Agronomy 615
Statistical Genetics
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SOLUTIONS TO EXERCISES FOR CHAPTER 12

Exercise 12.1.

N0TE: Although the basis for the solution to this exercise is discussed in Chapter 12, a much better, more polished and accurate presentation is given in my heritability article in Critical Rev. Plant Sci. 10:235-322, 1991, Section VII.B.1.c. This article was written many years after I wrote Chapter 12. I suggest that for the solution to this exercise we follow my heritability article where I equate Cov(X_f, Y) = Cov(X_m, Y) and the total covariance as Cov(X, Y) = 2Cov(X_f, Y) = 2Cov(X_m, Y). In contrast, in Chapter 12 I equate Cov(X_m, Y) = Cov(X_f, Y) = Cov(X, Y) [equations (12.40), (12.47), (12.50)]. I like what I did in my heritability article, for it is clearer.

a. For this part, see my heritability article, Section VII.B.1.c.ii.(a).(i), Half-sib, remnant-seed method, pp. 274-275. Referring to Fig. 1(b), p. 274 in my heritability article, we first calculate Cov(X_f, Y). I give what Cov(X_f, Y) is equal to in equation [48] for a *noninbred* parent P_f of a family [same as parent A_f in equation (12.49)]. The generalized expression for an *inbred* parent P_f is [equation (12.50) and above]

$$\begin{aligned}\operatorname{Cov}\left(X_f, Y\right) &= 2\theta_{X_f Y}\sigma_A^2 + \left(2\theta_{X_f Y}\right)^2 \sigma_{AA}^2 + \cdots \\ &= 2\left(\tfrac{1+F_P}{16}\right)\sigma_A^2 + \left(\tfrac{2(1+F_P)}{16}\right)^2 \sigma_{AA}^2 + \cdots \\ &= \left(\tfrac{1+F_P}{8}\right)\sigma_A^2 + \left(\tfrac{1+F_P}{8}\right)^2 \sigma_{AA}^2 + \cdots\end{aligned}$$

For our exercise, assuming all higher-order epistatic components, except σ_{AA}^2, equal zero, we have

$$\begin{aligned}\operatorname{Cov}\left(X_f, Y\right) &= \left(\frac{1+\frac{1}{2}}{8}\right)\sigma_A^2 + \left(\frac{1+\frac{1}{2}}{8}\right)^2 \sigma_{AA}^2 \\ &= \tfrac{3}{16}\sigma_A^2 + \left(\tfrac{3}{16}\right)^2 \sigma_{AA}^2 = \tfrac{3}{16}\sigma_A^2 + \tfrac{9}{256}\sigma_{AA}^2\end{aligned}$$

Next we calculate the half-sib family component [see equation (12.34)] because it is required in the denominator of the selection response equation:

$$\begin{aligned}\sigma_F^2 = \sigma_{\text{Half-sib families}}^2 &= 2\theta_{XY}\sigma_A^2 + \left(2\theta_{XY}\right)^2 \sigma_{AA}^2 \quad \text{[see equation (9.144) and Table 9.5, p. 9.52]} \\ &= \left(\frac{1+F_A}{4}\right)\sigma_A^2 + \left[\frac{1+F_A}{4}\right]^2 \sigma_{AA}^2 \\ &= \left(\frac{1+\frac{1}{2}}{4}\right)\sigma_A^2 + \left[\frac{\left(1+\frac{1}{2}\right)}{4}\right]^2 \sigma_{AA}^2 \\ &= \tfrac{3}{8}\sigma_A^2 + \left(\tfrac{3}{8}\right)^2 \sigma_{AA}^2 = \tfrac{3}{8}(3) + \tfrac{9}{64}(1) = \tfrac{9}{8} + \tfrac{9}{64} = \tfrac{81}{64}\end{aligned}$$

Then the selection response equation is (equation [49])

$$R_{1(a)}=\frac{2\text{Cov}\left(X_f,Y\right)}{\sigma_{\bar{X}}}i=\frac{2\left[\frac{3}{16}\sigma_A^2+\frac{9}{256}\sigma_{AA}^2\right]}{\sqrt{\frac{\sigma_E^2+\sigma_G^2-\sigma_F^2}{nr}+\frac{\sigma_\varepsilon^2}{r}+\sigma_F^2}}\left(1.75\right)$$ [R_1 (=Δ) is the response in my heritability article.]

$$=\frac{2\left[\frac{3}{16}(3)+\frac{9}{256}(1)\right]}{\sqrt{\frac{1+6-\frac{81}{64}}{10(2)}+\frac{4}{2}+\frac{81}{64}}}(1.75)=\frac{2.0917968}{\sqrt{3.5523437}}=\frac{2.0917968}{1.890005}=1.1067678$$

where $\sigma_G^2-\sigma_F^2=\ 6-\frac{81}{64}=\frac{303}{64}=4\ \frac{47}{64}=$ residual genotypic variance within a half-sib family

b. For this part, see my heritability article, Section VII.B.1.c.ii.(a).(iii), Half-sib, S_1 seed method, p. 275. Referring to Fig. 1(c), p. 274 in my heritability article, we first calculate Cov(X_f, Y). I give what Cov(X_f, Y) is equal to in equation [50] for a *noninbred* parent P_f of a family [same as parent A_f in equation (12.45)]. The generalized expression for an *inbred* parent P_f is [equation (12.46)]

$$\text{Cov}\left(X_f,Y\right)=2\theta_{X_fY}\sigma_A^2+\left(2\theta_{X_fY}\right)^2\sigma_{AA}^2+\cdots$$ [θ_{X_fY} is derived above equation (12.46)]

$$=2\left(\frac{1+F_P}{8}\right)\sigma_A^2+\left(\frac{2(1+F_P)}{8}\right)^2\sigma_{AA}^2+\cdots$$

$$=\left(\frac{1+F_P}{4}\right)\sigma_A^2+\left(\frac{1+F_P}{4}\right)^2\sigma_{AA}^2+\cdots$$

For our exercise, assuming all higher-order epistatic components, except σ_{AA}^2, equal zero, we have

$$\text{Cov}\left(X_f,Y\right)=\left(\frac{1+\frac{1}{2}}{4}\right)\sigma_A^2+\left(\frac{1+\frac{1}{2}}{4}\right)^2\sigma_{AA}^2$$

$$=\tfrac{3}{8}\sigma_A^2+\left(\tfrac{3}{8}\right)^2\sigma_{AA}^2=\tfrac{3}{8}\sigma_A^2+\tfrac{9}{64}\sigma_{AA}^2$$

The half-sib family component is the same as that in part (a):

$$\sigma_F^2=\sigma_{\text{Half-sib families}}^2=\tfrac{81}{64}$$

Then the selection response equation is (equation [51])

$$R_{1(b)}=\frac{2\text{Cov}\left(X_f,Y\right)}{\sigma_{\bar{X}}}i=\frac{2\left[\frac{3}{8}\sigma_A^2+\frac{9}{64}\sigma_{AA}^2\right]}{\sqrt{\frac{\sigma_E^2+\sigma_G^2-\sigma_F^2}{nr}+\frac{\sigma_\varepsilon^2}{r}+\sigma_F^2}}\left(1.75\right)$$

$$=\frac{2\left[\frac{3}{8}(3)+\frac{9}{64}(1)\right]}{\sqrt{\frac{1+6-\frac{81}{64}}{10(2)}+\frac{4}{2}+\frac{81}{64}}}(1.75)=\frac{4.4296875}{\sqrt{3.5523437}}=\frac{4.4296875}{1.890005}=2.3437437$$

where $\sigma_G^2-\sigma_F^2=\ 6-\frac{81}{64}=\frac{303}{64}=4\ \frac{47}{64}=$ residual genotypic variance within a half-sib family

c. For this part, see my heritability article, Section VII.B.1.c.ii.(b).(i), Full-sib, remnant-seed method, p. 277. Referring to Fig. 1(e), p. 274 in my heritability article, we first calculate Cov(X_f, Y). The generalized expression for $\text{Cov}\left(X_f,Y\right)$ for *inbred* parents is

$$\text{Cov}\left(X_f, Y\right) = 2\theta_{X_f Y}\sigma_A^2 + \left(2\theta_{X_f Y}\right)^2 \sigma_{AA}^2 + \cdots$$

$$= 2\left(\tfrac{2+F_P+F_{P'}}{16}\right)\sigma_A^2 + \left[2\left(\tfrac{2+F_P+F_{P'}}{16}\right)\right]^2 \sigma_{AA}^2 + \cdots$$

$$= \left(\tfrac{2+F_P+F_{P'}}{8}\right)\sigma_A^2 + \left(\tfrac{2+F_P+F_{P'}}{8}\right)^2 \sigma_{AA}^2 + \cdots$$

The expression for $\theta_{X_f Y}$ is derived in an unnumbered equation above equation (12.54) where the number 8 should be changed to 16 (see Errata for Statistical Genetics Notes). For our exercise, assuming all higher-order epistatic components, except σ_{AA}^2, equal zero, we have

$$\text{Cov}\left(X_f, Y\right) = \left(\tfrac{2+\frac{1}{2}+\frac{1}{2}}{8}\right)\sigma_A^2 + \left(\tfrac{2+\frac{1}{2}+\frac{1}{2}}{8}\right)^2 \sigma_{AA}^2$$

$$= \tfrac{3}{8}\sigma_A^2 + \left(\tfrac{3}{8}\right)^2 \sigma_{AA}^2 = \tfrac{3}{8}\sigma_A^2 + \tfrac{9}{64}\sigma_{AA}^2$$

which is the same as that in part (b) above. This agrees with the equality of the expressions for the half-sib, S_1 method and the full-sib, remnant seed method with no inbreeding of the parents. See full-sib, remnant seed method, p. 277.

Next we calculate the full-sib family component:

$$\sigma_F^2 = \sigma_{\text{Full-sib families}}^2 = 2\theta_{XY}\sigma_A^2 + \delta_{dXY}\sigma_D^2 + \left(2\theta_{XY}\right)^2 \sigma_{AA}^2 \qquad \text{[see equation (9.144) and Table 9.5, p. 9.52]}$$

$$= \left(\frac{2+F_P+F_{P'}}{4}\right)\sigma_A^2 + \frac{\left(1+F_P\right)\left(1+F_{P'}\right)}{4}\sigma_D^2 + \left[\frac{2+F_P+F_{P'}}{4}\right]^2 \sigma_{AA}^2$$

$$= \left(\frac{2+\frac{1}{2}+\frac{1}{2}}{4}\right)\sigma_A^2 + \frac{\left(1+\frac{1}{2}\right)\left(1+\frac{1}{2}\right)}{4}\sigma_D^2 + \left[\frac{2+\frac{1}{2}+\frac{1}{2}}{4}\right]^2 \sigma_{AA}^2$$

$$= \tfrac{3}{4}\sigma_A^2 + \tfrac{9}{16}\sigma_D^2 + \left(\tfrac{3}{4}\right)^2 \sigma_{AA}^2$$

$$= \tfrac{3}{4}(3) + \tfrac{9}{16}(2) + \tfrac{9}{16}(1) = \tfrac{36+18+9}{16} = \tfrac{63}{16}$$

Then the selection response equation is

$$R_{1(c)} = \frac{2\text{Cov}\left(X_f, Y\right)}{\sigma_{\bar{X}}} i = \frac{2\left[\frac{3}{8}\sigma_A^2 + \frac{9}{64}\sigma_{AA}^2\right]}{\sqrt{\frac{\sigma_E^2 + \sigma_G^2 - \sigma_F^2}{nr} + \frac{\sigma_\varepsilon^2}{r} + \sigma_F^2}}(1.75)$$

$$= \frac{2\left[\frac{3}{8}(3) + \frac{9}{64}(1)\right]}{\sqrt{\frac{1+6-\frac{63}{16}}{10(2)} + \frac{4}{2} + \frac{63}{16}}}(1.75) = \frac{4.4296875}{\sqrt{6.090625}} = \frac{4.4296875}{2.4679191} = 1.7949079$$

where $\sigma_G^2 - \sigma_F^2 = 6 - \frac{63}{16} = \frac{33}{16} = 2\ \frac{1}{16}$ = residual genotypic variance within a full-sib family

We compare R_1s: $R_{1(b)} = 2.3437 > R_{1(c)} = 1.7949 > R_{1(a)} = 1.1068$

Exercise 12.2.
For population 1:

From equation (12.24) we can write (also see Section VII.B.1.c in my heritability paper, Critical Reviews in Plant Sciences 10:235-322, 1991, for a more polished presentation)

$$\Delta_1 = \Delta_{m_1} + \Delta_{f_1} = k_m \frac{C_{1PO}}{\sigma_{X_{m_1}}} + k_f \frac{C_{1PO}}{\sigma_{X_{f_1}}} \quad \text{assume } k_m = k_f = k, \text{ and } \sigma_{X_{m_1}} = \sigma_{X_{f_1}} = \sigma_{X_1}$$

$$= 2k \frac{C_{1PO}}{\sigma_{X_1}}$$

$$= 2k \frac{\left(\frac{1}{2}\sigma^2_{A_1} + \frac{1}{4}\sigma^2_{AA_1}\right)}{\sqrt{\sigma^2_{A_1} + \sigma^2_{D_1} + \sigma^2_{AA_1} + \sigma^2_{AD_1} + \sigma^2_{DD_1} + \sigma^2_E}}$$

$$= k \frac{\left(\sigma^2_{A_1} + \frac{1}{2}\sigma^2_{AA_1}\right)}{\sqrt{\sigma^2_{A_1} + \sigma^2_{D_1} + \sigma^2_{AA_1} + \sigma^2_{AD_1} + \sigma^2_{DD_1} + \sigma^2_E}}$$

For population 2:

The genetic variation within the population is that within a full-sib family, namely,

$$\sigma^2_{X_2} = C_I - C_{fs}$$

$$= \sigma^2_{A_1} + \sigma^2_{D_1} + \sigma^2_{AA_1} + \sigma^2_{AD_1} + \sigma^2_{DD_1} - \left(\frac{1}{2}\sigma^2_{A_1} + \frac{1}{4}\sigma^2_{D_1} + \frac{1}{4}\sigma^2_{AA_1} + \frac{1}{8}\sigma^2_{AD_1} + \frac{1}{16}\sigma^2_{DD_1}\right)$$

$$= \frac{1}{2}\sigma^2_{A_1} + \frac{3}{4}\sigma^2_{D_1} + \frac{3}{4}\sigma^2_{AA_1} + \frac{7}{8}\sigma^2_{AD_1} + \frac{15}{16}\sigma^2_{DD_1}$$

From population 1 above we write

$$\Delta_2 = \Delta_{m_2} + \Delta_{f_2} = k \frac{\left(\sigma^2_{A_2} + \frac{1}{2}\sigma^2_{AA_2}\right)}{\sqrt{\sigma^2_{A_2} + \sigma^2_{D_2} + \sigma^2_{AA_2} + \sigma^2_{AD_2} + \sigma^2_{DD_2} + \sigma^2_E}}$$

where $\sigma^2_{A_2} = \frac{1}{2}\sigma^2_{A_1}$

$$\sigma^2_{D_2} = \frac{3}{4}\sigma^2_{D_1}$$

$$\sigma^2_{AA_2} = \frac{3}{4}\sigma^2_{AA_1}$$

$$\sigma^2_{AD_2} = \frac{7}{8}\sigma^2_{AD_1}$$

$$\sigma^2_{DD_2} = \frac{15}{16}\sigma^2_{DD_1}$$

$$\Delta_2 = k \frac{\left(\frac{1}{2}\sigma^2_{A_1} + \frac{1}{2}\left(\frac{3}{4}\sigma^2_{AA_1}\right)\right)}{\sqrt{\frac{1}{2}\sigma^2_{A_1} + \frac{3}{4}\sigma^2_{D_1} + \frac{3}{4}\sigma^2_{AA_1} + \frac{7}{8}\sigma^2_{AD_1} + \frac{15}{16}\sigma^2_{DD_1} + \sigma^2_E}}$$

Hence, the ratio of the gains are

$$\frac{\Delta_2}{\Delta_1}=\frac{k\dfrac{\left(\frac{1}{2}\sigma^2_{A_1}+\frac{3}{8}\sigma^2_{AA_1}\right)}{\sqrt{\frac{1}{2}\sigma^2_{A_1}+\frac{3}{4}\sigma^2_{D_1}+\frac{3}{4}\sigma^2_{AA_1}+\frac{7}{8}\sigma^2_{AD_1}+\frac{15}{16}\sigma^2_{DD_1}+\sigma^2_E}}}{k\dfrac{\left(\sigma^2_{A_1}+\frac{1}{2}\sigma^2_{AA_1}\right)}{\sqrt{\sigma^2_{A_1}+\sigma^2_{D_1}+\sigma^2_{AA_1}+\sigma^2_{AD_1}+\sigma^2_{DD_1}+\sigma^2_E}}}$$

$$=\frac{\left(\frac{1}{2}\sigma^2_{A_1}+\frac{3}{8}\sigma^2_{AA_1}\right)\sqrt{\sigma^2_{A_1}+\sigma^2_{D_1}+\sigma^2_{AA_1}+\sigma^2_{AD_1}+\sigma^2_{DD_1}+\sigma^2_E}}{\left(\sigma^2_{A_1}+\frac{1}{2}\sigma^2_{AA_1}\right)\sqrt{\frac{1}{2}\sigma^2_{A_1}+\frac{3}{4}\sigma^2_{D_1}+\frac{3}{4}\sigma^2_{AA_1}+\frac{7}{8}\sigma^2_{AD_1}+\frac{15}{16}\sigma^2_{DD_1}+\sigma^2_E}}$$

We calculate the relative gain in the two populations for $\sigma^2_A=\sigma^2_{A_1}=100$ and $\sigma^2_E=10$, assuming all other genetic variance components equal to zero

$$\frac{\Delta_2}{\Delta_1}=\frac{\frac{1}{2}(100)\sqrt{100+10}}{(100)\sqrt{\frac{1}{2}(100)+10}}=\frac{50\sqrt{110}}{100\sqrt{60}}=\frac{1}{2}\frac{\sqrt{110}}{\sqrt{60}}=\frac{1}{2}\frac{10.4881}{7.7460}=\frac{5.2440}{7.7460}=0.6770$$

Exercise 12.3.

The derivation of the basic expression for the prediction of selection response in the first generation, $R_1=\dfrac{\text{Cov}(X,Y)}{\sigma_X}i$, is given in my heritability article, W.E. Nyquist, 1991, Estimation of heritability and prediction of selection response in plant populations, Critical Rev. Plant Sci. 10:235-322, on p. 272. In my heritability article, I listed the female first and the male second, which is what I wish that I would have done in these notes (see my Preface and a discussion of this topic in Chapter 2, p. 2.18). Here I retain the order in my heritability article. The total response is equal to the response on the maternal side plus the response on the paternal side, namely,

$$R_1=R_{1f}+R_{1m}=b_{YX_f}S_f+b_{YX_m}S_m=\frac{\text{Cov}\left(X_f,Y\right)}{\sigma^2_{X_f}}i_f\sigma_{X_f}+\frac{\text{Cov}\left(X_m,Y\right)}{\sigma^2_{X_m}}i_m\sigma_{X_m}$$

$$=\frac{\text{Cov}\left(X_f,Y\right)}{\sigma_{X_f}}i_f+\frac{\text{Cov}\left(X_m,Y\right)}{\sigma_{X_m}}i_m$$

Then we assume no sexual dimorphism, so $\sigma^2_{X_f}=\sigma^2_{X_m}=\sigma^2_X$, and we assume the same relationship between X and Y on both the maternal and paternal sides of X, so $\text{Cov}\left(X_f,Y\right)=\text{Cov}\left(X_m,Y\right)$. Then we have

$$R_1=R_{1f}+R_{1m}=\frac{\text{Cov}\left(X_f,Y\right)}{\sigma_{X_f}}\left(i_f+i_m\right)$$

$$=\frac{2\text{Cov}\left(X_f,Y\right)}{\sigma_{X_f}}\left(\frac{i_f+i_m}{2}\right)$$

$$=\frac{\text{Cov}\left(X,Y\right)}{\sigma_X}\left(\frac{i_f+i_m}{2}\right)$$

where $\text{Cov}(X,Y) = 2\text{Cov}(X_f,Y) = \text{Cov}(X_f,Y) + \text{Cov}(X_m,Y)$, the total covariance from both the female and male sides

If $i_f = i_m = i$, we have $R_1 = R_{1f} + R_{1m} = \frac{\text{Cov}(X,Y)}{\sigma_X} i$.