributes the same amount of variance to the total additive-by-additive variance. Thus the total additive-by-additive variance is

$$\sigma_{AA}^2 = 4\sigma_{(\alpha\alpha)^{mm}}^2$$

Linkage equilibrium permits one to write the frequency of each $(\alpha\alpha)^{mm}$ as a product $p_a^m p_b^m$ and likewise for each $(\alpha\alpha)^{ff}$. Random mating permits one to write the frequency of each $(\alpha\alpha)^{mf}$ as a product $p_a^m p_b^f$ and likewise for each $(\alpha\alpha)^{fm}$.

Exercise 8.12.

There are various ways to assign genotypic values to the nine genotypic combinations from simply intuitively writing down a set of nine genotypic values to one or more formal approaches of assigning values to the effects in the genic factorial model given in equation (8.128). For instructional purposes we apply a more formal approach. Note that the e_{ij} are defined in (8.161) and are defined slightly differently from those in Cockerham, 1954, Genetics 39:859-882. The genotypic values assigned are not unique.

a. Only additive variance exists.

We write the model

$$G_{ijkl} = \mu + \alpha_{ai}^m + \alpha_{aj}^f + \alpha_{bk}^m + \alpha_{bl}^f$$

and assign values to the following effects: $\mu = 3$, $\alpha_{a1}^m = \frac{1}{2}$, $\alpha_{a2}^m = -\frac{1}{2}$, $\alpha_{a1}^f = \frac{1}{2}$, $\alpha_{a2}^f = -\frac{1}{2}$, $\alpha_{b1}^m = \frac{1}{2}$, $\alpha_{b2}^m = -\frac{1}{2}$, $\alpha_{b1}^f = \frac{1}{2}$, and $\alpha_{b2}^f = -\frac{1}{2}$. (Alternatively, we could have simply selected any value for the mean, say $\mu = 10$, and integers 1 and -1 for the α effects.) All other effects in (8.128) equal zero. The genotypic values are:

$$G_{1111} = 3 + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) = 5$$

$$G_{1112} = 3 + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 4$$

$$\vdots$$

$$G_{2222} = 3 + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 1$$

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij.}		e _{ij}
A ₁ A ₁ (1/4)	5	4	3	4		1 2
A ₁ A ₂ (1/2)	4	3	2	3	1	0 0
A ₂ A ₂ (1/4)	3	2	1	2	2	0 0
G _{.kl}	4	3	2	3		

b. Only dominance variance exists.

We write the model

$$G_{ijkl} = \mu + \delta_{aij} + \delta_{bkl}$$

and assign values to the following effects:

$\mu = 2$, $\delta_{a11} = -\frac{1}{2}$, $\delta_{a12} = \frac{1}{2}$, $\delta_{a22} = -\frac{1}{2}$, $\delta_{b11} = -\frac{1}{2}$, $\delta_{b12} = \frac{1}{2}$, $\delta_{b22} = -\frac{1}{2}$. (Alternatively, we could have simply selected any value for the mean, say $\mu = 10$, and integers 1 and -1 for the δ effects.) All other effects in (8.128) equal zero. The genotypic values are:

$$G_{1111} = 2 + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 1$$

$$G_{1112} = 2 + \left(-\frac{1}{2}\right) + \left(\frac{1}{2}\right) = 2$$

$$\vdots$$

$$G_{2222} = 2 + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 1$$

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij.}		e _{ij}
A ₁ A ₁ (1/4)	1	2	1	1.5		1 2
A ₁ A ₂ (1/2)	2	3	2	2.5	1	0 0
A ₂ A ₂ (1/4)	1	2	1	1.5	2	0 0
G _{.kl}	1.5	2.5	1.5	2		

c. Only additive and dominance variances exist.

We write the model

$$G_{ijkl} = \mu + \alpha_{ai}^m + \alpha_{aj}^f + \delta_{aij} + \alpha_{bk}^m + \alpha_{bl}^f + \delta_{bkl}$$

and use the same effects in (a) and (b) above. The genotypic values are:

$$\begin{aligned}
G_{1111} &= 4 + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 5 \\
G_{1112} &= 4 + \left(\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(\frac{1}{2}\right) = 5 \\
&\vdots \\
G_{2222} &= 4 + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) + \left(-\frac{1}{2}\right) = 1
\end{aligned}$$

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij.}		e _{ij}	
A ₁ A ₁ (1/4)	5	5	3	4.5		1	2
A ₁ A ₂ (1/2)	5	5	3	4.5	1	0	0
A ₂ A ₂ (1/4)	3	3	1	2.5	2	0	0
G _{.kl}	4.5	4.5	2.5	4			

More simply, one can simply add the corresponding genotypic values in (a) and (b) above to obtain a set of genotypic values for (c).

d. Only additive and additive-by-additive variances exist.

We write the model

$$G_{ijkl} = \mu + \alpha_{a_i}^m + \alpha_{a_j}^f + \alpha_{b_k}^m + \alpha_{b_l}^f + (\alpha\alpha)_{a_i b_k}^{mm} + (\alpha\alpha)_{a_i b_l}^{mf} + (\alpha\alpha)_{a_j b_k}^{fm} + (\alpha\alpha)_{a_j b_l}^{ff}$$

The same general principles developed in (a) to (c) above can be applied here, namely, regarding each term in the model as a variable which takes on a different value depending upon the allele in the genotype. With equal male and female allelic frequencies at each locus, which we are assuming here, $\alpha_{a_i}^m$ and $\alpha_{a_j}^f$ are the same variable

$(\alpha_{a_i} = \alpha_{a_i}^m = \alpha_{a_i}^f)$, as are $\alpha_{b_k}^m$ and $\alpha_{b_l}^f$ ($\alpha_{b_k} = \alpha_{b_k}^m = \alpha_{b_k}^f$), and likewise

$(\alpha\alpha)_{a_i b_k}^{mm}$, $(\alpha\alpha)_{a_i b_l}^{mf}$, $(\alpha\alpha)_{a_j b_k}^{fm}$, and $(\alpha\alpha)_{a_j b_l}^{ff}$ are the same variables

$(\alpha\alpha)_{a_i b_k} = (\alpha\alpha)_{a_i b_k}^{mm} = (\alpha\alpha)_{a_i b_l}^{mf} = (\alpha\alpha)_{a_j b_k}^{fm} = (\alpha\alpha)_{a_j b_l}^{ff}$. We assign the following values to the effects: $\mu = 4$,

$\alpha_{a_1}^m = 1$, $\alpha_{a_2}^m = -1$, $\alpha_{a_1}^f = 1$, $\alpha_{a_2}^f = -1$, $\alpha_{b_1}^m = 1$, $\alpha_{b_2}^m = -1$, $\alpha_{b_1}^f = 1$, and $\alpha_{b_2}^f = -1$. For the additive-by-additive

effects, we assigned the following values: $(\alpha\alpha)_{a_1 b_1} = \frac{1}{4}$, $(\alpha\alpha)_{a_1 b_2} = -\frac{1}{4}$, $(\alpha\alpha)_{a_2 b_1} = -\frac{1}{4}$, $(\alpha\alpha)_{a_2 b_2} = \frac{1}{4}$.

(Alternatively, we could have simply selected any value for the mean, say $\mu = 10$, and integers 1 and -1 for the α effects and likewise 1 and -1 for the $\alpha\alpha$ effects.) All other effects in (8.128) equal zero. The genotypic values are:

$$\begin{aligned}
G_{1111} &= 4 + 1 + 1 + 1 + 1 + \left(\frac{1}{4}\right) + \left(\frac{1}{4}\right) + \left(\frac{1}{4}\right) + \left(\frac{1}{4}\right) = 9 \\
G_{1112} &= 4 + 1 + 1 + 1 + 1 - \frac{1}{4} - \frac{1}{4} + \frac{1}{4} - \frac{1}{4} = 6 \\
&\vdots \\
G_{2222} &= 4 - 1 - 1 - 1 - 1 + \frac{1}{4} + \frac{1}{4} + \frac{1}{4} + \frac{1}{4} = 1
\end{aligned}$$

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij..}	e _{ij}			
A ₁ A ₁ (1/4)	9	6	3	6		1	2	e _{i1} - e _{i2}
A ₁ A ₂ (1/2)	6	4	2	4	1	1	1	0
A ₂ A ₂ (1/4)	3	2	1	2	2	1	1	0
G _{..kl}	6	4	2	4	e _{1j} - e _{2j}	0	0	

Every e_{ij} equals one, and all row and column differences equal zero, as required for only additive-by-additive epistatic variance (see Section 8.3.3, pp. 9.98 to 9.119).

Or, intuitively, from statistical knowledge of the response surface of a two-factor factorial experiment involving quantitative factors with only A -linear and B -linear main effects and A -linear by B -linear interaction effect, one can simply write down the above genotypic values.

e. Additive, dominance, and only additive (at the A locus)-by-dominance (at the B locus) epistatic variances exist.

In a similar manner to the above one can devise a table of genotypic values by simply adding the corresponding terms in the genic factorial model. Or, more simply from intuition, one can write down the following genotypic values.

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij..}	e _{ij}			
A ₁ A ₁ (1/4)	3	1	2	1.75		1	2	e _{i1} - e _{i2}
A ₁ A ₂ (1/2)	3	2	2	2.25	1	1	-1	2
A ₂ A ₂ (1/4)	2	2	1	1.75	2	1	-1	2
G _{..kl}	2.75	1.75	1.75	2	e _{1j} - e _{2j}	0	0	

We note that from the marginal means for the B locus we have both additive and dominance variances. Also we have additional dominance variance from the marginal means for the A locus. There is no additive-by-additive, no dominance-by-additive, and no dominance-by-dominance epistatic variances because with equal allelic frequencies $e_{11} + e_{12} + e_{21} + e_{22} = 0$, $e_{11} + e_{12} - e_{21} - e_{22} = 0$, and $e_{11} - e_{12} - e_{21} + e_{22} = 0$ [see equation (8.163), p. 9.103].

f. Additive, dominance, and only dominance (at the A locus)-by-additive (at the B locus) epistatic variances exist.

In a similar manner to the above one can devise a table of genotypic values by simply adding the corresponding terms in the genic factorial model. Or, more simply from intuition, one can write down the following genotypic values.

	B ₁ B ₁ (1/4)	B ₁ B ₂ (1/2)	B ₂ B ₂ (1/4)	G _{ij..}	e _{ij}			
A ₁ A ₁ (1/4)	4	3	2	3		1	2	e _{i1} - e _{i2}
A ₁ A ₂ (1/2)	2	2	2	2	1	1	1	0
A ₂ A ₂ (1/4)	2	1	0	1	2	-1	-1	0
G _{..kl}	3	2	1	2	e _{1j} - e _{2j}	2	2	

We note that we have additive variance only from the marginal means for the A locus and additive variance only from the marginal means for the B locus. There is no additive-by-additive, no additive-by-dominance, and no dominance-by-dominance epistatic variances because with equal allelic frequencies $e_{11} + e_{12} + e_{21} + e_{22} = 0$, $e_{11} - e_{12} + e_{21} - e_{22} = 0$, and $e_{11} - e_{12} - e_{21} + e_{22} = 0$.

g. Additive, dominance, and only dominance-by-dominance epistatic variances exist.

In a similar manner to the above one can devise a table of genotypic values by simply adding the corresponding terms in the genic factorial model. Or, more simply from intuition, one can write down the following genotypic values.

	B_1B_1 (1/4)	B_1B_2 (1/2)	B_2B_2 (1/4)	$G_{ij..}$	e_{ij}			
A_1A_1 (1/4)	3	3	2	2.75		1	2	$e_{i1} - e_{i2}$
A_1A_2 (1/2)	3	4	2	3.25	1	1	-1	2
A_2A_2 (1/4)	2	2	1	1.75	2	-1	1	-2
$G_{..kl}$	2.75	3.25	1.75	2.75	$e_{1j} - e_{2j}$	2	-2	

We note that we have both additive and dominance variances from the marginal means for both the A and B loci. There is no additive-by-additive, no additive-by-dominance, and no dominance-by-additive epistatic variances because with equal allelic frequencies $e_{11} + e_{12} + e_{21} + e_{22} = 0$, $e_{11} - e_{12} + e_{21} - e_{22} = 0$, and $e_{11} + e_{12} - e_{21} - e_{22} = 0$.

Exercise 8.13. This exercise is similar to Example 8.5, pp. 8.105 to 8.117.

	B ₁ B ₁ 1/4	B ₁ B ₂ 1/2	B ₂ B ₂ 1/4	
A ₁ A ₁	$G_{22} = G_{1111}$ = 4	$G_{21} = G_{1112}$ = 2	$G_{20} = G_{1122}$ = 3	$G_{2.} = G_{11..} = \frac{1}{4} \cdot 4 + \frac{1}{2} \cdot 2 + \frac{1}{4} \cdot 3 = 2\frac{3}{4}$ $G_{2.} - G_{..} = \frac{3}{16}$
1/4	1/16	2/16	1/16	
	$\frac{23}{16}$	$-\frac{9}{16}$	$\frac{7}{16}$	
A ₁ A ₂	$G_{12} = G_{1211}$ = 4	$G_{11} = G_{1212}$ = 3	$G_{10} = G_{1222}$ = 1	$G_{1.} = G_{12..} = \frac{1}{4} \cdot 4 + \frac{1}{2} \cdot 3 + \frac{1}{4} \cdot 1 = 2\frac{3}{4}$ $G_{1.} - G_{..} = \frac{3}{16}$
1/2	2/16	4/16	2/16	
	$\frac{23}{16}$	$\frac{7}{16}$	$-\frac{25}{16}$	
A ₂ A ₂	$G_{02} = G_{2211}$ = 3	$G_{01} = G_{2212}$ = 2	$G_{00} = G_{2222}$ = 1	$G_{0.} = G_{22..} = \frac{1}{4} \cdot 3 + \frac{1}{2} \cdot 2 + \frac{1}{4} \cdot 1 = 2$ $G_{0.} - G_{..} = -\frac{9}{16}$
1/4	1/16	2/16	1/16	
	$\frac{7}{16}$	$-\frac{9}{16}$	$-\frac{25}{16}$	

$$G_{.2} = G_{..11} \quad G_{.1} = G_{..12} \quad G_{.0} = G_{..22} \quad G_{..} = G_{....} = \frac{41}{16} = 2\frac{9}{16}$$

$$\frac{1}{4} \cdot 4 + \frac{1}{2} \cdot 4 + \frac{1}{4} \cdot 3 \quad \frac{1}{4} \cdot 2 + \frac{1}{2} \cdot 3 + \frac{1}{4} \cdot 2 \quad \frac{1}{4} \cdot 3 + \frac{1}{2} \cdot 1 + \frac{1}{4} \cdot 1$$

$$= 3\frac{3}{4} \quad = 2\frac{1}{2} \quad = 1\frac{1}{2}$$

$$G_{.2} - G_{..} = \frac{19}{16} \quad G_{.1} - G_{..} = -\frac{1}{16} \quad G_{.0} - G_{..} = -\frac{17}{16}$$

a.i. The total genotypic variance by the definition formula is

$$\sigma_G^2 = \sum_i \sum_j p_{ij} (G_{ij} - G_{..})^2 = \frac{1}{16} \left(\frac{23}{16}\right)^2 + \frac{2}{16} \left(-\frac{9}{16}\right)^2 + \dots + \frac{1}{16} \left(-\frac{25}{16}\right)^2 = \frac{255}{256}$$

a.ii. The genotypic variance due to locus *a* by the definition formula is

$$\sigma_{y_a}^2 = \sum_i p_i (G_i - G_{..})^2 = \frac{1}{4} \left(\frac{3}{16}\right)^2 + \frac{1}{2} \left(\frac{3}{16}\right)^2 + \frac{1}{4} \left(-\frac{9}{16}\right)^2 = \frac{27}{256}$$

a.iii. The genotypic variance due to locus *b* by the definition formula is

$$\sigma_{y_b}^2 = \sum_j p_j (G_{.j} - G_{..})^2 = \frac{1}{4} \left(\frac{19}{16}\right)^2 + \frac{1}{2} \left(-\frac{1}{16}\right)^2 + \frac{1}{4} \left(-\frac{17}{16}\right)^2 = \frac{163}{256}$$

a.iv. The interlocus or epistatic variance between loci a and b by definition formula is

	B ₁ B ₁ 1/4	B ₁ B ₂ 1/2	B ₂ B ₂ 1/4
A ₁ A ₁	4 $\hat{G}_{22} = \frac{41}{16} + \frac{3}{16} + \frac{19}{16} = \frac{63}{16}$	2 $\hat{G}_{21} = \frac{41}{16} + \frac{3}{16} + \left(-\frac{1}{16}\right) = \frac{43}{16}$	3 $\hat{G}_{20} = \frac{41}{16} + \frac{3}{16} + \left(-\frac{17}{16}\right) = \frac{27}{16}$
1/4	1/16 $\frac{1}{16}$	2/16 $-\frac{11}{16}$	1/16 $\frac{21}{16}$
A ₁ A ₂	4 $\hat{G}_{12} = \frac{41}{16} + \frac{3}{16} + \frac{19}{16} = \frac{63}{16}$	3 $\hat{G}_{11} = \frac{41}{16} + \frac{3}{16} + \left(-\frac{1}{16}\right) = \frac{43}{16}$	1 $\hat{G}_{10} = \frac{41}{16} + \frac{3}{16} + \left(-\frac{17}{16}\right) = \frac{27}{16}$
1/2	2/16 $\frac{1}{16}$	4/16 $\frac{5}{16}$	2/16 $-\frac{11}{16}$
A ₂ A ₂	3 $\hat{G}_{02} = \frac{41}{16} + \left(-\frac{9}{16}\right) + \frac{19}{16} = \frac{51}{16}$	2 $\hat{G}_{01} = \frac{41}{16} + \left(-\frac{9}{16}\right) + \left(-\frac{1}{16}\right) = \frac{31}{16}$	1 $\hat{G}_{00} = \frac{41}{16} + \left(-\frac{9}{16}\right) + \left(-\frac{17}{16}\right) = \frac{15}{16}$
1/4	1/16 $-\frac{3}{16}$	2/16 $\frac{1}{16}$	1/16 $\frac{1}{16}$

$$\sigma_{yyab}^2 = \sum_i \sum_j p_{ij} (G_{ij} - G_{..})^2 = \frac{1}{16} \left(\frac{1}{16}\right)^2 + \frac{2}{16} \left(-\frac{11}{16}\right)^2 + \dots + \frac{1}{16} \left(\frac{1}{16}\right)^2 = \frac{65}{256}$$

Check:

$$\sigma_G^2 = \sigma_{y_a}^2 + \sigma_{y_b}^2 + \sigma_{yyab}^2 = \frac{27}{256} + \frac{163}{256} + \frac{65}{256} = \frac{255}{256}$$

a.v. The additive variance at locus a by definition formula is

	A ₁ 1/2	A ₂ 1/2	
A ₁	$G_2 = G_{11..} = \frac{11}{4} = 2\frac{3}{4}$	$G_1 = G_{12..} = \frac{11}{4} = 2\frac{3}{4}$	$G_{1...} = \frac{1}{2} \frac{11}{4} + \frac{1}{2} \frac{11}{4} = \frac{11}{4} = 2\frac{3}{4}$ $G_{1...} - G_{....} = \frac{3}{16}$
1/2	$p_2 = p_{11..} = \frac{1}{4}$	$\frac{p_1}{2} = p_{12..} = \frac{1}{4}$	
A ₂	$G_1 = G_{12..} = \frac{11}{4} = 2\frac{3}{4}$	$G_0 = G_{22..} = 2$	$G_{2...} = \frac{1}{2} \frac{11}{4} + \frac{1}{2} \cdot 2 = \frac{19}{8} = 2\frac{3}{8}$ $G_{2...} - G_{....} = -\frac{3}{16}$
1/2	$\frac{p_1}{2} = p_{21..} = \frac{1}{4}$	$p_0 = p_{22..} = \frac{1}{4}$	
	$G_{1..} = \frac{1}{2} \frac{11}{4} + \frac{1}{2} \frac{11}{4}$ $= \frac{11}{4}$ $= 2\frac{3}{4}$	$G_{2..} = \frac{1}{2} \frac{11}{4} + \frac{1}{2} \cdot 2$ $= \frac{19}{8}$ $= 2\frac{3}{8}$	$G_{..} = G_{....} = \frac{1}{2} \frac{11}{4} + \frac{1}{2} \frac{19}{8}$ $= \frac{41}{16}$ $= 2\frac{9}{16}$
	$G_{1..} - G_{....} = \frac{3}{16}$	$G_{2..} - G_{....} = -\frac{3}{16}$	

$$\sigma_{A_a}^2 = 2 \sum_{i=1}^2 p_i (G_{i\dots} - G_{\dots})^2 = 2 \left[\frac{1}{2} \left(\frac{3}{16} \right)^2 + \frac{1}{2} \left(-\frac{3}{16} \right)^2 \right] = \frac{18}{256}$$

a.vi. The dominance variance at the locus a is:

	A ₁ 1/2	A ₂ 1/2
A ₁ 1/2	$G_{2.} = G_{11..} = \frac{11}{4} = 2\frac{3}{4}$ $\hat{G}_{11..} = \frac{41}{16} + \frac{3}{16} + \frac{3}{16} = \frac{47}{16}$ $-3/16$	$G_{1.} = G_{12..} = \frac{11}{4} = 2\frac{3}{4}$ $\hat{G}_{12..} = \frac{41}{16} + \frac{3}{16} + \left(-\frac{3}{16}\right) = \frac{41}{16}$ $3/16$
A ₂ 1/2	$G_{1.} = G_{21..} = \frac{11}{4} = 2\frac{3}{4}$ $\hat{G}_{21} = \frac{41}{16} + \left(-\frac{3}{16}\right) + \frac{3}{16} = \frac{41}{16}$ $3/16$	$G_{0.} = G_{22..} = 2$ $\hat{G}_{22..} = \frac{41}{16} + \left(-\frac{3}{16}\right) + \left(-\frac{3}{16}\right) = \frac{35}{16}$ $-3/16$

$$G_{\dots} = 2\frac{9}{16}$$

$$\sigma_{D_a}^2 = \sum_i \sum_j p_{ij} (G_{ij..} - G_{\dots})^2 = \frac{1}{4} \left(-\frac{3}{16}\right)^2 + \frac{1}{4} \left(\frac{3}{16}\right)^2 + \frac{1}{4} \left(\frac{3}{16}\right)^2 + \frac{1}{4} \left(-\frac{3}{16}\right)^2 = \frac{9}{256}$$

a.vii. The total additive-by-additive variance is equal to

$$\sigma_{AA_{ab}}^2 = \sigma_{(\alpha\alpha)_{ab}^{mm}}^2 + \sigma_{(\alpha\alpha)_{ab}^{mf}}^2 + \sigma_{(\alpha\alpha)_{ab}^{fm}}^2 + \sigma_{(\alpha\alpha)_{ab}^{ff}}^2$$

We must calculate each of the four variances separately. We consider $\sigma_{(\alpha\alpha)_{ab}^{mm}}^2$ first. To do so we must construct

a 2×2 table where one side or factor of the table represents the possible A alleles contributed by the male parent and the other side or factor of the table represents the possible B alleles contributed by the male parent. We desire the genotypic value in each cell in such a 2×2 table. To visualize this procedure, it is convenient to expand the initial 3×3 table to a 4×4 table so that we can clearly identify all male alleles of loci a and b .

	$B_1^m B_1^f$	$B_1^m B_2^f$	$B_2^m B_1^f$	$B_2^m B_2^f$
	1/4	1/4	1/4	1/4
$A_1^m A_1^f$	$G_{22} = G_{1111}$	$G_{21} = G_{1112}$	$G_{21} = G_{1121}$	$G_{20} = G_{1122}$
1/4	4 1/16	2 1/16	2 1/16	3 1/16
$A_1^m A_2^f$	$G_{12} = G_{1211}$	$G_{11} = G_{1212}$	$G_{11} = G_{1221}$	$G_{10} = G_{1222}$
1/4	4 1/16	3 1/16	3 1/16	1 1/16
$A_2^m A_1^f$	$G_{12} = G_{2111}$	$G_{11} = G_{2112}$	$G_{11} = G_{2121}$	$G_{10} = G_{2122}$
1/4	4 1/16	3 1/16	3 1/16	1 1/16
$A_2^m A_2^f$	$G_{02} = G_{2211}$	$G_{01} = G_{2212}$	$G_{01} = G_{2221}$	$G_{00} = G_{2222}$
1/4	3 1/16	2 1/16	2 1/16	1 1/16

Thus, to calculate the genotypic value for any combination of A alleles from the male parent with any combination of B alleles from the male parent, we have

$$G_{i.k.} = \sum_j \sum_l p_j p_l G_{ijkl}$$

$$\text{For example, } G_{1.1.} = \frac{1}{4}G_{1111} + \frac{1}{4}G_{1112} + \frac{1}{4}G_{1211} + \frac{1}{4}G_{1212} = \frac{1}{4}(4) + \frac{1}{4}(2) + \frac{1}{4}(4) + \frac{1}{4}(3) = 3\frac{1}{4}$$

Note that this is the upper left 2×2 table in the above 4×4 table. In like manner, we obtain the genotypic values for the three remaining cells in the 2×2 table:

	B_1^m	B_2^m	
	$p_{.1.} = \frac{1}{2}$	$p_{.2.} = \frac{1}{2}$	
A_1^m	$G_{1.1.}$ $= \frac{1}{4}4 + \frac{1}{4}2 + \frac{1}{4}4 + \frac{1}{4}3 = 3\frac{1}{4}$ $\hat{G}_{1.1.} = \frac{41}{16} + \frac{3}{16} + \frac{9}{16} = \frac{53}{16}$ $(\alpha\alpha)_{11}^{mm} = -\frac{1}{16}$	$G_{1.2.}$ $= \frac{1}{4}2 + \frac{1}{4}3 + \frac{1}{4}3 + \frac{1}{4}1 = 2\frac{1}{4}$ $\hat{G}_{1.2.} = \frac{41}{16} + \frac{3}{16} + (-\frac{9}{16}) = \frac{35}{16}$ $(\alpha\alpha)_{12}^{mm} = \frac{1}{16}$	$G_{1\dots} = \frac{1}{2}\frac{13}{4} + \frac{1}{2}\frac{9}{4} = 2\frac{3}{4}$ $\alpha_{a_1}^m = \frac{3}{16}$
A_2^m	$G_{2.1.}$ $= \frac{1}{4}4 + \frac{1}{4}3 + \frac{1}{4}3 + \frac{1}{4}2 = 3$ $\hat{G}_{2.1.} = \frac{41}{16} + (-\frac{3}{16}) + \frac{9}{16} = \frac{47}{16}$ $(\alpha\alpha)_{21}^{mm} = \frac{1}{16}$	$G_{2.2.}$ $= \frac{1}{4}3 + \frac{1}{4}1 + \frac{1}{4}2 + \frac{1}{4}1 = 1\frac{3}{4}$ $\hat{G}_{2.2.} = \frac{41}{16} + (-\frac{3}{16}) + (-\frac{9}{16}) = \frac{29}{16}$ $(\alpha\alpha)_{22}^{mm} = -\frac{1}{16}$	$G_{2\dots} = \frac{1}{2}\frac{12}{4} + \frac{1}{2}\frac{7}{4} = 2\frac{3}{8}$ $\alpha_{a_2}^m = -\frac{3}{16}$
$p_{1\dots} = \frac{1}{2}$	$G_{.1.} = 3\frac{1}{8}$	$G_{.2.} = 2$	$G_{\dots} = 2\frac{9}{16}$
$p_{2\dots} = \frac{1}{2}$	$\alpha_{b_1}^m = \frac{9}{16}$	$\alpha_{b_1}^m = -\frac{9}{16}$	

$$\sigma_{(\alpha\alpha)_{ab}^{mm}}^2 = \sum_i \sum_k p_i p_k (G_{i.k.} - \hat{G}_{i.k.})^2 = \sum_i \sum_k [(\alpha\alpha)_{a_i b_k}^{mm}]^2 = \frac{1}{4}(-\frac{1}{16})^2 + \frac{1}{4}(\frac{1}{16})^2 + \frac{1}{4}(\frac{1}{16})^2 + \frac{1}{4}(-\frac{1}{16})^2 = \frac{1}{256}$$

Since $p_{a_i}^m = p_{a_i}^f$ for $i = 1, 2$, and $p_{b_k}^m = p_{b_k}^f$ for $k = 1, 2$, then

$$\sigma_{(\alpha\alpha)_{ab}^{mm}}^2 = \sigma_{(\alpha\alpha)_{ab}^{mf}}^2 = \sigma_{(\alpha\alpha)_{ab}^{fm}}^2 = \sigma_{(\alpha\alpha)_{ab}^{ff}}^2$$

For example, for $\sigma_{(\alpha\alpha)_{ab}^{mf}}^2$ consider the following table:

	B_1^f	B_2^f
A_1^m	$G_{1.1}$	$G_{1.2}$
A_2^m	$G_{2.1}$	$G_{2.2}$

The genotypic value for each $G_{i.l}$ cell is equal to the average of four cells in the above 4×4 table which have the same values for i and l . Hence, the total additive-by-additive variance is

$$\sigma_{AAab}^2 = 4\sigma_{(\alpha\alpha)_{ab}^{mm}}^2 = 4\frac{1}{256} = \frac{4}{256}$$

a.viii. The total additive (at locus a)-by-dominance (at locus b) variance is equal to

$$\sigma_{ADab}^2 = \sigma_{(\alpha\delta)_{abb}^{mmf}}^2 + \sigma_{(\alpha\delta)_{abb}^{fmf}}^2$$

We must calculate each of the two variances separately. We consider $\sigma_{(\alpha\delta)_{abb}^{mf}}^2$ by constructing a $2 \times 2 \times 2$ table.

In the three-way table each genotypic value is averaged over the two levels of the A^f factor. The predicted genotypic value for each cell in the $2 \times 2 \times 2$ three-way table is calculated as follows:

$$\hat{G}_{i.kl} = \mu + \alpha_i^m + \alpha_k^m + \alpha_l^f + (\alpha\alpha)_{ik}^{mm} + (\alpha\alpha)_{il}^{mf} + \delta_{kl}^{mf}$$

To calculate these effects we construct three two-way tables—two of which we have already constructed. The three two-way tables are

(1) $A^m - B^m$ --averaged over the levels of the A^f and B^f factors

This table has already been constructed in part a.vii in which we obtained values for the following effects:

$$\alpha_{a_1}^m = \frac{3}{16}, \alpha_{a_2}^m = -\frac{3}{16}, \alpha_{b_1}^m = \frac{9}{16}, \alpha_{b_2}^m = -\frac{9}{16}, (\alpha\alpha)_{11}^{mm} = -\frac{1}{16}, (\alpha\alpha)_{12}^{mm} = \frac{1}{16}, (\alpha\alpha)_{21}^{mm} = \frac{1}{16}, (\alpha\alpha)_{22}^{mm} = -\frac{1}{16}$$

(2) $A^m - B^f$ --averaged over the levels of the A^f and B^m factors

This table provides the same values for the effects as the $A^m - B^m$ table above (because the allelic frequencies for the male side is the same as that for the female side for locus b), namely,

$$\alpha_{a_1}^m = \frac{3}{16}, \alpha_{a_2}^m = -\frac{3}{16}, \alpha_{b_1}^f = \frac{9}{16}, \alpha_{b_2}^f = -\frac{9}{16}, (\alpha\alpha)_{11}^{mf} = -\frac{1}{16}, (\alpha\alpha)_{12}^{mf} = \frac{1}{16}, (\alpha\alpha)_{21}^{mf} = \frac{1}{16}, (\alpha\alpha)_{22}^{mf} = -\frac{1}{16}$$

(3) $B^m - B^f$ --averaged over the levels of the A^m and A^f factors

The table is

	B_1^f	B_2^f	
B_1^m	$G_{..11}$ $= \frac{1}{4}4 + \frac{1}{4}4 + \frac{1}{4}4 + \frac{1}{4}3 = 3\frac{3}{4}$ $\hat{G}_{..11} = \frac{41}{16} + \frac{9}{16} + \frac{9}{16} = \frac{59}{16}$ $\delta_{b_1b_1}^{mf} = \frac{1}{16}$	$G_{..12}$ $= \frac{1}{4}2 + \frac{1}{4}3 + \frac{1}{4}3 + \frac{1}{4}2 = 2\frac{1}{2}$ $\hat{G}_{..12} = \frac{41}{16} + \frac{9}{16} + \left(-\frac{9}{16}\right) = \frac{41}{16}$ $\delta_{b_1b_2}^{mf} = -\frac{1}{16}$	$G_{..1} = 3\frac{1}{8}$ $\alpha_{b_1}^m = \frac{9}{16}$
B_2^m	$G_{..21}$ $= \frac{1}{4}2 + \frac{1}{4}3 + \frac{1}{4}3 + \frac{1}{4}2 = 2\frac{1}{2}$ $\hat{G}_{..21} = \frac{41}{16} + \left(-\frac{9}{16}\right) + \frac{9}{16} = \frac{41}{16}$ $\delta_{b_2b_1}^{mf} = -\frac{1}{16}$	$G_{..22}$ $= \frac{1}{4}3 + \frac{1}{4}1 + \frac{1}{4}1 + \frac{1}{4}1 = 1\frac{1}{2}$ $\hat{G}_{..22} = \frac{41}{16} + \left(-\frac{9}{16}\right) + \left(-\frac{9}{16}\right) = \frac{23}{16}$ $\delta_{b_2b_2}^{mf} = \frac{1}{16}$	$G_{..2} = 2$ $\alpha_{b_2}^m = -\frac{9}{16}$
	$G_{...1} = 3\frac{1}{8}$ $\alpha_{b_1}^f = \frac{9}{16}$	$G_{...2} = 2$ $\alpha_{b_2}^f = -\frac{9}{16}$	$G_{....} = 2\frac{9}{16}$

This table is analogous to that constructed in a.v for locus a . From this table we obtain the values of the following effects:

$$\alpha_{b_1}^m = \frac{9}{16}, \alpha_{b_2}^m = -\frac{9}{16}, \alpha_{b_1}^f = \frac{9}{16}, \alpha_{b_2}^f = -\frac{9}{16}, \delta_{b_1b_1}^{mf} = \frac{1}{16}, \delta_{b_1b_2}^{mf} = -\frac{1}{16}, \delta_{b_2b_1}^{mf} = -\frac{1}{16}, \delta_{b_2b_2}^{mf} = \frac{1}{16}$$

Using the effects from these three tables we can construct the predicted genotypic value for each of the eight cells in the desired $2 \times 2 \times 2$ table for the additive (at locus a)-by-dominance (at locus b) effects. The desired predicted genotypic values are

$$\hat{G}_{i.kl} = \mu + \alpha_i^m + \alpha_k^m + \alpha_l^f + (\alpha\alpha)_{ik}^{mm} + (\alpha\alpha)_{il}^{mf} + \delta_{kl}^{mf}$$

$$\hat{G}_{1.11} = \frac{41}{16} + \frac{3}{16} + \frac{9}{16} + \frac{9}{16} - \frac{1}{16} - \frac{1}{16} + \frac{1}{16} = \frac{61}{16}$$

$$\hat{G}_{1.12} = \frac{41}{16} + \frac{3}{16} + \frac{9}{16} - \frac{9}{16} - \frac{1}{16} + \frac{1}{16} - \frac{1}{16} = \frac{43}{16}$$

$$\hat{G}_{1.21} = \frac{41}{16} + \frac{3}{16} - \frac{9}{16} + \frac{9}{16} + \frac{1}{16} - \frac{1}{16} - \frac{1}{16} = \frac{43}{16}$$

$$\hat{G}_{1.22} = \frac{41}{16} + \frac{3}{16} - \frac{9}{16} - \frac{9}{16} + \frac{1}{16} + \frac{1}{16} + \frac{1}{16} = \frac{29}{16}$$

$$\hat{G}_{2.11} = \frac{41}{16} - \frac{3}{16} + \frac{9}{16} + \frac{9}{16} + \frac{1}{16} + \frac{1}{16} + \frac{1}{16} = \frac{59}{16}$$

$$\hat{G}_{2.12} = \frac{41}{16} - \frac{3}{16} + \frac{9}{16} - \frac{9}{16} + \frac{1}{16} - \frac{1}{16} - \frac{1}{16} = \frac{37}{16}$$

$$\hat{G}_{2.21} = \frac{41}{16} - \frac{3}{16} - \frac{9}{16} + \frac{9}{16} - \frac{1}{16} + \frac{1}{16} - \frac{1}{16} = \frac{37}{16}$$

$$\hat{G}_{2.22} = \frac{41}{16} - \frac{3}{16} - \frac{9}{16} - \frac{9}{16} - \frac{1}{16} - \frac{1}{16} + \frac{1}{16} = \frac{19}{16}$$

For the desired $2 \times 2 \times 2$ table for the additive (at locus a)-by-dominance (at locus b) we present two 2×2 tables. The first 2×2 table is one for the $A^m \times B^m$ factors at the first level of the B^f factor, i.e., B_1^f . The second 2×2 table is one for the $A^m \times B^m$ factors at the second level of the B^f factor, i.e., B_2^f . The first 2×2 table at the B_1^f level is

	B_1^m	B_2^m	
A_1^m	$G_{1.11} = \frac{1}{2}4 + \frac{1}{2}4 = 4$	$G_{1.21} = \frac{1}{2}2 + \frac{1}{2}3 = 2\frac{1}{2}$	$G_{1..1} = \frac{1}{2}4 + \frac{1}{2}5 = 3\frac{1}{4}$
	$\hat{G}_{1.11} = \frac{61}{16}$	$\hat{G}_{1.21} = \frac{43}{16}$	
	$(\alpha\delta)_{111} = \frac{3}{16}$	$(\alpha\delta)_{121} = -\frac{3}{16}$	
A_2^m	$G_{2.11} = \frac{1}{2}4 + \frac{1}{2}3 = 3\frac{1}{2}$	$G_{2.21} = \frac{1}{2}3 + \frac{1}{2}2 = 2\frac{1}{2}$	$G_{2..1} = \frac{1}{2}7 + \frac{1}{2}5 = 3$
	$\hat{G}_{2.11} = \frac{59}{16}$	$\hat{G}_{2.21} = \frac{37}{16}$	
	$(\alpha\delta)_{211} = -\frac{3}{16}$	$(\alpha\delta)_{221} = \frac{3}{16}$	
	$G_{..11} = \frac{1}{2}4 + \frac{1}{2}7 = 3\frac{3}{4}$	$G_{..21} = \frac{1}{2}5 + \frac{1}{2}5 = 2\frac{1}{2}$	$G_{..2} = \frac{1}{2}13 + \frac{1}{2}3 = 3\frac{1}{8}$

The second 2×2 table at the B_2^f level is

	B_1^m	B_2^m	
A_1^m	$G_{1.12} = \frac{1}{2}2 + \frac{1}{2}3 = 2\frac{1}{2}$	$G_{1.22} = \frac{1}{2}3 + \frac{1}{2}1 = 2$	$G_{2..1} = \frac{1}{2}\frac{5}{2} + \frac{1}{2}2 = 2\frac{1}{4}$
	$\hat{G}_{1.12} = \frac{43}{16}$	$\hat{G}_{1.22} = \frac{29}{16}$	
	$(\alpha\delta)_{112} = -\frac{3}{16}$	$(\alpha\delta)_{122} = \frac{3}{16}$	
A_2^m	$G_{2.12} = \frac{1}{2}3 + \frac{1}{2}2 = 2\frac{1}{2}$	$G_{2.22} = \frac{1}{2}1 + \frac{1}{2}1 = 1$	$G_{2..2} = \frac{1}{2}\frac{5}{2} + \frac{1}{2}1 = 1\frac{3}{4}$
	$\hat{G}_{2.12} = \frac{37}{16}$	$\hat{G}_{2.22} = \frac{19}{16}$	
	$(\alpha\delta)_{212} = \frac{3}{16}$	$(\alpha\delta)_{222} = -\frac{3}{16}$	
	$G_{..11} = \frac{1}{2}\frac{5}{2} + \frac{1}{2}\frac{5}{2} = 2\frac{1}{2}$	$G_{..22} = \frac{1}{2}2 + \frac{1}{2}1 = 1\frac{1}{2}$	$G_{...2} = \frac{1}{2}\frac{9}{4} + \frac{1}{2}\frac{7}{4} = 2$

Then

$$\sigma_{(\alpha\delta)_{abb}^{mmf}}^2 = \frac{1}{8}\left(\frac{3}{16}\right)^2 + \frac{1}{8}\left(-\frac{3}{16}\right)^2 + \frac{1}{8}\left(-\frac{3}{16}\right)^2 + \frac{1}{8}\left(\frac{3}{16}\right)^2 + \frac{1}{8}\left(-\frac{3}{16}\right)^2 + \frac{1}{8}\left(\frac{3}{16}\right)^2 + \frac{1}{8}\left(\frac{3}{16}\right)^2 + \frac{1}{8}\left(-\frac{3}{16}\right)^2 = \left(\frac{3}{16}\right)^2 = \frac{9}{256}$$

Since $p_i^m = p_i^f$, $\sigma_{(\alpha\delta)_{abb}^{mmf}}^2 = \sigma_{(\alpha\delta)_{abb}^{fmf}}^2$, $\sigma_{AD}^2 = \sigma_{(\alpha\delta)_{abb}^{mmf}}^2 + \sigma_{(\alpha\delta)_{abb}^{fmf}}^2 = 2\left(\frac{9}{256}\right) = \frac{18}{256}$

Check:

check i. $\sigma_G^2 = \sigma_{y_a}^2 + \sigma_{y_b}^2 + \sigma_{yy_{ab}}^2 = \frac{27}{256} + \frac{163}{256} + \frac{65}{256} = \frac{255}{256}$

check ii. $\sigma_{y_a}^2 = \sigma_{A_a}^2 + \sigma_{D_a}^2 = \frac{18}{256} + \frac{9}{256} = \frac{27}{256}$

b.i. Additive variance at locus b by the computing formula, equation (8.51), is (see marginal column means in first 3×3 diagram above)

$$\begin{aligned} \sigma_{A_b}^2 &= 2p_1p_2 \left[p_1(G_{11} - G_{12}) + p_2(G_{12} - G_{22}) \right]^2 \\ &= 2\left(\frac{1}{2}\right)\left(\frac{1}{2}\right) \left[\frac{1}{2}\left(\frac{15}{4} - \frac{5}{2}\right) + \frac{1}{2}\left(\frac{5}{2} - \frac{3}{2}\right) \right]^2 = \frac{1}{2} \left[\frac{1}{2}\left(\frac{5}{4}\right) + \frac{1}{2}\left(\frac{2}{2}\right) \right]^2 = \frac{81}{128} \end{aligned}$$

b.ii. Dominance variance at locus b by the computing formula, equation (8.52) is (see marginal column means in first 3×3 diagram above)

$$\begin{aligned} \sigma_{D_b}^2 &= p_1^2 p_2^2 \left[2G_{12} - G_{11} - G_{22} \right]^2 \\ &= \left(\frac{1}{2}\right)^2 \left(\frac{1}{2}\right)^2 \left[2\left(\frac{5}{2}\right) - \frac{15}{4} - \frac{3}{2} \right]^2 = \frac{1}{16} \left[\frac{20-15-6}{4} \right]^2 = \frac{1}{256} \end{aligned}$$

b.iii. Additive-by-additive variance by the computing formula, equation (8.163a), is

$$\begin{aligned} \sigma_{AA_{ab}}^2 &= 4p_{A_1}p_{A_2}p_{B_1}p_{B_2} \left(p_{A_1}p_{B_1}e_{11} + p_{A_1}p_{B_2}e_{12} + p_{A_2}p_{B_1}e_{21} + p_{A_2}p_{B_2}e_{22} \right)^2 \\ &= 4\left(\frac{1}{2}\right)\left(\frac{1}{2}\right)\left(\frac{1}{2}\right)\left(\frac{1}{2}\right) \left[\frac{1}{2}\left(\frac{1}{2}\right)(4-2-4+3) + \frac{1}{2}\left(\frac{1}{2}\right)(2-3-3+1) + \frac{1}{2}\left(\frac{1}{2}\right)(4-3-3+2) + \frac{1}{2}\left(\frac{1}{2}\right)(3-1-2+1) \right]^2 \\ &= \frac{1}{4} \left[\frac{1}{4}(1) + \frac{1}{4}(-3) + \frac{1}{4}(0) + \frac{1}{4}(1) \right]^2 = \frac{1}{64} \end{aligned}$$

b.iv. Additive (at locus a)-by-dominance (at locus b) variance by the computing formula, equation (8.163b), is

$$\begin{aligned}\sigma_{AD_{ab}}^2 &= 2p_{A_1}p_{A_2}p_{B_1}^2p_{B_2}^2 \left[p_{A_1}(e_{11} - e_{12}) + p_{A_2}(e_{21} - e_{22}) \right]^2 \\ &= 2\left(\frac{1}{2}\right)\left(\frac{1}{2}\right)\left(\frac{1}{4}\right)\left(\frac{1}{4}\right) \left[\frac{1}{2}(1 - (-3)) + \frac{1}{2}(0 - 1) \right]^2 = \frac{1}{32} \left[2 - \frac{1}{2} \right]^2 = \frac{9}{128}\end{aligned}$$

b.v. Dominance (at locus a)-by-additive (at locus b) variance by the computing formula, equation (8.163c) is

$$\begin{aligned}\sigma_{DA_{ab}}^2 &= 2p_{A_1}^2p_{A_2}^2p_{B_1}p_{B_2} \left[p_{B_1}(e_{11} - e_{21}) + p_{B_2}(e_{12} - e_{22}) \right]^2 \\ &= 2\left(\frac{1}{4}\right)\left(\frac{1}{4}\right)\left(\frac{1}{2}\right)\left(\frac{1}{2}\right) \left[\frac{1}{2}(1 - 0) + \frac{1}{2}((-3) - 1) \right]^2 = \frac{1}{32} \left[\frac{1}{2} - \frac{4}{2} \right]^2 = \frac{9}{128}\end{aligned}$$

b.vi. Dominance-by-dominance variance by the computing formula, equation (8.163d), is

$$\begin{aligned}\sigma_{DD_{ab}}^2 &= p_{A_1}^2p_{A_2}^2p_{B_1}^2p_{B_2}^2 \left[e_{11} - e_{12} - e_{21} + e_{22} \right]^2 \\ &= \left(\frac{1}{4}\right)\left(\frac{1}{4}\right)\left(\frac{1}{4}\right)\left(\frac{1}{4}\right) \left[1 - (-3) - 0 + 1 \right]^2 = \frac{25}{256}\end{aligned}$$

Checks:

$$\text{check iii. } \sigma_{y_b}^2 = \sigma_{A_b}^2 + \sigma_{D_b}^2 = \frac{81}{128} + \frac{1}{256} = \frac{163}{256}$$

$$\text{check iv. } \sigma_{yy_{ab}}^2 = \sigma_{AA_{ab}}^2 + \sigma_{AD_{ab}}^2 + \sigma_{DA_{ab}}^2 + \sigma_{DD_{ab}}^2 = \frac{1}{64} + \frac{9}{128} + \frac{9}{128} + \frac{25}{256} = \frac{65}{256}$$

c.i. The total additive variance is

$$\sigma_A^2 = \sigma_{A_a}^2 + \sigma_{A_b}^2 = \frac{18}{256} + \frac{81}{128} = \frac{9}{128} + \frac{81}{128} = \frac{90}{128} = \frac{45}{64}$$

c.ii. The total dominance variance is

$$\sigma_D^2 = \sigma_{D_a}^2 + \sigma_{D_b}^2 = \frac{9}{256} + \frac{1}{256} = \frac{10}{256} = \frac{5}{128}$$

c.iii. The epistatic variance is

$$\sigma_I^2 = \sigma_G^2 - \sigma_A^2 - \sigma_D^2 = \frac{255}{256} - \frac{45}{64} - \frac{5}{128} = \frac{255}{256} - \frac{180}{256} - \frac{10}{256} = \frac{65}{256}$$

Exercise 8.14.

a.	B_1B_1	B_1B_2	B_2B_2
	$2s$	$s - r$	$-2r$
	r^2	$2rs$	s^2
A_1A_1	G_{22}	G_{21}	G_{20}
p^2	$4qs$	$2q(s - r)$	$-4qr$
$2q$	p^2r^2	$2p^2rs$	p^2s^2
A_1A_2	G_{12}	G_{11}	G_{10}
$2pq$	$2(q - p)s$	$(q - p)(s - r)$	$-2(q - p)r$
$q - p$	$2pqr^2$	$4pqrs$	$2pqs^2$
A_2A_2	G_{02}	G_{01}	G_{00}
q^2	$-4ps$	$-2p(s - r)$	$4pr$
$-2p$	q^2r^2	$2q^2rs$	q^2s^2

b.

$$\begin{aligned}
\text{cov}(c_{12}, G) &= p^2 r^2 (4qs)G_{22} + 2p^2 rs [2q(s-r)]G_{21} + p^2 s^2 (-4qr)G_{20} \\
&\quad (qs - qr - ps + pr) \\
&\quad + 2pqr^2 [2(q-p)s]G_{12} + 4pqrs [(q-p)(s-r)]G_{11} + 2pqs^2 [-2(q-p)r]G_{10} \\
&\quad + q^2 r^2 (-4ps)G_{02} + 2q^2 rs [-2p(s-r)]G_{01} + q^2 s^2 (4pr)G_{00} \\
&= 4p^2 \overset{11}{qr^2 s} G_{22} + 4p^2 \overset{12}{qrs^2} G_{21} - 4p^2 \overset{11}{qr^2 s} G_{21} - 4p^2 \overset{12}{qrs^2} G_{20} \\
&\quad + 4p \overset{21}{q^2 r^2 s} G_{12} - 4p^2 \overset{11}{qr^2 s} G_{12} \\
&\quad + 4p \overset{22}{q^2 rs^2} G_{11} - 4p \overset{21}{q^2 r^2 s} G_{11} - 4p^2 \overset{12}{qrs^2} G_{11} + 4p^2 \overset{11}{qr^2 s} G_{11} \\
&\quad - 4p \overset{21}{q^2 rs^2} G_{10} + 4p^2 \overset{12}{qrs^2} G_{10} \\
&\quad - 4p \overset{21}{q^2 r^2 s} G_{02} - 4p \overset{22}{q^2 rs^2} G_{01} + 4p \overset{21}{q^2 r^2 s} G_{01} + 4p \overset{22}{q^2 rs^2} G_{00} \\
&= 4pqrs \left\{ \left[\overset{21}{pr} G_{22} - \overset{21}{pr} G_{21} - \overset{21}{pr} G_{12} + \overset{21}{pr} G_{11} \right] + \left[\overset{22}{ps} G_{21} - \overset{22}{ps} G_{20} - \overset{22}{ps} G_{11} + \overset{22}{ps} G_{10} \right] \right\} \\
&\quad + 4pqrs \left\{ \left[\overset{21}{qr} G_{12} - \overset{21}{qr} G_{11} - \overset{21}{qr} G_{02} + \overset{21}{qr} G_{01} \right] + \left[\overset{22}{qs} G_{11} - \overset{22}{qs} G_{10} - \overset{22}{qs} G_{01} + \overset{22}{qs} G_{00} \right] \right\} \\
&= 4pqrs \left\{ \begin{aligned} &pr(G_{22} - G_{21} - G_{12} + G_{11}) + ps(G_{21} - G_{20} - G_{11} + G_{10}) \\ &+ qr(G_{12} - G_{11} - G_{02} + G_{01}) + qs(G_{11} - G_{10} - G_{01} + G_{00}) \end{aligned} \right\} \\
&= 4pqrs (pre_{11} + pse_{12} + qre_{21} + qse_{22})
\end{aligned}$$

c. Note: The subscript 12 on c follows the notation in statistics of linear (additive) for factor 1 (locus A) and linear (additive) for factor 2 (locus B). The quadratic (dominance) for factor 1 would be denoted by two 1s.

$$\begin{aligned}
&= 16p^2 q^2 r^2 s^2 + 8p^2 q^2 rs (s^2 - 2sr + r^2) + 16p^2 q^2 r^2 s^2 \\
&\quad + 8pqr^2 s^2 (q^2 - 2qp + p^2) + 4pqrs (q^2 - 2pq + p^2) (s^2 - 2rs + r^2) + 8pqr^2 s^2 (q^2 - 2pq + p^2) \\
&\quad + 16p^2 q^2 r^2 s^2 + 8p^2 q^2 rs (s^2 - 2rs + r^2) + 16p^2 q^2 r^2 s^2 \\
&= 4pqrs \left[\begin{aligned} &4pqrs + 2pq(s^2 - 2sr + r^2) + 4pqrs \\ &+ 2rs(q^2 - 2pq + p^2) + (q^2 - 2pq + p^2)(s^2 - 2rs + r^2) + 2rs(q^2 - 2pq + p^2) \\ &+ 4pqrs + 2pq(s^2 - 2rs + r^2) + 4pqrs \end{aligned} \right]
\end{aligned}$$

$$\begin{aligned}
&= 4pqrs \left[16pqrs + 4pq(s^2 - 2sr + r^2) + 4rs(q^2 - 2pq + p^2) + (q^2 - 2pq + p^2)(s^2 - 2rs + r^2) \right] \\
&= 4pqrs \left[16pqrs + 4pq(s^2 - 2sr + r^2) + 4q^2rs - 8pqrs + 4p^2rs + (q^2 - 2pq + p^2)(s^2 - 2rs + r^2) \right] \\
&= 4pqrs \left[\begin{array}{cccccccccc} 16pqrs & + & 4pqs^2 & - & 8pqrs & + & 4pqr^2 & + & 4q^2rs & - & 8pqrs & + & 4p^2rs \\ + & q^2s^2 & - & 2q^2rs & + & q^2r^2 & - & 2pqs^2 & + & 4pqrs & - & 2pqr^2 & + & p^2s^2 & - & 2p^2rs & + & p^2r^2 \end{array} \right] \\
&= 4pqrs \left[\begin{array}{cccccccccc} 2pqs^2 & + & 2pqr^2 & + & 2q^2rs & + & 2p^2rs & + & q^2s^2 & + & q^2r^2 & + & 4pqrs & + & p^2s^2 & + & p^2r^2 \end{array} \right] \\
&= 4pqrs \left[\begin{array}{cccccccccc} p^2 & (r^2 & + & 2rs & + & s^2) & + & 2pq & (r^2 & + & 2rs & + & s^2) & + & q^2 & (r^2 & + & 2rs & + & s^2) \end{array} \right] \\
&= 4pqrs \left[(p^2 + 2pq + q^2)(r^2 + 2rs + s^2) \right] \\
&= 4pqrs
\end{aligned}$$

d.

$$\begin{aligned}
\text{regression coefficient} = \alpha_{1,2} &= \frac{\text{cov}(c_{12}, G)}{\sigma_{c_{12}}^2} = \frac{4pqrs(pre_{11} + pse_{12} + qre_{21} + qse_{22})}{4pqrs} \\
&= pre_{11} + pse_{12} + qre_{21} + qse_{22}
\end{aligned}$$

e.

$$\begin{aligned}
\sigma_{AA}^2 &= \alpha_{1,2} \text{cov}(c_{12}, G) = \frac{\text{cov}(c_{12}, G)}{\sigma_{c_{12}}^2} \text{cov}(c_{12}, G) = \frac{[\text{cov}(c_{12}, G)]^2}{\sigma_{c_{12}}^2} \\
&= \frac{[4pqrs(pre_{11} + pse_{12} + qre_{21} + qse_{22})]^2}{4pqrs} \\
&= 4pqrs(pre_{11} + pse_{12} + qre_{21} + qse_{22})^2
\end{aligned}$$

which is equation (8.163a).

Exercise 8.15.

a. We construct the following diagram so that we can calculate the gametic values.

	A ₁ B ₁ 0.25	A ₁ B ₂ 0.25	A ₂ B ₁ 0.25	A ₂ B ₂ 0.25	
A ₁ B ₁ 0.25	G ₁₁₁₁ 4	G ₁₁₁₂ 4	G ₁₂₁₁ 4	G ₁₂₁₂ 4	G _{1.1.} = 4
A ₁ B ₂ 0.25	G ₁₁₂₁ 4	G ₁₁₂₂ 2	G ₁₂₂₁ 4	G ₁₂₂₂ 2	G _{1.2.} = 3
A ₂ B ₁ 0.25	G ₂₁₁₁ 4	G ₂₁₁₂ 4	G ₂₂₁₁ 2	G ₂₂₁₂ 2	G _{2.1.} = 3
A ₂ B ₂ 0.25	G ₂₁₂₁ 4	G ₂₁₂₂ 2	G ₂₂₂₁ 2	G ₂₂₂₂ 2	G _{2.2.} = 2.5

$$G_{\dots} = \frac{9}{16}(4) + \frac{7}{16}(2) = \frac{50}{16} = \frac{25}{8} = 3.125$$

$$\sigma_g^2 = \frac{1}{4}(4)^2 + \frac{1}{2}(3)^2 + \frac{1}{4}(2.5)^2 - (3.125)^2 = 4 + \frac{9}{2} + \frac{25}{16} - \left(\frac{25}{8}\right)^2 = \frac{256+288+100-625}{64} = \frac{19}{64} = 0.296875$$

b.i. We construct the following diagram for the case of linkage disequilibrium so that we can calculate the overall mean.

	A ₁ B ₁ 0.35	A ₁ B ₂ 0.15	A ₂ B ₁ 0.15	A ₂ B ₂ 0.35	
A ₁ B ₁ 0.35	G ₁₁₁₁ 4 0.1225	G ₁₁₁₂ 4 0.0525	G ₁₂₁₁ 4 0.0525	G ₁₂₁₂ 4 0.1225	G _{1.1.} = 4
A ₁ B ₂ 0.15	G ₁₁₂₁ 4 0.0525	G ₁₁₂₂ 2 0.0225	G ₁₂₂₁ 4 0.0225	G ₁₂₂₂ 2 0.0525	G _{1.2.} = 3
A ₂ B ₁ 0.15	G ₂₁₁₁ 4 0.0525	G ₂₁₁₂ 4 0.0225	G ₂₂₁₁ 2 0.0225	G ₂₂₁₂ 2 0.0525	G _{2.1.} = 3
A ₂ B ₂ 0.35	G ₂₁₂₁ 4 0.1225	G ₂₁₂₂ 2 0.0525	G ₂₂₂₁ 2 0.0525	G ₂₂₂₂ 2 0.1225	G _{2.2.} = 2.7

G_{....} = 3.245

$$G_{\dots} = [3(0.1225) + 4(0.0525) + 2(0.0225)]4 + [1(0.1225) + 4(0.0525) + 2(0.0225)]2 = 3.245$$

We can also calculate the overall mean from equation (8.171):

$$\begin{aligned}
G_{\dots} &= \hat{G}_{\dots} + 2\Delta \sum_i \sum_k p_{A_i} p_{B_k} e_{ik} + \Delta^2 (e_{11} - e_{12} - e_{21} + e_{22}) \\
&= 3.125 + 2(0.10) \left[\frac{1}{4}(0) + \frac{1}{4}(0) + \frac{1}{4}(0) + \frac{1}{4}(2) \right] + (0.10)^2 (0 - 0 - 0 + 2) \\
&= 3.125 + 0.20 \frac{1}{2} + (0.01)2 \\
&= 3.125 + 0.10 + 0.02 \\
&= 3.245
\end{aligned}$$

Yes, the mean has changed because both linkage disequilibrium and epistasis exist.

b.ii. The genetic gametic variance is

$$\begin{aligned}
\sigma_g^2 &= 0.35(4)^2 + 0.15(3)^2 + 0.15(3)^2 + 0.35(2.7)^2 - (3.245)^2 \\
&= 10.8515 - 10.530025 \\
&= 0.321475
\end{aligned}$$

Exercise 8.16.

a. The genic factorial model for this situation is

$$G_{ijkl} = \mu + \alpha_{ai}^m + \alpha_{aj}^f + \delta_{aij} + \alpha_{bk}^m + \alpha_{bl}^f + \delta_{bkl}$$

b. The variance of each term in the model, calculated by definition, is:

For the A locus:

	A ₁	A ₂	
A ₁	5.5 5 $\delta_{11} = +0.5$	3.5 4 $\delta_{12} = -0.5$	4.5 $\alpha_1 = +0.5$
A ₂	3.5 4 $\delta_{12} = -0.5$	3.5 3 $\delta_{22} = +0.5$	3.5 $\alpha_2 = -0.5$
	4.5 $\alpha_1 = +0.5$	3.5 $\alpha_2 = -0.5$	4

$$\sigma_{\alpha_a^m}^2 = \frac{1}{2}(+0.5)^2 + \frac{1}{2}(-0.5)^2 = \frac{1}{8} + \frac{1}{8} = \frac{1}{4}$$

$$\alpha_a^f = \frac{1}{4}$$

$$\sigma_{\delta_a}^2 = \frac{1}{4}(+0.5)^2 + \frac{1}{4}(-0.5)^2 + \frac{1}{4}(-0.5)^2 + \frac{1}{4}(+0.5)^2 = \frac{1}{4}$$

For the B locus: A diagram similar to that for the A locus can be set up, and it is observed that the corresponding variances are the same as for the A locus, namely,

$$\alpha_b^m = \frac{1}{4}$$

$$\alpha_b^f = \frac{1}{4}$$

$$\sigma_{\delta_b}^2 = \frac{1}{4}$$

c. The total genotypic variance can be calculated by simply adding the six variances in (b) together. The linear combination theorem for independent random variables permits the addition. The minimal genetic conditions which must exist for the application of the theorem is random mating and linkage equilibrium. These two genetic conditions insure independence between all of the six terms.

d. If the population represented an F_2 population, the minimal genetic condition to insure the application of the linear combination theorem is independence between the two loci, i.e., for the two loci to be located on two separate chromosomes. This insures linkage equilibrium in the F_2 population [see equation (3.102)]. Random mating is also required, but random mating always occurs for an F_2 population.

e. If selection were initiated in both directions, the expected response would be the same in both directions. The nature of locus A for earliness with respect to genetic variances (additive and total genotypic, and allelic frequencies) is equivalent to locus B for lateness, and likewise the nature of locus B for earliness with respect to genetic variances (additive and total genotypic, and allelic frequencies) is equivalent to locus A for lateness.

f. The frequencies of both A_2 and B_2 would increase, but the increase in frequency of A_2 , the dominant allele, would be less than that for B_2 , the recessive allele, assuming initial allelic frequencies of $1/2$ for both loci. That is, the frequency of the recessive allele B_2 would be greater than the frequency of the dominant allele A_2 .

Exercise 8.17.

a. The theorem states that if one has a linear combination $Y_i = \sum_{j=1}^n c_j X_{ij}$ of n different random variables

with variances $\sigma_1^2, \dots, \sigma_j^2, \dots, \sigma_n^2$, then the variance of the linear combination is $\sigma_Y^2 = \sum_{j=1}^n c_j^2 \sigma_j^2$ when all the

random variables are uncorrelated. If the variables are correlated, then the variance of the linear combination Y is

$$\sigma_Y^2 = \sum_{j=1}^n c_j^2 \sigma_j^2 + 2 \sum_{j=1}^n \sum_{\substack{j'=1 \\ j < j'}}^n c_j c_{j'} \text{cov}(X_j, X_{j'})$$

b. The theorem is extremely important in statistical genetics because we deal with many variables. The exact relation among these variables is unknown, but we usually assume that they have a linear relationship, i.e., one variable can be expressed as a linear combination of several other variables. Estimation of the variance of different variables is a common important task in statistical genetics, so the variance of the linear combination theorem is frequently used in estimating variances.

c. Some examples of the application of the linear combination theorem for uncorrelated variables are:
Phenotypic variance

$$P = G + E \quad \text{equation (8.1)--} G \text{ is assumed to be uncorrelated with } E$$

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2$$

Genotypic variance

1. One locus, random mating so α^m and α^f are uncorrelated

i. $p_i^m \neq p_i^f$ Section 8.1.1--two populations crossed

$$G_{ij} = \mu + \alpha_i^m + \alpha_j^f + \delta_{ij}$$

$$\sigma_G^2 = \sigma_{\alpha^m}^2 + \sigma_{\alpha^f}^2 + \sigma_{\delta}^2 \quad \text{equation (8.22)}$$

ii. $p_i^m = p_i^f$ Section 8.1.2--one population

$$G_{ij} = \mu + \alpha_i^m + \alpha_j^f + \delta_{ij}$$

$$\sigma_G^2 = 2\sigma_\alpha^2 + \sigma_\delta^2 \quad \text{equation (8.29)}$$

2. Two or more loci, random mating, no epistasis, and linkage equilibrium so all α^m effects are uncorrelated, all α^f effects are uncorrelated, and all δ effects are uncorrelated as well as the individual total-locus effects are uncorrelated

i. $p_i^m \neq p_i^f$ Section 8.1.6--two populations crossed

$$G = \mu + \sum_{k=1}^n (\alpha_k^m + \alpha_k^f + \delta_k)$$

$$\sigma_G^2 = \sum_{k=1}^n \sigma_{\alpha_k^m}^2 + \sum_{k=1}^n \sigma_{\alpha_k^f}^2 + \sum_{k=1}^n \sigma_{\delta_k}^2$$

ii. $p_i^m = p_i^f$ Section 8.1.7--one population

$$G = \mu + \sum_{k=1}^n (\alpha_k^m + \alpha_k^f + \delta_k)$$

$$\sigma_G^2 = 2 \sum_{k=1}^n \sigma_{\alpha_k}^2 + \sum_{k=1}^n \sigma_{\delta_k}^2$$

3. Two loci, random mating, epistasis, linkage equilibrium so different epistatic effects are uncorrelated

i. $p_i^m \neq p_i^f$ Section 8.3.1--two populations crossed

$$\begin{aligned} \sigma_G^2 = & \sigma_{\alpha_a^m}^2 + \sigma_{\alpha_a^f}^2 + \sigma_{\delta_a}^2 + \sigma_{\alpha_b^m}^2 + \sigma_{\alpha_b^f}^2 + \sigma_{\delta_b}^2 + \sigma_{(\alpha\alpha)_{ab}^{mm}}^2 + \sigma_{(\alpha\alpha)_{ab}^{mf}}^2 + \sigma_{(\alpha\alpha)_{ab}^{fm}}^2 + \sigma_{(\alpha\alpha)_{ab}^{ff}}^2 \\ & + \sigma_{(\alpha\delta)_{abb}^{mmf}}^2 + \sigma_{(\alpha\delta)_{abb}^{fmf}}^2 + \sigma_{(\delta\alpha)_{aab}^{mfm}}^2 + \sigma_{(\delta\alpha)_{aab}^{mff}}^2 + \sigma_{(\delta\delta)_{abab}^{mfmf}}^2 \end{aligned}$$

ii. $p_i^m = p_i^f$ Section 8.3.2--one population

$$\sigma_G^2 = 2\sigma_{\alpha_a}^2 + \sigma_{\delta_a}^2 + 2\sigma_{\alpha_b}^2 + \sigma_{\delta_b}^2 + 4\sigma_{(\alpha\alpha)_{ab}}^2 + 2\sigma_{(\alpha\delta)_{ab}}^2 + 2\sigma_{(\delta\alpha)_{ab}}^2 + \sigma_{(\delta\delta)_{ab}}^2$$

4. Two or more traits, indexes, one locus, random mating, no epistasis

i. $p_i^m \neq p_i^f$ Section 8.4.2.1 --two populations crossed

$$I = b_1 G_1 + b_2 G_2 \quad \text{equation (8.192)}$$

$$\sigma_I^2 = \sigma_{\alpha_I^m}^2 + \sigma_{\alpha_I^f}^2 + \sigma_{\delta_I}^2 \quad \text{equation (8.194)}$$

ii. $p_i^m = p_i^f$ Section 8.4.2.2 --one population

$$\sigma_I^2 = 2\sigma_{\alpha_I}^2 + \sigma_{\delta_I}^2 \quad \text{equation (8.195)}$$

There are many other applications of the linear combination theorem of uncorrelated variables.

Some examples of the application of the linear combination theorem for correlated variables are:

Phenotypic variance

$$P = G + E \quad \text{equation (8.1)--G is assumed to be correlated with E}$$

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + 2\text{cov}(G, E)$$

Genotypic variance

1. One locus, nonrandom mating so α^m and α^f are correlated

- i. $p_i^m \neq p_i^f$ Section 8.1.1--two populations crossed

$$G_{ij} = \mu + \alpha_i^m + \alpha_j^f + \delta_{ij}$$

$$\sigma_G^2 = \sigma_{\alpha^m}^2 + \sigma_{\alpha^f}^2 + \sigma_{\delta}^2 + 2 \operatorname{cov}(\alpha^m, \alpha^f) + 2 \operatorname{cov}(\alpha^m, \delta) + 2 \operatorname{cov}(\alpha^f, \delta)$$

- ii. $p_i^m = p_i^f$ Section 8.1.2--one population

$$G_{ij} = \mu + \alpha_i^m + \alpha_j^f + \delta_{ij}$$

$$\sigma_G^2 = 2\sigma_{\alpha}^2 + \sigma_{\delta}^2 + 2 \operatorname{cov}(\alpha^m, \alpha^f) + 2 \left[2 \operatorname{cov}(\alpha^m, \delta) \right]$$

2. Two or more locus, random mating so α^m and α^f are uncorrelated, no epistasis, linkage disequilibrium

- i. $p_i^m \neq p_i^f$ Section 8.1.6--two populations crossed

$$y_k = \mu_k + \alpha_k^m + \alpha_k^f + \delta_k$$

$$\sigma_G^2 = \sum_{k=1}^n \sigma_{y_k}^2 + 2 \sum_k \sum_{\substack{k' \\ k < k'}} \operatorname{cov}(y_k, y_{k'})$$

- ii. $p_i^m = p_i^f$ Section 8.1.7--one population

$$y_k = \mu_k + \alpha_k^m + \alpha_k^f + \delta_k$$

$$\sigma_G^2 = \sum_{k=1}^n \sigma_{y_k}^2 + 2 \sum_k \sum_{\substack{k' \\ k < k'}} \operatorname{cov}(y_k, y_{k'})$$

3. Two or more loci, random mating, epistasis, linkage disequilibrium

Gametic effect

$$g^m = \sum_{k=1}^n \alpha_k^m + \sum_{k=1}^n (\alpha\alpha)_k^m + \dots$$

$$\sigma_{g^m}^2 = \sigma_{A^m}^2 + \sigma_{AA^m}^2 + \dots + \text{all possible covariances between epistatic effects}$$

4. Two loci, two alleles, random mating, no epistasis

$$\sigma_g^2 = \sigma_{\alpha_a}^2 + \sigma_{\alpha_b}^2 + \frac{2\Delta}{\sqrt{p_{A_1} p_{A_1} p_{B_1} p_{B_1}}} \sigma_{\alpha_a} \sigma_{\alpha_b} = \sigma_{\alpha_a}^2 + \sigma_{\alpha_b}^2 + 2 \operatorname{cov}(\alpha_a, \alpha_b) \quad \text{equation (8.173)}$$

Exercise 8.18.

The genic factorial model provides the framework whereby all effects and variances are defined. The genic factorial model treats gene action involving several loci as a factorial experiment with several factors. This allows one to use the ideas of factorial experiments, as exists in statistics, and apply them to genetics using the simultaneous inheritance of Mendelian factors. It allows complex genetic interactions to be reduced to a linear model which is fitted to the genotypic values in terms of additive, dominance, and epistatic gene effects, corresponding to main effects of factors and to the interactions between various factors. See Chapter 8, particularly equation (8.2) for a two-factor (one-locus) model, equation (8.128) for a four-factor (two-locus) model with all possible interactions, and equation (8.175) for a multiple-factor (n-locus) model with all possible interactions.

There are many assumptions involving the genic factorial model, but probably the three most important assumptions are random mating, linkage equilibrium, and no linkage between loci.

Exercise 8.19.

In discussing the question “Is heredity or environment more important?”, one must define the trait, have a proper measure of variation (variance), measure in principle the environmental variance for a fixed genotype, measure in principle the genotypic variance for a fixed environment, add the two variances together only if the genotypic and environmental variables are independent, and form the ratio $\sigma_G^2 / (\sigma_G^2 + \sigma_E^2) = H$ which is the broad-sense heritability. It is a measure from zero to one where zero would indicate no genetic variation for the trait whereas one would indicate no environmental variation for the trait.