

SOLUTIONS TO EXERCISES FOR CHAPTER 7

**Exercise 7.1.**

For the  $u$  series we set up two equations in two unknown,  $b$  and  $c$ , and solve for the two unknowns:

$$u_2 = bu_1 + cu_0$$

$$u_3 = bu_2 + cu_1$$

Substituting the values for the  $u$  series in the two equations above, we have

$$\frac{16}{72} = b \frac{8}{36} + c(0)$$

$$\frac{248}{1296} = b \frac{16}{72} + c \frac{8}{36}$$

Solving the two equations simultaneously, the two unknowns for the  $u$  series are  $b = 1$  and  $c = -\frac{5}{36}$ . (I solved the first equation for  $b = 1$ , and substituted that value for  $b$  in the second equation from which I obtained  $c = -\frac{5}{36}$ .)

$$\text{Check: } u_4 = \frac{416}{2592} = (1) \frac{248}{1296} + \left(-\frac{5}{36}\right) \frac{16}{72} = \frac{416}{2592}$$

For the  $v$  series we set up two equations in two unknown,  $b$  and  $c$ , and solve for the two unknowns:

$$v_2 = bv_1 + cv_0$$

$$v_3 = bv_2 + cv_1$$

Substituting the values for the  $v$  series in the two equations above, we have

$$\frac{26}{72} = b \frac{18}{36} + c(1)$$

$$\frac{378}{1296} = b \frac{26}{72} + c \frac{18}{36}$$

Solving the two equations simultaneously, the two unknowns for the  $v$  series are  $b = 1$  and  $c = -\frac{5}{36}$ . (To solve the system of equations, I first multiplied the second equation by  $-\frac{36}{18}$  and added the two equations together, thereby eliminating  $c$ . Then I obtained  $b = 1$ , and substituted that value for  $b$  in one of the original equations to obtain  $c = -\frac{5}{36}$ .) The scales of relation are the same for the two series.

The next step is to find the common ratio for each of the two geometric series with the same scales of relation (see p. 7.4).

$$u_t = bu_{t-1} + cu_{t-2} = (1)u_{t-1} - \frac{5}{36}u_{t-2}$$

$$x\lambda^t = bx\lambda^{t-1} + cx\lambda^{t-2}$$

$$x\lambda^t - bx\lambda^{t-1} - cx\lambda^{t-2} = 0$$

$$\lambda^2 - b\lambda - c = 0$$

$$\lambda^2 - (1)\lambda - \left(-\frac{5}{36}\right) = 0$$

$$\lambda^2 - \lambda + \frac{5}{36} = 0$$

Solving the quadratic equation for its two roots,  $\lambda_1$  and  $\lambda_2$ , we obtain

$$\lambda_1 = \frac{-b + \sqrt{b^2 - 4ac}}{2a} = \frac{-(-1) + \sqrt{(-1)^2 - 4\left(\frac{5}{36}\right)}}{2} = \frac{1 + \sqrt{1 - \frac{20}{36}}}{2} = \frac{1 + \sqrt{\frac{16}{36}}}{2} = \frac{1 + \frac{2}{3}}{2} = \frac{5}{6}$$

$$\lambda_2 = \frac{-b - \sqrt{b^2 - 4ac}}{2a} = \frac{-(-1) - \sqrt{(-1)^2 - 4\left(\frac{5}{36}\right)}}{2} = \frac{1 - \sqrt{1 - \frac{20}{36}}}{2} = \frac{1 - \sqrt{\frac{16}{36}}}{2} = \frac{1 - \frac{2}{3}}{2} = \frac{1}{6}$$

The two geometric series are

$$x, x\lambda_1, x\lambda_1^2, x\lambda_1^3, \dots, x\lambda_1^t, \dots \quad \text{where } \lambda_1 = \frac{5}{6}$$

$$y, y\lambda_2, y\lambda_2^2, y\lambda_2^3, \dots, y\lambda_2^t, \dots \quad \text{where } \lambda_2 = \frac{1}{6}$$

By Proposition 1 (p. 7.3) we add the corresponding terms of the two geometric series to obtain another series, say, the  $u$  series from which we can find the initial values of the two geometric series,  $x$  and  $y$ .

For the  $u$  series we have two equations in the two unknowns,  $x$  and  $y$ , for which we solve.

$$u_0 = x + y$$

$$u_1 = x\lambda_1 + y\lambda_2$$

Substituting the values for the  $u$  series and the common ratios in the two equations above, we have

$$0 = x + y$$

$$\frac{8}{36} = x\left(\frac{5}{6}\right) + y\left(\frac{1}{6}\right)$$

Solving the two equations simultaneously, the values for the two unknowns are  $x = \frac{1}{3}$  and  $y = -\frac{1}{3}$ . (To solve the system of equations, I first multiplied the first equation by  $-\frac{5}{6}$  and added the two equations together, thereby eliminating  $x$ . Then I obtained  $y = -\frac{1}{3}$ , and substituted that value for  $y$  in one of the original equations to obtain  $x = \frac{1}{3}$ .) The general term for the  $u$  series is

$$\begin{aligned} u_t &= x\lambda_1^t + y\lambda_2^t \\ &= \frac{1}{3}\left(\frac{5}{6}\right)^t + \left(-\frac{1}{3}\right)\left(\frac{1}{6}\right)^t \\ &= \frac{1}{3}\left(\frac{5}{6}\right)^t - \frac{1}{3}\left(\frac{1}{6}\right)^t \end{aligned}$$

For the  $v$  series we have two equations in the two unknowns,  $x$  and  $y$ , for which we solve.

$$v_0 = x + y$$

$$v_1 = x\lambda_1 + y\lambda_2$$

Substituting the values for the  $v$  series and the common ratios in the two equations above, we have

$$1 = x + y$$

$$\frac{18}{36} = x\left(\frac{5}{6}\right) + y\left(\frac{1}{6}\right)$$

Solving the two equations simultaneously, the values for the two unknowns are  $x = \frac{1}{2}$  and  $y = \frac{1}{2}$ . (To solve the system of equations, I first multiplied the first equation by  $-\frac{1}{6}$  and added the two equations together, thereby eliminating  $y$ . Then I obtained  $x = \frac{1}{2}$ , and substituted that value for  $x$  in one of the original equations to obtain  $y = \frac{1}{2}$ .) The general term for the  $v$  series is

$$\begin{aligned}
v_t &= x\lambda_1^t + y\lambda_2^t \\
&= \frac{1}{2}\left(\frac{5}{6}\right)^t + \frac{1}{2}\left(\frac{1}{6}\right)^t \\
&= \frac{1}{2}\left(\frac{5}{6}\right)^t + \frac{1}{2}\left(\frac{1}{6}\right)^t
\end{aligned}$$

**Exercise 7.2.**

a. We note that in Example 7.2, p. 7.7, which has the same recurrence relation as that given in this Exercise, the roots or common ratios are  $\lambda_1 = \frac{1+\sqrt{5}}{4}$  and  $\lambda_2 = \frac{1-\sqrt{5}}{4}$ .

The general term is  $u_t = x\lambda_1^t + y\lambda_2^t$  [see equation (7.13)]. Solve for  $x$  and  $y$  in the general term by solving the two simultaneous equations as follows:

$$\begin{aligned}
u_0 &= x(1) + y(1) \\
u_1 &= x\lambda_1 + y\lambda_2
\end{aligned}$$

$$\begin{aligned}
1 &= u_0 = x(1) + y(1) &&= (1)x + (1)y \\
1 &= u_1 = x\frac{1+\sqrt{5}}{4} + y\frac{1-\sqrt{5}}{4} = \frac{1+\sqrt{5}}{4}x + \frac{1-\sqrt{5}}{4}y
\end{aligned}$$

We eliminated  $y$  by multiplying the second equation by  $-\frac{4}{1-\sqrt{5}}$  and then by adding the two equations together to obtain  $x = \frac{5+3\sqrt{5}}{10}$ . Next we obtain  $y = \frac{5-3\sqrt{5}}{10}$  from the first equation..

The general term for the  $u$  series is

$$u_t = x\lambda_1^t + y\lambda_2^t = \frac{5+3\sqrt{5}}{10}\left(\frac{1+\sqrt{5}}{4}\right)^t + \frac{5-3\sqrt{5}}{10}\left(\frac{1-\sqrt{5}}{4}\right)^t$$

For the  $v$  series  $v_0 = 1/2$  and  $v_1 = 1/2$ , which are one-half of the corresponding terms in the  $u$  series, so  $x$  and  $y$  are one-half of those in the  $u$  series, i.e.,  $x = \frac{5+3\sqrt{5}}{20}$  and  $y = \frac{5-3\sqrt{5}}{20}$ . Hence, the general term is

$$v_t = x\lambda_1^t + y\lambda_2^t = \frac{5+3\sqrt{5}}{20}\left(\frac{1+\sqrt{5}}{4}\right)^t + \frac{5-3\sqrt{5}}{20}\left(\frac{1-\sqrt{5}}{4}\right)^t$$

b. Yes, the general terms for the two series are different, because the two series are different.

**Exercise 7.3.**

The  $P$  series for full-sib mating from equation (6.32) is: 1, 1, 3/4, 5/8, 8/16, 13/32, ... . The recurrence relation from equation (6.30) is

$$P_t = \frac{1}{2}P_{t-1} + \frac{1}{4}P_{t-2}$$

From Proposition 2 (p. 7.3) we can equate the  $t$ th term in the  $P$  series to the  $t$ th term in a geometric series and express that  $t$ th term in the form of a recurrence relation with two scales of relation, namely,

$$\begin{aligned}
P_t &= x\lambda^t = \frac{1}{2}x\lambda^{t-1} + \frac{1}{4}x\lambda^{t-2} \\
x\lambda^t - \frac{1}{2}x\lambda^{t-1} - \frac{1}{4}x\lambda^{t-2} &= 0 \\
\lambda^2 - \frac{1}{2}\lambda - \frac{1}{4} &= 0
\end{aligned}$$

Solving the quadratic equation for its two roots,  $\lambda_1$  and  $\lambda_2$ , we obtain

$$\lambda_1 = \frac{-b + \sqrt{b^2 - 4ac}}{2a} = \frac{-(-\frac{1}{2}) + \sqrt{(-\frac{1}{2})^2 - 4(-\frac{1}{4})}}{2} = \frac{\frac{1}{2} + \sqrt{\frac{5}{4}}}{2} = \frac{\frac{1}{2} + \frac{1}{2}\sqrt{5}}{2} = \frac{1}{4}(1 + \sqrt{5}) = 0.809017 = \varepsilon$$

$$\lambda_2 = \frac{-b - \sqrt{b^2 - 4ac}}{2a} = \frac{-(-\frac{1}{2}) - \sqrt{(-\frac{1}{2})^2 - 4(-\frac{1}{4})}}{2} = \frac{\frac{1}{2} - \sqrt{\frac{5}{4}}}{2} = \frac{\frac{1}{2} - \frac{1}{2}\sqrt{5}}{2} = \frac{1}{4}(1 - \sqrt{5}) = -0.309017 = \varepsilon'$$

Solving for the initial values,  $x$  and  $y$ , in the two geometric series with common ratios  $\lambda_1 = \varepsilon$  and  $\lambda_2 = \varepsilon'$ , we have

$$u_0 = x + y$$

$$u_1 = x\lambda_1 + y\lambda_2$$

Substituting the values for the panmictic series for the  $u$  terms and for the common ratios in the two equations above, we have

$$1 = x + y$$

$$1 = x \frac{1 + \sqrt{5}}{4} + y \frac{1 - \sqrt{5}}{4} = x\varepsilon + y\varepsilon'$$

Multiplying the first equation by  $-\varepsilon'$ , adding the first and second equations together, solving for  $x$ , and then solving for  $y$  by substituting the value for  $x$  in the first equation, we obtain

$$x = \frac{1 - \varepsilon'}{\varepsilon - \varepsilon'} = \frac{1 - \frac{1 - \sqrt{5}}{4}}{\frac{1 + \sqrt{5}}{4} - \frac{1 - \sqrt{5}}{4}} = \frac{4 - 1 + \sqrt{5}}{4} = \frac{3 + \sqrt{5}}{4} = \frac{3 + \sqrt{5}}{2\sqrt{5}} \frac{\sqrt{5}}{\sqrt{5}} = \frac{5 + 3\sqrt{5}}{10} = 1.1708204$$

$$y = 1 - \frac{5 + 3\sqrt{5}}{10} = \frac{5 - 3\sqrt{5}}{10} = -0.1708204$$

$$\text{Check: } 1 = x + y = \frac{5 + 3\sqrt{5}}{10} + \frac{5 - 3\sqrt{5}}{10} = \frac{5 + 5}{10} = 1$$

The general term for the panmictic series is (see Example 7.2, pp. 7.7 to 7.8)

$$P_t = \frac{5 + 3\sqrt{5}}{10} \left( \frac{1 + \sqrt{5}}{4} \right)^t + \frac{5 - 3\sqrt{5}}{10} \left( \frac{1 - \sqrt{5}}{4} \right)^t$$

$$= 1.1708204(0.809017)^t - 0.1708204(-0.309017)^t$$

The general term for the inbreeding series is

$$F_t = 1 - P_t = 1 - \frac{5 + 3\sqrt{5}}{10} \left( \frac{1 + \sqrt{5}}{4} \right)^t + \frac{5 - 3\sqrt{5}}{10} \left( \frac{1 - \sqrt{5}}{4} \right)^t$$

$$= 1 - 1.1708204(0.809017)^t + 0.1708204(-0.309017)^t$$

#### Exercise 7.4.

An eigenvalue  $\lambda_i$  is one possible value such that when one premultiplies a vector, called an eigenvector, by a square matrix  $\mathbf{A}$ , the product is another vector in which every element is  $\lambda_i$  times the elements in the original vector. The eigenvalues are the roots of the so-called characteristic equation.

An eigenvector is that nonzero vector which will satisfy the above multiplication.

We have used them to diagonalize a matrix so that we may find the  $t$ th power of a matrix very easily by simply raising every element on the diagonal to the  $t$  power. We have been interested in this for two reasons: 1) to describe the state of affairs in generation  $t$  and 2) to determine in an analytical way what happens as  $t \rightarrow \infty$ .

**Exercise 7.5.**

The eigenvalues, or latent or characteristic roots, of the matrix are [see equations (7.106) and (7.107)]

$$\begin{aligned} \begin{vmatrix} 2-\lambda & 1 \\ 5 & 6-\lambda \end{vmatrix} &= (2-\lambda)(6-\lambda) - 5 = 12 - 2\lambda - 6\lambda + \lambda^2 - 5 \\ &= \lambda^2 - 8\lambda + 7 \\ &= (\lambda - 7)(\lambda - 1) \\ \lambda - 7 &= 0 \\ \lambda_1 &= 7 \\ \lambda - 1 &= 0 \\ \lambda_2 &= 1 \end{aligned}$$

**Exercise 7.6.**

a. The  $6 \times 6$  transition matrix given in equation (7.40) is

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2} & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{16} & \frac{1}{16} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

b. Conceptually the eigenvalues are the solution to the sixth power polynomial equation, called the characteristic equation of the matrix  $\mathbf{P}$ , defined as

$$|(\mathbf{P} - \lambda \mathbf{I})| = 0$$

Expanding that equation we have

$$\begin{vmatrix} 1-\lambda & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-\lambda & 0 & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{2}-\lambda & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{2}-\lambda & \frac{1}{4} & 0 \\ \frac{1}{16} & \frac{1}{16} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4}-\lambda & \frac{1}{8} \\ 0 & 0 & 0 & 0 & 1 & 0-\lambda \end{vmatrix} = (1-\lambda)^2 \begin{vmatrix} \frac{1}{2}-\lambda & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{2}-\lambda & \frac{1}{4} & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{4}-\lambda & \frac{1}{8} \\ 0 & 0 & 1 & -\lambda \end{vmatrix} = 0$$

Setting each of the first two factors  $(1-\lambda)^2$  equal to zero, we have  $\lambda_1 = 1$  and  $\lambda_2 = 1$ . Using the hint given in the exercise, we have

$$\begin{aligned} & \left(\frac{1}{2}-\lambda\right) \begin{vmatrix} \frac{1}{2}-\lambda & \frac{1}{4} & 0 \\ \frac{1}{4} & \frac{1}{4}-\lambda & \frac{1}{8} \\ 0 & 1 & -\lambda \end{vmatrix} + \frac{1}{4} \begin{vmatrix} 0 & \frac{1}{2}-\lambda & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & -\lambda \end{vmatrix} \\ &= \left(\frac{1}{2}-\lambda\right) \left[ \left(\frac{1}{2}-\lambda\right) \left(\frac{1}{4}-\lambda\right) (-\lambda) - \left(\frac{1}{2}-\lambda\right) \frac{1}{8} (1) - \frac{1}{4} \frac{1}{4} (-\lambda) \right] + \frac{1}{4} \left[ -\left(\frac{1}{2}-\lambda\right) \frac{1}{4} (-\lambda) \right] \\ &= \left(\frac{1}{2}-\lambda\right) \left[ \left(\frac{1}{8} - \frac{1}{2}\lambda - \frac{1}{4}\lambda + \lambda^2\right) (-\lambda) - \frac{1}{16} + \frac{1}{8}\lambda + \frac{1}{16}\lambda \right] + \frac{1}{4} \left[ \lambda \left(\frac{1}{8} - \frac{1}{4}\lambda\right) \right] \end{aligned}$$

$$\begin{aligned}
&= \left(\frac{1}{2} - \lambda\right) \left[ -\frac{1}{8}\lambda + \frac{3}{4}\lambda^2 - \lambda^3 - \frac{1}{16} + \frac{3}{16}\lambda \right] + \frac{1}{4} \left[ \frac{1}{8}\lambda - \frac{1}{4}\lambda^2 \right] \\
&= \left(\frac{1}{2} - \lambda\right) \left[ -\frac{1}{16} + \frac{1}{16}\lambda + \frac{3}{4}\lambda^2 - \lambda^3 \right] + \frac{1}{32}\lambda - \frac{1}{16}\lambda^2 \\
&= \left(\frac{1}{2} - \lambda\right) \left[ -\frac{1}{16} + \frac{1}{16}\lambda + \frac{3}{4}\lambda^2 - \lambda^3 \right] + \frac{1}{16}\lambda \left(\frac{1}{2} - \lambda\right) \\
&= \left(\frac{1}{2} - \lambda\right) \left\{ \left[ -\frac{1}{16} + \frac{1}{16}\lambda + \frac{3}{4}\lambda^2 - \lambda^3 \right] + \frac{1}{16}\lambda \right\} \\
&= \left(\frac{1}{2} - \lambda\right) \left[ -\frac{1}{16} + \frac{1}{8}\lambda + \frac{3}{4}\lambda^2 - \lambda^3 \right] = 0
\end{aligned}$$

The cubic equation is the same as that in equation (7.140) and its roots are  $\varepsilon = \frac{1+\sqrt{5}}{4}$ ,  $\varepsilon' = \frac{1-\sqrt{5}}{4}$ , and  $\frac{1}{4}$  as given in equations (7.142) and (7.143). Hence, the roots to the sixth degree polynomial or characteristic equation of the matrix  $\mathbf{P}$  are

$$\lambda_1 = 1, \lambda_2 = 1, \lambda_3 = \frac{1}{2}, \lambda_4 = \varepsilon = \frac{1+\sqrt{5}}{4}, \lambda_5 = \varepsilon' = \frac{1-\sqrt{5}}{4}, \text{ and } \lambda_6 = \frac{1}{4}$$

### Exercise 7.7.

a. The individual element  $p_{ij}$  in the  $\mathbf{P}$  matrix is the conditional probability of being in state  $j$  in the next generation ( $t$ ), given that the process was in state  $i$  in the previous generation ( $t-1$ ) (see p. 7.12).

b. The individual element  $p_{ij}^{(2)}$  in the  $\mathbf{P}^2$  matrix is the probability of being in state  $j$  in any generation  $t$ , given that the process was in state  $i$  in two previous generations ( $t-2$ ). It is called a two-step transitional probability.

Any  $p_{ij}$  element in the  $\mathbf{P}^2$  matrix can be expressed as a function of the  $p_{ij}$  elements in the  $\mathbf{P}$  matrix itself (for  $s = 4$ ) as follows:

$$p_{ij}^{(2)} = \sum_{k=1}^4 p_{ik} p_{kj} \quad [\text{see equation (7.46)}]$$

For example, for full-sib mating we have

$$\mathbf{P}^2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 1 & 0 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{13}{32} & \frac{3}{8} & \frac{3}{16} & \frac{1}{32} \\ \frac{9}{32} & \frac{3}{8} & \frac{5}{16} & \frac{1}{32} \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \end{bmatrix} \quad [\text{see equation (7.45)}]$$

c. The individual element  $p_{ij}^{(3)}$  in the  $\mathbf{P}^3$  matrix is the probability of being in state  $j$  in any generation  $t$ , given that the process was in state  $i$  in three previous generations ( $t-3$ ). It is called a three-step transitional probability.

$$\begin{aligned}
P_{ij}^{(3)} &= \sum_{l=1}^4 P_{il}^{(2)} P_{lj} \\
&= \sum_{l=1}^4 \left( \sum_{k=1}^4 P_{ik} P_{kl} \right) P_{lj} \\
\mathbf{P}^3 &= \mathbf{P}^2 \mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{13}{32} & \frac{3}{8} & \frac{3}{16} & \frac{1}{32} \\ \frac{9}{32} & \frac{3}{8} & \frac{5}{16} & \frac{1}{32} \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 1 & 0 \end{bmatrix} \\
&= \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{67}{128} & \frac{9}{32} & \frac{11}{64} & \frac{3}{128} \\ \frac{53}{128} & \frac{11}{32} & \frac{13}{64} & \frac{5}{128} \\ \frac{9}{32} & \frac{3}{8} & \frac{5}{16} & \frac{1}{32} \end{bmatrix}
\end{aligned}$$

**Exercise 7.8.**

a. From equation (7.112) we have  $\mathbf{C} = \begin{bmatrix} 1 & 0 \\ 1 & 1 \end{bmatrix}$ , and from equation (7.114) we have  $\mathbf{C}^{-1} = \begin{bmatrix} 1 & 0 \\ -1 & 1 \end{bmatrix}$ .

$$\begin{aligned}
\text{Thus, } \mathbf{P} &= \mathbf{K} \boldsymbol{\lambda} \mathbf{K}^{-1} = \begin{bmatrix} 0 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} \frac{1}{2} & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} -1 & 1 \\ 1 & 0 \end{bmatrix} \\
&= \begin{bmatrix} 0 & 1 \\ \frac{1}{2} & 1 \end{bmatrix} \begin{bmatrix} -1 & 1 \\ 1 & 0 \end{bmatrix} \\
&= \begin{bmatrix} 1 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix} \quad \text{which is equation (7.28)}
\end{aligned}$$

b. The C matrix is defined in equation (7.174) as

$$\mathbf{C} = (\mathbf{c}_1 \ \mathbf{c}_2 \ \mathbf{c}_3 \ \mathbf{c}_4) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 1 & \varepsilon & \varepsilon' & -1 \\ 1 & 1 & 1 & 1 \\ 1 & 4\varepsilon - 2 & 4\varepsilon' - 2 & 4 \end{bmatrix}$$

and its inverse is defined in equation (7.179) as

$$\mathbf{C}^{-1} = \mathbf{D} = \begin{bmatrix} \mathbf{d}'_1 \\ \mathbf{d}'_2 \\ \mathbf{d}'_3 \\ \mathbf{d}'_4 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{-10\varepsilon-3}{10} & \frac{4\varepsilon}{5} & \frac{2}{5} & \frac{2\varepsilon-1}{10} \\ \frac{5\varepsilon-4}{5} & \frac{-4\varepsilon+2}{5} & \frac{2}{5} & \frac{-\varepsilon}{5} \\ \frac{1}{10} & \frac{-2}{5} & \frac{1}{5} & \frac{1}{10} \end{bmatrix}$$

If we express

$$\mathbf{P} = \mathbf{K}\boldsymbol{\lambda}\mathbf{K}^{-1}$$

$$\begin{aligned}
&= (\mathbf{c}_3 \ \mathbf{c}_1 \ \mathbf{c}_4 \ \mathbf{c}_2) \boldsymbol{\lambda} \begin{bmatrix} \mathbf{d}'_3 \\ \mathbf{d}'_1 \\ \mathbf{d}'_4 \\ \mathbf{d}'_2 \end{bmatrix} \\
&= \begin{bmatrix} 0 & 1 & 0 & 0 \\ \varepsilon' & 1 & -1 & \varepsilon \\ 1 & 1 & 1 & 1 \\ 4\varepsilon' - 2 & 1 & 4 & 4\varepsilon - 2 \end{bmatrix} \begin{bmatrix} \varepsilon' & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & \varepsilon \end{bmatrix} \begin{bmatrix} \frac{5\varepsilon-4}{5} & \frac{-4\varepsilon+2}{5} & \frac{2}{5} & -\frac{\varepsilon}{5} \\ 1 & 0 & 0 & 0 \\ \frac{1}{10} & -\frac{2}{5} & \frac{1}{5} & \frac{1}{10} \\ \frac{-10\varepsilon-3}{10} & \frac{4\varepsilon}{5} & \frac{2}{5} & \frac{2\varepsilon-1}{10} \end{bmatrix} \\
&= \begin{bmatrix} 0 & 1 & 0 & 0 \\ \varepsilon'^2 & 1 & -\frac{1}{4} & \varepsilon^2 \\ \varepsilon' & 1 & \frac{1}{4} & \varepsilon \\ 4\varepsilon'^2 - 2\varepsilon' & 1 & 1 & 4\varepsilon^2 - 2\varepsilon \end{bmatrix} \begin{bmatrix} \frac{5\varepsilon-4}{5} & \frac{-4\varepsilon+2}{5} & \frac{2}{5} & -\frac{\varepsilon}{5} \\ 1 & 0 & 0 & 0 \\ \frac{1}{10} & -\frac{2}{5} & \frac{1}{5} & \frac{1}{10} \\ \frac{-10\varepsilon-3}{10} & \frac{4\varepsilon}{5} & \frac{2}{5} & \frac{2\varepsilon-1}{10} \end{bmatrix} \\
&= \begin{bmatrix} 0 & 1 & 0 & 0 \\ \frac{1+2\varepsilon'}{4} & 1 & -\frac{1}{4} & \frac{1+2\varepsilon}{4} \\ \varepsilon' & 1 & \frac{1}{4} & \varepsilon \\ 1 & 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} \frac{5\varepsilon-4}{5} & \frac{-4\varepsilon+2}{5} & \frac{2}{5} & -\frac{\varepsilon}{5} \\ 1 & 0 & 0 & 0 \\ \frac{1}{10} & -\frac{2}{5} & \frac{1}{5} & \frac{1}{10} \\ \frac{-10\varepsilon-3}{10} & \frac{4\varepsilon}{5} & \frac{2}{5} & \frac{2\varepsilon-1}{10} \end{bmatrix} \\
&= \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{2} & \frac{1}{4} & 0 \\ \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} \\ 0 & 0 & 1 & 0 \end{bmatrix}
\end{aligned}$$

The algebra to obtain the last matrix is omitted except that associated with the (21) element.

$$\begin{aligned}
(21) \text{ element} &= \frac{1+2\varepsilon'}{4} \left( \frac{5\varepsilon-4}{5} \right) + 1 - \frac{1}{40} + \frac{1+2\varepsilon}{4} \left( \frac{-10\varepsilon-3}{10} \right) \\
&= \frac{5\varepsilon-4+10\varepsilon\varepsilon'-8\varepsilon'}{20} + 1 - \frac{1}{40} + \frac{-10\varepsilon-3-20\varepsilon^2-6\varepsilon}{40} \\
&= \frac{10\varepsilon-8+20\left(-\frac{1}{4}\right)-16\varepsilon'-10\varepsilon-3-20\varepsilon^2-6\varepsilon}{40} + 1 - \frac{1}{40} \\
&= \frac{-16-16\varepsilon'-20\varepsilon^2-6\varepsilon}{40} + 1 - \frac{1}{40} \\
&= \frac{-16-16\left(\frac{1}{2}-\varepsilon\right)-20\left(\frac{1}{4}+\frac{1}{2}\varepsilon\right)-6\varepsilon}{40} + 1 - \frac{1}{40} \\
&= \frac{-16-8+16\varepsilon-5-10\varepsilon-6\varepsilon}{40} + 1 - \frac{1}{40} \\
&= \frac{-29}{40} - \frac{1}{40} + 1 \\
&= \frac{1}{4}
\end{aligned}$$

c. The order in which you arrange the right eigenvectors in the C matrix, the left eigenvectors in the inverse, and the eigenvalues in the diagonal matrix, is immaterial as long as the order is the same or consistent in all three matrices.

**Exercise 7.9.**

a. The matrix  $\mathbf{A}_1$  which transforms the probabilities,  $\delta_{\ddot{A}\ddot{B}t-1}, \Delta_{\ddot{A}\ddot{B}t-1}, \dots, \theta_{ABt-1}$ , in the  $t-1$  generation to those in the  $t$  generation can be written as follows from the functional relations given in Example 4.11 (p. 4.110).

$$\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)}$$

$$\begin{bmatrix} \delta_{\ddot{A}\ddot{B}t} \\ \Delta_{\ddot{A}\ddot{B}t} \\ \Delta_{\ddot{A}+\ddot{B}t} \\ \gamma_{\ddot{A}Bt} \\ \gamma_{\ddot{A}\ddot{B}t} \\ F_{\ddot{A}t} \\ F_{\ddot{B}t} \\ \theta_{ABt} \\ 1 \end{bmatrix} = \begin{bmatrix} \delta_{\ddot{A}\ddot{B}} & \Delta_{\ddot{A}+\ddot{B}} & \gamma_{\ddot{A}\ddot{B}} & F_{\ddot{B}} & 1 \\ \frac{1}{4} & 0 & 0 & \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{4} & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} & \frac{1}{8} \\ 0 & 0 & 0 & \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{1}{8} & \frac{1}{8} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \delta_{\ddot{A}\ddot{B}t-1} \\ \Delta_{\ddot{A}\ddot{B}t-1} \\ \Delta_{\ddot{A}+\ddot{B}t-1} \\ \gamma_{\ddot{A}Bt-1} \\ \gamma_{\ddot{A}\ddot{B}t-1} \\ F_{\ddot{A}t-1} \\ F_{\ddot{B}t-1} \\ \theta_{ABt-1} \\ 1 \end{bmatrix} \quad \text{equation (1)}$$

$$\begin{matrix} \Delta_{\ddot{A}\ddot{B}} & \gamma_{\ddot{A}\ddot{B}} & F_{\ddot{A}} & \theta_{AB} \end{matrix}$$

b.i. The matrix  $\mathbf{T}$  which transforms the probabilities,  $\delta_{\ddot{A}\ddot{B}t}, \Delta_{\ddot{A}\ddot{B}t}, \dots, \theta_{ABt}$ , to the condensed coefficients of identity in generation  $t$  can be written from the functional relations given in equation (4.82).

$$\mathbf{f}_2^{(t)} = \mathbf{T} \mathbf{f}_1^{(t)}$$

$$\begin{bmatrix} \Delta_1 \\ \Delta_2 \\ \Delta_3 \\ \Delta_4 \\ \Delta_5 \\ \Delta_6 \\ \Delta_7 \\ \Delta_8 \\ \Delta_9 \end{bmatrix} = \begin{bmatrix} \delta_{\ddot{A}\ddot{B}} & \Delta_{\ddot{A}+\ddot{B}} & \gamma_{\ddot{A}\ddot{B}} & F_{\ddot{B}} & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -2 & 0 & 0 & 2 & 0 & 0 & 0 & 0 & 0 \\ -2 & 0 & 0 & 0 & 2 & 0 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -2 & 0 & 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ -2 & -1 & 0 & -2 & 0 & 1 & 0 & 0 & 0 \\ 2 & -1 & 0 & 0 & -2 & 0 & 1 & 0 & 0 \\ 8 & 0 & -4 & -4 & -4 & 0 & 0 & 4 & 0 \\ -6 & 1 & 2 & 4 & 4 & -1 & -1 & -4 & 1 \end{bmatrix} \begin{bmatrix} \delta_{\ddot{A}\ddot{B}} \\ \Delta_{\ddot{A}\ddot{B}} \\ \Delta_{\ddot{A}+\ddot{B}} \\ \gamma_{\ddot{A}\ddot{B}} \\ \gamma_{\ddot{A}\ddot{B}} \\ F_{\ddot{A}} \\ F_{\ddot{B}} \\ \theta_{AB} \\ 1 \end{bmatrix} \quad \text{equation (2)}$$

$$\begin{matrix} \Delta_{\ddot{A}\ddot{B}} & \gamma_{\ddot{A}\ddot{B}} & F_{\ddot{A}} & \theta_{AB} \end{matrix}$$

b.ii. Part (a) gives the relation, say, equation (1),  $\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)}$ , for vector  $\mathbf{f}_1$  from generation  $t-1$  to generation  $t$ , and part b.i gives the relation, say, equation (2),  $\mathbf{f}_2^{(t)} = \mathbf{T} \mathbf{f}_1^{(t)}$ , between vectors  $\mathbf{f}_1$  and  $\mathbf{f}_2$  in any

generation. We desire to find the matrix  $\mathbf{A}_2$  which relates vector  $\mathbf{f}_2$  from generation  $t - 1$  to generation  $t$ , i.e.,  $\mathbf{f}_2^{(t)} = \mathbf{A}_2 \mathbf{f}_2^{(t-1)}$ . Equation (1) relates one generation to the next, but it is in terms of  $\mathbf{f}_1$ . We desire an equation that relates one generation to the next in terms of  $\mathbf{f}_2$ . Hence, we solve equation (2) for  $\mathbf{f}_1$  as a function of  $\mathbf{f}_2$ , substitute it in equation (1), and solve for  $\mathbf{f}_2$ . Starting with equation (2) we solve for  $\mathbf{f}_1$  in generation  $t$  (and similarly for generation  $t - 1$ )

$$\begin{aligned}\mathbf{f}_2^{(t)} &= \mathbf{T} \mathbf{f}_1^{(t)} \\ \mathbf{T}^{-1} \mathbf{f}_2^{(t)} &= \mathbf{T}^{-1} \mathbf{T} \mathbf{f}_1^{(t)} \\ &= \mathbf{f}_1^{(t)} \\ \mathbf{f}_1^{(t)} &= \mathbf{T}^{-1} \mathbf{f}_2^{(t)} \quad \text{equation (3a)}\end{aligned}$$

and similarly for generation  $t - 1$

$$\mathbf{f}_1^{(t-1)} = \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} \quad \text{equation (3b)}$$

Then we substitute equation (3a) on the left side of equation (1) for generation  $t$  and likewise we substitute equation (3b) on the right side of equation (1) for generation  $t - 1$ , namely.

$$\begin{aligned}\mathbf{f}_1^{(t)} &= \mathbf{A}_1 \mathbf{f}_1^{(t-1)} \\ \mathbf{T}^{-1} \mathbf{f}_2^{(t)} &= \mathbf{A}_1 \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)}\end{aligned}$$

Premultiplying both sides by  $\mathbf{T}$ , we obtain

$$\begin{aligned}\mathbf{T} \mathbf{T}^{-1} \mathbf{f}_2^{(t)} &= \mathbf{T} \mathbf{A}_1 \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} \\ \mathbf{f}_2^{(t)} &= \mathbf{T} \mathbf{A}_1 \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} \\ &= \mathbf{A}_2 \mathbf{f}_2^{(t-1)}\end{aligned}$$

Therefore  $\mathbf{A}_2 = \mathbf{T} \mathbf{A}_1 \mathbf{T}^{-1}$ .

An alternative, more succinct solution is the following:

$$\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)} \quad \text{equation (1) \quad between generations (we know)}$$

$$\mathbf{f}_2^{(t)} = \mathbf{T} \mathbf{f}_1^{(t)} \quad \text{equation (2) \quad within any generation (we know)}$$

Substitute equation (1) in equation (2)

$$\mathbf{f}_2^{(t)} = \mathbf{T} \mathbf{A}_1 \mathbf{f}_1^{(t-1)} \quad \text{equation (3)}$$

Equation (2) can be rewritten as

$$\mathbf{f}_2^{(t-1)} = \mathbf{T} \mathbf{f}_1^{(t-1)} \quad \text{equation (4)}$$

Solving equation (4) for  $\mathbf{f}_1^{(t-1)}$ , we premultiply both sides of equation (4) by  $\mathbf{T}^{-1}$

$$\mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} = \mathbf{T}^{-1} \mathbf{T} \mathbf{f}_1^{(t-1)}$$

$$\mathbf{f}_1^{(t-1)} = \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} \quad \text{equation (5)}$$

Substituting equation (5) in equation (3)

$$\mathbf{f}_2^{(t)} = \mathbf{T} \mathbf{A}_1 \mathbf{T}^{-1} \mathbf{f}_2^{(t-1)} \quad \text{equation (6)}$$

Thus,  $\mathbf{A}_2 = \mathbf{T} \mathbf{A}_1 \mathbf{T}^{-1}$

**Exercise 7.10.**

We are given the  $\mathbf{P}$  matrix. We suppose that there exists a nonsingular  $\mathbf{C}$  matrix and its inverse  $\mathbf{C}^{-1}$  which will diagonalize the  $\mathbf{P}$  matrix, i.e.,

$$\lambda = \mathbf{C}^{-1}\mathbf{P}\mathbf{C}$$

where  $\lambda$  is a diagonal matrix. Hence

$$\mathbf{P} = \mathbf{C}\lambda\mathbf{C}^{-1}$$

We can rewrite that equation (for  $s = 4$ ) as

$$\begin{aligned} \mathbf{P} &= (\mathbf{c}_1 \ \mathbf{c}_2 \ \mathbf{c}_3 \ \mathbf{c}_4) \begin{bmatrix} \lambda_1 & 0 & 0 & 0 \\ 0 & \lambda_2 & 0 & 0 \\ 0 & 0 & \lambda_3 & 0 \\ 0 & 0 & 0 & \lambda_4 \end{bmatrix} \begin{bmatrix} \mathbf{d}'_1 \\ \mathbf{d}'_2 \\ \mathbf{d}'_3 \\ \mathbf{d}'_4 \end{bmatrix} \\ &= (\mathbf{c}_1\lambda_1 \ \mathbf{c}_2\lambda_2 \ \mathbf{c}_3\lambda_3 \ \mathbf{c}_4\lambda_4) \begin{bmatrix} \mathbf{d}'_1 \\ \mathbf{d}'_2 \\ \mathbf{d}'_3 \\ \mathbf{d}'_4 \end{bmatrix} \\ &= \lambda_1\mathbf{c}_1\mathbf{d}'_1 + \lambda_2\mathbf{c}_2\mathbf{d}'_2 + \lambda_3\mathbf{c}_3\mathbf{d}'_3 + \lambda_4\mathbf{c}_4\mathbf{d}'_4 \\ &= \sum_{j=1}^s \lambda_j \mathbf{c}_j \mathbf{d}'_j \\ &= \sum_{j=1}^s \lambda_j \mathbf{A}_j \end{aligned}$$

This is known as the spectral resolution or spectral decomposition of  $\mathbf{P}$  (see pp. 7.31 to 7.38). Before this method offers any simplicity in powering the  $\mathbf{P}$  matrix, the  $\mathbf{A}$  matrices must possess some simplifying features. Otherwise  $\mathbf{P}^2$  involves  $s^2 = 4^2 = 16$  sums each of four product terms,  $\mathbf{P}^3$  involves  $4^3 = 64$  sums each of 16 product terms, etc. Fortunately it can be shown that  $\mathbf{A}_i\mathbf{A}_j = \mathbf{0}$  for  $i \neq j$  (see Box 7.1, pp. 7.35-7.36), so all cross product terms equal zero and  $\mathbf{A}_i\mathbf{A}_j = \mathbf{A}_j$  for  $i = j$ , so all squares or any power of  $\mathbf{A}_j$  equals  $\mathbf{A}_j$  itself. These properties of the  $\mathbf{A}_j$  matrices permit easy powering of the  $\mathbf{P}$  matrix. For example,

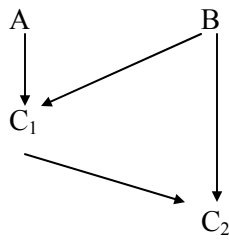
$$\begin{aligned} \mathbf{P}^2 &= \left( \sum_{j=1}^s \lambda_j \mathbf{A}_j \right)^2 \\ &= \sum_{j=1}^s \lambda_j^2 \mathbf{A}_j \end{aligned}$$

or

$$\mathbf{P}^t = \sum_{j=1}^s \lambda_j^t \mathbf{A}_j$$

**Exercise 7.11.**

The younger parent to offspring mating system is diagrammed in Fig. 6.8 (p. 6.53) and the first two generations are repeated here



If we start with individuals  $A$  and  $B$  and assume that both may be either  $AA$ ,  $Aa$ , or  $aa$ , we would have nine mating kinds [see equation (7.39) for full sibs].

		Individual B		
		AA	Aa	aa
Ind. A	AA	1	3a	6a
	Aa	3b	5	4a
	aa	6b	4b	2

However, we realize that after  $A \times B$  mating, we can have no matings of the kind  $AA \times aa$ , because one is always mating a parent with an offspring and the offspring must always receive a gene from the parent. Hence matings 6a and 6b can not occur after the  $A \times B$  mating.

We have the following mating kinds for generation 1:

		Individual B (= parent)		
		AA	Aa	aa
Individual $C_1$ (= offspring)	AA	1	3a	
	Aa	3b	5	4a
	aa		4b	2

Hence, we consider the genotypic outcomes from the possible  $B \times C_1$  mating and write their frequencies in the  $\mathbf{P}$  matrix as follows:

$C_1 \times C_2$  mating

(parent×offsp) $B \times C_1$	AA×AA 1	aa×aa 2	Aa×AA 3a	AA×Aa 3b	aa×Aa 4a	Aa×aa 4b	Aa×Aa 5
1 AA × AA	$\mathbf{P} =$	(					
2 aa × aa							
3a Aa × AA							
3b AA × Aa							
4a aa × Aa							
4b Aa × aa							
5 Aa × Aa							

Next we permute the rows and columns in like manner to bring the matings of a similar type together, i.e., heterozygous parent by homozygous offspring (matings 3a,  $Aa \times AA$ , and 4b,  $Aa \times aa$ ) and homozygous parent by heterozygous offspring (matings 3b,  $AA \times Aa$ , and 4a,  $aa \times Aa$ ). First, we permute the rows to obtain order 1, 2, 3a, 4b, 3b, 4a, 5

(parent×offsp) $B \times C_1$	AA×AA 1	aa×aa 2	Aa×AA 3a	AA×Aa 3b	aa×Aa 4a	Aa×aa 4b	Aa×Aa 5
1 AA × AA	$\mathbf{P} =$	(					
2 aa × aa							
3a Aa × AA							
4b Aa × aa							
3b AA × Aa							
4a aa × Aa							
5 Aa × Aa							

Then we permute the columns to the same order as that of the rows as follows:

(parent×offsp) B × C <sub>1</sub>	AA×AA 1	aa×aa 2	Aa×AA 3a	Aa×aa 4b	AA×Aa 3b	aa×Aa 4a	Aa×Aa 5
1 AA × AA	1						
2 aa × aa		1					
3a Aa × AA	$\frac{1}{2}$				$\frac{1}{2}$		
4b Aa × aa		$\frac{1}{2}$				$\frac{1}{2}$	
3b AA × Aa			$\frac{1}{2}$				$\frac{1}{2}$
4a aa × Aa				$\frac{1}{2}$			$\frac{1}{2}$
5 Aa × Aa			$\frac{1}{4}$	$\frac{1}{4}$			$\frac{1}{2}$

It would appear that one can collapse mating kinds 1 and 2 (homozygote by homozygote), 3a and 4b (parental heterozygote by offspring homozygote), and 3b and 4a (parental homozygote by offspring heterozygote), so that one would have four mating types:

Type	Kind
1 same homozygote by homozygote	(1) AA × AA (2) aa × aa
2 parental heterozygote by offspring homozygote	(3a) Aa × AA (4b) Aa × aa
3 parental homozygote by offspring heterozygote	(3b) AA × Aa (4a) aa × Aa
4 parental heterozygote by offspring heterozygote	(5) Aa × Aa

The dimensions of the **P** matrix would be reduced from a  $7 \times 7$  to a  $4 \times 4$  matrix. Thus the **P** matrix would appear to be

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \frac{1}{2} & 0 & \frac{1}{2} & 0 \\ 0 & \frac{1}{2} & 0 & \frac{1}{2} \\ 0 & \frac{1}{2} & 0 & \frac{1}{2} \end{bmatrix}$$

It would appear that this matrix is singular and that one could collapse this matrix further. At this point I am unclear what the solution is. Fisher (R. A. Fisher, 1949, *The Theory of Inbreeding*, Oliver & Boyd, London, pp. 67-69) discussed this mating system. I believe that he assumed multiple alleles and had five mating types, but I do not profess to understand what Fisher has done.

**Exercise 7.12.**

The mating types for an X-linked locus with multiple alleles are

Type	Male	Female	Example
1	a	aa	$A_1 \times A_1A_1$ $A_2 \times A_2A_2$
2	a	ab	$A_1 \times A_1A_2$ $A_2 \times A_2A_3$
3	a	bb	$A_1 \times A_2A_2$ $A_3 \times A_2A_2$
4	a	bc	$A_1 \times A_2A_3$ $A_3 \times A_1A_2$

**Exercise 7.13.**

a.i. The frequencies of the nine genotypes in the  $F_2$  population are

AABB	$(1/4)(1/4) = 1/16$
AABb	$(1/4)(1/2) = 1/8$
AAbb	$(1/4)(1/4) = 1/16$
AaBB	$(1/2)(1/4) = 1/8$
AaBb	$(1/2)(1/2) = 1/4$
Aabb	$(1/2)(1/4) = 1/8$
aaBB	$(1/4)(1/4) = 1/16$
aaBb	$(1/4)(1/2) = 1/8$
aabb	$(1/4)(1/4) = 1/16$
Total	$16/16 = 1$

a.ii. The frequencies of the nine genotypes in the  $F_3$  population, assuming self-fertilization, are

AABB	$(3/8)(3/8) = 9/64$
AABb	$(3/8)(1/4) = 3/32$
AAbb	$(3/8)(3/8) = 9/64$
AaBB	$(1/4)(3/8) = 3/32$
AaBb	$(1/4)(1/4) = 1/16$
Aabb	$(1/4)(3/8) = 3/32$
aaBB	$(3/8)(3/8) = 9/64$
aaBb	$(3/8)(1/4) = 3/32$
aabb	$(3/8)(3/8) = 9/64$
Total	$64/64 = 1$

a.iii. To calculate the frequency of each of the nine genotypes in any  $F_{2+t}$  generation, we desire to express the frequency of either homozygote or the heterozygote at any locus as a function of the inbreeding coefficient which in turn is expressed as a function of generation  $t$ . First, for the  $i$ th homozygote expressed as a deviation from panmixia we have

$$p_{iiF} = p_i^2 + Fp_i(1 - p_i) \quad \text{equation (5.19)}$$

Then from equation (6.23) for self-fertilization we express  $F$  as a function of the  $t$ th generation. Thus,

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

Substituting that expression in the one above for  $p_{iiF}$ , we have

$$p_{iiF} = p_i^2 + \left[1 - \left(\frac{1}{2}\right)^t\right] p_i(1 - p_i)$$

Substituting  $p_i = \frac{1}{2}$ , we obtain

$$p_{iiF} = \left(\frac{1}{2}\right)^2 + \left[1 - \left(\frac{1}{2}\right)^t\right] \frac{1}{2} \cdot \frac{1}{2} = \frac{1}{4} + \left[1 - \left(\frac{1}{2}\right)^t\right] \frac{1}{4} = \frac{1}{4} \left[1 + 1 - \left(\frac{1}{2}\right)^t\right] = \frac{1}{4} \left[2 - \frac{2}{2}\left(\frac{1}{2}\right)^t\right] = \frac{1}{2} \left[1 - \left(\frac{1}{2}\right)^{t+1}\right]$$

Second, for the  $ij$ th heterozygote expressed as a deviation from panmixia we have

$$2p_{ijF} = 2p_i p_j - (2p_i p_j)F = 2p_i p_j - (2p_i p_j) \left[1 - \left(\frac{1}{2}\right)^t\right]$$

Substituting  $p_i = \frac{1}{2}$ , we obtain

$$2p_{ijF} = 2p_i p_j - (2p_i p_j) \left[1 - \left(\frac{1}{2}\right)^t\right] = 2 \cdot \frac{1}{2} \cdot \frac{1}{2} - \left(2 \cdot \frac{1}{2} \cdot \frac{1}{2}\right) \left[1 - \left(\frac{1}{2}\right)^t\right] = \frac{1}{2} - \frac{1}{2} \left[1 - \left(\frac{1}{2}\right)^t\right] = \frac{1}{2} \left[1 - 1 + \left(\frac{1}{2}\right)^t\right] = \left(\frac{1}{2}\right)^{t+1}$$

Using these expressions for the homozygotes and the heterozygotes, the frequencies of the nine genotypes in any generation  $t$  are

$$\begin{aligned} AABB & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\}^2 \\ AABb & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\} \left\{ \left(\frac{1}{2}\right)^{t+1} \right\} \\ AAbb & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\}^2 \\ AaBB & \left(\frac{1}{2}\right)^{t+1} \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\} \\ AaBb & \left\{ \left(\frac{1}{2}\right)^{t+1} \right\}^2 \\ Aabb & \left(\frac{1}{2}\right)^{t+1} \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\} \\ aaBB & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\}^2 \\ aaBb & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\} \left(\frac{1}{2}\right)^{t+1} \\ aabb & \left\{ \frac{1}{2} \left[ 1 - \left(\frac{1}{2}\right)^{t+1} \right] \right\}^2 \end{aligned}$$

I have not attempted to simplify these expressions.

a.iv. When the population is fully inbred, there are only four double homozygotes—each with equal frequency of  $\frac{1}{4}$ .

b.i. From equation (2.118),  $i = k = 1, j = l = 2$ , one can easily obtain the frequencies of the ten genotypes in the  $F_2$  or random-mating population as follows:

Each of the four double homozygotes is represented by a single cell out of 16 in equation (2.118).

$$P\left(\frac{A_1B_1}{A_1B_1}\right) = P\left(\frac{AB}{AB}\right) = P\left(\frac{A_2B_2}{A_2B_2}\right) = P\left(\frac{ab}{ab}\right) = \left(\frac{1-\rho}{2}\right)^2, \quad P\left(\frac{A_1B_2}{A_1B_2}\right) = P\left(\frac{Ab}{Ab}\right) = P\left(\frac{A_2B_1}{A_2B_1}\right) = P\left(\frac{aB}{aB}\right) = \left(\frac{\rho}{2}\right)^2$$

The four single heterozygotes are equally frequent and each is represented by two equally frequent cells out of 16 in equation (2.118).

$$P\left(\frac{AB}{Ab}\right) = P\left(\frac{aB}{ab}\right) = P\left(\frac{AB}{aB}\right) = P\left(\frac{Ab}{ab}\right) = 2\left(\frac{1-\rho}{2}\right)\left(\frac{\rho}{2}\right)$$

Each of the coupling and repulsion phase double heterozygotes are represented by two equally frequent cells out of 16 in equation (2.118).

$$P\left(\frac{AB}{ab}\right) = 2\left(\frac{1-\rho}{2}\right)^2, \quad P\left(\frac{Ab}{aB}\right) = 2\left(\frac{\rho}{2}\right)^2$$

b.ii. The 10 x 10 transition matrix  $\mathbf{P}$  is given in equation (7.318) and will not be repeated here.

b.iii. With  $\rho_1 = 0.2$  the frequencies of the ten genotypes in the  $F_2$  generation are

$$P\left(\frac{AB}{AB}\right) = P\left(\frac{ab}{ab}\right) = \left(\frac{1-\rho}{2}\right)^2 = \left(\frac{1-0.2}{2}\right)^2 = (0.4)^2 = 0.16 = f_1 = f_4, \text{ respectively}$$

$$P\left(\frac{Ab}{Ab}\right) = P\left(\frac{aB}{aB}\right) = \left(\frac{\rho}{2}\right)^2 = \left(\frac{0.2}{2}\right)^2 = (0.1)^2 = 0.01 = f_2 = f_3, \text{ respectively}$$

$$P\left(\frac{AB}{Ab}\right) = P\left(\frac{aB}{ab}\right) = P\left(\frac{AB}{aB}\right) = P\left(\frac{Ab}{ab}\right) = 2\left(\frac{1-\rho}{2}\right)\left(\frac{\rho}{2}\right) = 2(0.4)(0.1) = 0.08 = f_5 = f_8 = f_6 = f_7, \text{ respectively}$$

$$P\left(\frac{AB}{ab}\right) = 2\left(\frac{1-\rho}{2}\right)^2 = 2(0.16) = 0.32 = f_9$$

$$P\left(\frac{Ab}{aB}\right) = 2\left(\frac{\rho}{2}\right)^2 = 2(0.01) = 0.02 = f_{10}$$

The  $\mathbf{P}$  matrix in equation (7.318), evaluated for  $\rho = 0.2$ , is

$$\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 & 0 & 0 \\ \frac{1}{4} & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{4} & \frac{1}{4} & 0 & 0 & 0 & \frac{1}{2} & 0 & 0 \\ 0.16 & 0.01 & 0.01 & 0.16 & 0.08 & 0.08 & 0.08 & 0.08 & 0.32 & 0.02 \\ 0.01 & 0.16 & 0.16 & 0.01 & 0.08 & 0.08 & 0.08 & 0.08 & 0.02 & 0.32 \end{bmatrix}$$

The frequencies of the ten genotypes in the  $F_3$  generation, using the  $\mathbf{P}$  matrix, is

$$\mathbf{f}'^{(0)}\mathbf{P} = \mathbf{f}'^{(1)}$$

$$\begin{aligned}
 & [0.16 \ 0.01 \ 0.01 \ 0.16 \ 0.08 \ 0.08 \ 0.08 \ 0.08 \ 0.32 \ 0.02] \\
 & \begin{bmatrix}
 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
 \frac{1}{4} & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 & 0 & 0 \\
 \frac{1}{4} & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 & 0 \\
 0 & \frac{1}{4} & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{2} & 0 & 0 & 0 \\
 0 & 0 & \frac{1}{4} & \frac{1}{4} & 0 & 0 & 0 & \frac{1}{2} & 0 & 0 \\
 0.16 & 0.01 & 0.01 & 0.16 & 0.08 & 0.08 & 0.08 & 0.08 & 0.32 & 0.02 \\
 0.01 & 0.16 & 0.16 & 0.01 & 0.08 & 0.08 & 0.08 & 0.08 & 0.02 & 0.32
 \end{bmatrix}
 \end{aligned}$$

$$= [0.2514 \ 0.0564 \ 0.0564 \ 0.2514 \ 0.0672 \ 0.0672 \ 0.0672 \ 0.0672 \ 0.1028 \ 0.0128]$$

**Exercise 7.14.**

Genotypic disequilibrium (see pp. 7.135 to 7.137) is a phenomenon that arises in partial inbred populations when two loci are linked ( $\rho_1 < 0.5$ ), but yet linkage equilibrium exists with respect to gametic frequencies. The frequency of the double homozygotes and double heterozygotes are each individually higher, and those frequencies of the single heterozygotes are individually lower, compared to those frequencies under independence ( $\rho_1 = 0.5$ ). This is true for any  $F$  value greater than zero but less than 1, but yet for any generation gametic frequencies are those expected based upon linkage equilibrium. With a fully inbred population, the genotypic disequilibrium disappears, so genotypic disequilibrium is an ephemeral condition which exists only during the inbreeding process itself.

**Exercise 7.15.**

Genotypic disequilibrium exists when the frequencies of the genotypes involving two or more loci are not equal to the product of the corresponding gametic frequencies that produce the individuals. It occurs in partially inbred populations when loci are linked. See pp. 7.135 to 7.137.

**Exercise 7.16.**

Genotypic disequilibrium is equal to the departure of any genotypic frequency from that expected value based upon the product of the corresponding gametic frequencies in a population in linkage equilibrium. It occurs only during inbreeding when  $F$  is greater than zero but less than one, and when loci are linked. See pp. 7.135-7.137.

**Exercise 7.17.**

a. The transition matrix is (see Section 7.2.1)

$$\mathbf{P} = \begin{bmatrix}
 1 & 0 & 0 \\
 0 & 1 & 0 \\
 \frac{1}{4} & \frac{1}{4} & \frac{1}{2}
 \end{bmatrix}$$

b. The eigenvalues are (see Section 7.2.3)

$$\begin{vmatrix} 1-\lambda & 0 & 0 \\ 0 & 1-\lambda & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{2}-\lambda \end{vmatrix} = (1-\lambda)^2 \left(\frac{1}{2}-\lambda\right) + 0 + 0 - (0)(1-\lambda)\left(\frac{1}{4}\right) - (1-\lambda)(0)\left(\frac{1}{4}\right) - (0)(0)\left(\frac{1}{2}-\lambda\right) = 0$$

$$\lambda_1 = 1, \lambda_2 = 1, \lambda_3 = \frac{1}{2}$$

c. For the right-hand eigenvectors one possible solution for the eigenvectors is

$$(\mathbf{P} - \lambda_j \mathbf{I}) \mathbf{c}_j = 0 \quad [\text{equation (7.67)}]$$

$$\begin{bmatrix} 1-1 & 0 & 0 \\ 0 & 1-1 & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{2}-1 \end{bmatrix} \begin{bmatrix} c_{11} \\ c_{21} \\ c_{31} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{1}{4} & \frac{1}{4} & -\frac{1}{2} \end{bmatrix} \begin{bmatrix} c_{11} \\ c_{21} \\ c_{31} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\frac{1}{4}c_{11} + \frac{1}{4}c_{21} - \frac{1}{2}c_{31} = 0$$

$$\frac{1}{4}c_{11} + \frac{1}{4}c_{21} = \frac{1}{2}c_{31}$$

$$\frac{1}{4}(1) + \frac{1}{4}(0) = \frac{1}{2}c_{31}$$

let  $c_{21}$  be zero, so  $\mathbf{c}_1$  vector is independent of  $\mathbf{c}_2$  vector

$$c_{31} = \frac{1}{2}$$

$$\text{so } \mathbf{c}'_1 = \begin{pmatrix} 1 & 0 & \frac{1}{2} \end{pmatrix}.$$

$$\text{Similarly, } \mathbf{c}'_2 = \begin{pmatrix} 0 & 1 & \frac{1}{2} \end{pmatrix}.$$

Then  $\mathbf{c}_3$  vector is

$$\begin{bmatrix} 1-\frac{1}{2} & 0 & 0 \\ 0 & 1-\frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{2}-\frac{1}{2} \end{bmatrix} \begin{bmatrix} c_{13} \\ c_{23} \\ c_{33} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{2} & 0 \\ \frac{1}{4} & \frac{1}{4} & 0 \end{bmatrix} \begin{bmatrix} c_{13} \\ c_{23} \\ c_{33} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\frac{1}{2}c_{13} = 0 \quad \text{so } c_{13} \text{ must be zero}$$

$$\frac{1}{2}c_{23} = 0 \quad \text{so } c_{23} \text{ must be zero}$$

$$\text{then } \frac{1}{4}c_{13} + \frac{1}{4}c_{23} + (0)c_{33} = 0$$

$$\frac{1}{4}(0) + \frac{1}{4}(0) + (0)c_{33} = 0$$

so we can set  $c_{33} = 1$

$$\text{Thus, } \mathbf{c}'_3 = \begin{pmatrix} 0 & 0 & 1 \end{pmatrix}$$

The matrix  $\mathbf{C}$  composed of the three column, right-hand eigenvectors is

$$\mathbf{C} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{1}{2} & \frac{1}{2} & 1 \end{bmatrix}$$

Its determinant is  $|\mathbf{C}|=1$ , so the matrix  $\mathbf{C}$  is nonsingular.

d. For the left-hand eigenvectors we have

$$\mathbf{d}'_j (\mathbf{P} - \lambda_j \mathbf{I}) = \mathbf{0}' \quad [\text{equation (7.74)}]$$

$$\begin{bmatrix} d_{1j} & d_{2j} & d_{3j} \end{bmatrix} \begin{bmatrix} 1-\lambda_j & 0 & 0 \\ 0 & 1-\lambda_j & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{2}-\lambda_j \end{bmatrix} = [0+0+0]$$

Taking the transpose of both sides, we have

$$(\mathbf{P}' - \lambda_j \mathbf{I}) \mathbf{d}_j = \mathbf{0} \quad [\text{equation (7.75)}]$$

$$\begin{bmatrix} 1-\lambda_j & 0 & \frac{1}{4} \\ 0 & 1-\lambda_j & \frac{1}{4} \\ 0 & 0 & \frac{1}{2}-\lambda_j \end{bmatrix} \begin{bmatrix} d_{1j} \\ d_{2j} \\ d_{3j} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} 1-1 & 0 & \frac{1}{4} \\ 0 & 1-1 & \frac{1}{4} \\ 0 & 0 & \frac{1}{2}-1 \end{bmatrix} \begin{bmatrix} d_{11} \\ d_{21} \\ d_{31} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} 0 & 0 & \frac{1}{4} \\ 0 & 0 & \frac{1}{4} \\ 0 & 0 & -\frac{1}{2} \end{bmatrix} \begin{bmatrix} d_{11} \\ d_{21} \\ d_{31} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

The elements  $d_{11}$  and  $d_{21}$  can be equal to any value, but  $d_{31}$  must be equal to zero. Similar conditions must exist for  $\mathbf{d}_2$  vector. Therefore

$$\mathbf{d}'_1 = (1 \ 0 \ 0)$$

$$\mathbf{d}'_2 = (0 \ 1 \ 0)$$

The  $\mathbf{d}_3$  vector is

$$\begin{bmatrix} 1-\frac{1}{2} & 0 & \frac{1}{4} \\ 0 & 1-\frac{1}{2} & \frac{1}{4} \\ 0 & 0 & \frac{1}{2}-\frac{1}{2} \end{bmatrix} \begin{bmatrix} d_{13} \\ d_{23} \\ d_{33} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\begin{bmatrix} \frac{1}{2} & 0 & \frac{1}{4} \\ 0 & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} d_{13} \\ d_{23} \\ d_{33} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}$$

$$\frac{1}{2}d_{13} + \frac{1}{4}d_{33} = 0$$

$$\frac{1}{2}d_{13} = -\frac{1}{4}d_{33}$$

$$d_{13} = -\frac{1}{2}(1) = -\frac{1}{2} \quad \text{setting } d_{33} \text{ equal to } 1$$

$$\frac{1}{2}d_{23} + \frac{1}{4}d_{33} = 0$$

$$\frac{1}{2}d_{23} = -\frac{1}{4}d_{33}$$

$$d_{23} = -\frac{1}{2}(1) = -\frac{1}{2} \quad \text{having set } d_{33} \text{ equal to } 1$$

$$\text{So } \mathbf{d}'_3 = \left(-\frac{1}{2} \quad -\frac{1}{2} \quad 1\right)$$

Check to see that  $\mathbf{d}'_j \mathbf{c}_j = 1$ .

$$\text{For } j = 1, \mathbf{d}'_1 \mathbf{c}_1 = (1 \quad 0 \quad 0) \begin{bmatrix} 1 \\ 0 \\ \frac{1}{2} \end{bmatrix} = 1$$

$$\text{For } j = 2, \mathbf{d}'_2 \mathbf{c}_2 = (0 \quad 1 \quad 0) \begin{bmatrix} 0 \\ 1 \\ \frac{1}{2} \end{bmatrix} = 1$$

$$\text{For } j = 3, \mathbf{d}'_3 \mathbf{c}_3 = \left(-\frac{1}{2} \quad -\frac{1}{2} \quad 1\right) \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} = 1$$

So the matrix  $\mathbf{D}$  composed of the three column, left-hand eigenvectors is

$$\mathbf{D} = \begin{bmatrix} 1 & 0 & -\frac{1}{2} \\ 0 & 1 & -\frac{1}{2} \\ 0 & 0 & 1 \end{bmatrix}$$

Again the same check is

$$\mathbf{D}'\mathbf{C} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{1}{2} & \frac{1}{2} & 1 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

e. The spectral matrices are  $\mathbf{A}_j = \mathbf{c}_j \mathbf{d}'_j$  [see equation (7.79)]

$$\mathbf{A}_1 = \begin{bmatrix} 1 \\ 0 \\ \frac{1}{2} \end{bmatrix} [1 \ 0 \ 0] = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{1}{2} & 0 & 0 \end{bmatrix}$$

$$\mathbf{A}_2 = \begin{bmatrix} 0 \\ 1 \\ \frac{1}{2} \end{bmatrix} [0 \ 1 \ 0] = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & \frac{1}{2} & 0 \end{bmatrix}$$

$$\mathbf{A}_3 = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} \begin{bmatrix} -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix}$$

One can also check that  $\mathbf{A}_1 + \mathbf{A}_2 + \mathbf{A}_3 = \mathbf{I}$

f. The fifth power of the transition matrix by use of the spectral matrices is [see equation (7.84)]

$$\begin{aligned} \mathbf{P}^5 &= (1)^5 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{1}{2} & 0 & 0 \end{bmatrix} + (1)^5 \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & \frac{1}{2} & 0 \end{bmatrix} + \left(\frac{1}{2}\right)^5 \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 \end{bmatrix} \\ &= \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{1}{2} & 0 & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & \frac{1}{2} & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ -\frac{1}{64} & -\frac{1}{64} & \frac{1}{32} \end{bmatrix} \\ &= \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{1}{2} - \frac{1}{64} & \frac{1}{2} - \frac{1}{64} & \frac{1}{32} \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{31}{64} & \frac{31}{64} & \frac{1}{32} \end{bmatrix} \end{aligned}$$

g. The fifth power of the transition matrix by the partitioning method follows. The transition matrix itself is

$$\mathbf{P} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{1}{4} & \frac{1}{4} & \frac{1}{2} \end{bmatrix} = \begin{bmatrix} \mathbf{I} & \mathbf{O} \\ \mathbf{R} & \mathbf{Q} \end{bmatrix} \quad \begin{matrix} 2 \times 2 & 2 \times 1 \\ 1 \times 2 & 1 \times 1 \end{matrix} \quad \text{[equation (7.90)]}$$

and

$$\mathbf{P}^t = \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ (\mathbf{I} - \mathbf{Q}^t)(\mathbf{I} - \mathbf{Q})^{-1} \mathbf{R} & \mathbf{Q}^t \end{bmatrix} \quad \text{[equation (7.97)]}$$

We find the lower right  $1 \times 1$  submatrix  $\mathbf{Q}^t = \left(\frac{1}{2}\right)^5 = \frac{1}{32}$ . Then from equation (7.134) we calculate the quantity

$(\mathbf{I} - \mathbf{Q})^{-1} = 2$  which is needed to calculate the fixation probability and the lower left  $1 \times 2$  submatrix. The fixation probability [equation (7.135)] is

$$(\mathbf{I} - \mathbf{Q})^{-1} \mathbf{R} = 2 \begin{pmatrix} \frac{1}{4} & \frac{1}{4} \end{pmatrix} = \begin{pmatrix} \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

The lower-left  $1 \times 2$  submatrix is

$$\begin{aligned}
 & (\mathbf{I} - \mathbf{Q}^t)(\mathbf{I} - \mathbf{Q})^{-1} \mathbf{R} \\
 & = \left(1 - \left(\frac{1}{2}\right)^5\right) \begin{pmatrix} \frac{1}{2} & \frac{1}{2} \end{pmatrix} = \frac{31}{32} \begin{pmatrix} \frac{1}{2} & \frac{1}{2} \end{pmatrix} = \begin{pmatrix} \frac{31}{64} & \frac{31}{64} \end{pmatrix}
 \end{aligned}$$

Putting the submatrices together we obtain the fifth power of the transition matrix.

$$\mathbf{P}^5 = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{31}{64} & \frac{31}{64} & \frac{1}{32} \end{bmatrix}$$

h. The frequencies of the genotypes in the fifth generation are

$$\mathbf{f}^{(5)} = \mathbf{f}^{(0)} \mathbf{P}^5 = (0.38 \quad 0.11 \quad 0.51) \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ \frac{31}{64} & \frac{31}{64} & \frac{1}{32} \end{bmatrix} = [0.62703125 \quad 0.35703125 \quad 0.01593750]$$

i. No, it is not essential to use this  $3 \times 3$  form for the self-fertilizing mating system because the transition probabilities for an  $Aa \times Aa$  mating type gives equal values of  $\frac{1}{4}$  for each of the two homozygotes, i.e., every time a heterozygous individual is selfed, it produces equal proportions of each of the two homozygotes. Hence, if we know the sum of the two homozygous mating frequencies, we can calculate the mating frequency of each

homozygote. For our example, the  $2 \times 2$  transition matrix is  $\begin{bmatrix} 1 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix}$  and that for  $\mathbf{P}^5 = \begin{bmatrix} 1 & 0 \\ \frac{31}{32} & \frac{1}{32} \end{bmatrix}$ . The sum of

the frequencies of the two homozygotes is  $0.38 + 0.11 = 0.49$ . Hence,  $\mathbf{f}^{(0)} = (0.49 \quad 0.51)$ . Then

$$\mathbf{f}^{(5)} = (0.49 \quad 0.51) \begin{bmatrix} 1 & 0 \\ \frac{31}{32} & \frac{1}{32} \end{bmatrix} = (0.9840625 \quad 0.0159375)$$

$$\text{So } p(AA \times AA) = 0.38 + \frac{0.9840625 - 0.49}{2} = 0.62703125$$

$$p(aa \times aa) = 0.11 + \frac{0.9840625 - 0.49}{2} = 0.35703125$$

An alternative way of calculating the frequencies of the homozygous mating types in generation 5 from the initial frequencies is by the use of the inbreeding coefficient, namely,

$$p(AA \times AA) = f_1^{(0)} + F \frac{1}{2} f_3^{(0)} = 0.38 + \frac{31}{32} \cdot \frac{1}{2} \cdot 0.51 = 0.62703125$$

$$p(aa \times aa) = f_2^{(0)} + F \frac{1}{2} f_3^{(0)} = 0.11 + \frac{31}{32} \cdot \frac{1}{2} \cdot 0.51 = 0.35703125$$

I am unable to cite an equation number in my notes for the above. It seems that the use of the inbreeding coefficient per se to calculate the frequencies of mating kinds from the frequencies of mating types has not been discussed in Chapter 7—even for the selfing system. It would seem that some potential exists for the use of  $F$  in this area for other mating systems, but the topic has not been explored.

**Exercise 7.18.**

a. From equations (6.23) and (6.18) the inbreeding coefficient of a random  $F_7$  individual is  $31/32$  where  $t = 7 - 2 = 5$ , namely,  $F_t = 1 - \left(\frac{1}{2}\right)^t = 1 - \left(\frac{1}{2}\right)^5 = \frac{31}{32}$ .

b. From equations (6.7) and (6.21) the frequency of heterozygotes is  $H_{F_7} = H_5 = H_0(1 - F_5) = H_0P_5 = 0.5 \frac{1}{32} = \frac{1}{64}$ .

c. To calculate the expected frequency of recombinant inbred lines still segregating for that particular locus, we need the frequency of heterozygotes in the previous generation, i.e.,  $H_{F_6} = H_4 = H_0P_4 = 0.5 \frac{1}{16} = \frac{1}{32}$ . The expected frequency of lines homozygous for that particular locus equals  $1 - \frac{1}{32} = \frac{31}{32}$ .

d. The proportion of loci in a random individual in the  $F_7$  generation expected to be homozygous is the same as the expected frequency of homozygotes at any locus. Thus, from equation (6.6c) we have  $\bar{H}_t = \bar{H}_0 + F_t H_0 = 0.5 + \frac{31}{32}(0.5) = \frac{1}{2} + \frac{31}{32}\left(\frac{1}{2}\right) = \frac{1}{2} + \frac{31}{64} = \frac{63}{64}$ . That is, when  $t = 0$  the proportion of homozygotes at any locus is 0.5. Thus, we have the series for the probability of homozygotes for  $t = 0, 1, 2, 3, 4, 5$  as follows:  $\bar{H}_t = \frac{1}{2}, \frac{3}{4}, \frac{7}{8}, \frac{15}{16}, \frac{31}{32}, \frac{63}{64}$ .

e. Of all loci segregating in the cross, the expected frequency of those loci still heterozygous in a random individual in the  $F_7$  generation is  $H_5 = 1 - \bar{H}_5 = 1 - \frac{63}{64} = \frac{1}{64}$ , or from equation (6.6d)

$$H_t = (1 - F_t)H_0 = \left(1 - \frac{31}{32}\right)\left(\frac{1}{2}\right) = \frac{1}{32}\left(\frac{1}{2}\right) = \frac{1}{64}.$$