

EXERCISES FOR CHAPTER 7

Exercise 7.1. Derive the two scales of relation for each of the two following recurrent series:

$$u: 0, \frac{8}{36}, \frac{16}{72}, \frac{248}{1296}, \frac{416}{2592}, \dots$$

$$v: 1, \frac{18}{36}, \frac{26}{72}, \frac{378}{1296}, \frac{626}{2592}, \dots$$

Are the scales of relation for the two series the same or different? Obtain the general term for each series. Use fractions (to avoid rounding errors) -- not decimals.

Exercise 7.2. Suppose that you are given the following two recurrent series:

$$\begin{array}{cccccccc} & 0 & 1 & 2 & 3 & 4 & 5 & 6 \\ \text{Series } u: & 1, & \frac{2}{2}, & \frac{3}{4}, & \frac{5}{8}, & \frac{8}{16}, & \frac{13}{32}, & \frac{21}{64}, \dots \end{array}$$

$$\text{Series } v: \frac{1}{2}, \frac{2}{4}, \frac{3}{8}, \frac{5}{16}, \frac{8}{32}, \frac{13}{64}, \frac{21}{128}, \dots$$

The recurrence relation for both series is

$$u_t = v_t = \frac{1}{2}u_{t-1} + \frac{1}{4}u_{t-2}$$

- Give the general term for each of the two recurrent series.
- Are they different? Why or why not?

Exercise 7.3. Obtain the general term for F for the recurrent series for full-sib mating given in equation (6.29), namely,

$$F: 0, 0, \frac{1}{4}, \frac{3}{8}, \frac{8}{16}, \frac{19}{32}, \dots$$

Hint: Since the recurrence relation for F has a constant term, use the P series and its recurrence relation and then change back to a series in terms of F by substitution.

Exercise 7.4. Define an eigenvalue and eigenvector. In what way have we used them and why have we been interested in their use?

Exercise 7.5. What are the eigenvalues, or latent, or characteristic roots of the following matrix?

$$\begin{bmatrix} 2 & 1 \\ 5 & 6 \end{bmatrix}$$

Exercise 7.6. In Chapter 7 [equations (7.40) and (7.41)] we collapsed the two different homozygous kinds and the two different homozygous-by-heterozygous kinds of full-sib matings into two different mating types, so that we dealt with only a 4×4 transition matrix. Instead of doing that, keep the different mating kinds separate, so that one has a 6×6 transition matrix.

- Give the 6×6 transition matrix.
- Find the eigenvalues. [Hint: The determinant of a 4×4 matrix is equal to elements in any row (or column) times the corresponding cofactor, e.g., $a_{11}A_{11} + a_{12}A_{12} + a_{13}A_{13} + a_{14}A_{14}$. If the derivation of anything is given in my notes, you do not need to repeat it; simply refer to the appropriate equation(s).]

Exercise 7.7.

- a. Give the meaning of an individual element p_{ij} in the \mathbf{P} transition matrix.
 b. Give the meaning of an individual element in the \mathbf{P}^2 matrix. What is such a probability called?

Express any p_{ij} element in the \mathbf{P}^2 matrix as a function of the p_{ij} elements in the \mathbf{P} matrix itself.

What is every element in the \mathbf{P}^2 matrix equal to numerically for full-sib mating with two alleles.

- c. Repeat (b) for the \mathbf{P}^3 matrix.

Exercise 7.8.

- a. In the transition matrix method for self-fertilization, the \mathbf{P} matrix was defined $\begin{bmatrix} 1 & 0 \\ \frac{1}{2} & \frac{1}{2} \end{bmatrix}$ [see equation

(7.28)], and the eigenvalues, 1 and $\frac{1}{2}$, were labeled λ_1 and λ_2 , respectively. Then in obtaining the corresponding eigenvectors, \mathbf{c}_1 and \mathbf{c}_2 , we constructed $\mathbf{C} = (\mathbf{c}_1 \ \mathbf{c}_2)$, and were careful to write the corresponding eigenvalues, $\lambda_1 = 1$ and $\lambda_2 = \frac{1}{2}$, in the 11 and 22 positions on the diagonal of $\boldsymbol{\lambda}$, so that \mathbf{P} was defined

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

$$= (\mathbf{c}_1 \ \mathbf{c}_2) \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix} \begin{bmatrix} \mathbf{d}'_1 \\ \mathbf{d}'_2 \end{bmatrix}$$

where $\mathbf{C}^{-1} = \mathbf{D} = \begin{bmatrix} \mathbf{d}'_1 \\ \mathbf{d}'_2 \end{bmatrix}$

Show that \mathbf{P} remains unchanged, if \mathbf{P} were set equal to

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

$$= (\mathbf{c}_2 \ \mathbf{c}_1) \begin{bmatrix} \lambda_2 & 0 \\ 0 & \lambda_1 \end{bmatrix} \begin{bmatrix} \mathbf{d}'_2 \\ \mathbf{d}'_1 \end{bmatrix}$$

where $\mathbf{K} = (\mathbf{c}_2 \ \mathbf{c}_1)$, and

$$\mathbf{K}^{-1} = \begin{bmatrix} \mathbf{d}'_2 \\ \mathbf{d}'_1 \end{bmatrix}$$

Note that the inverse of \mathbf{K} can be easily obtained by permuting the rows of \mathbf{C}^{-1} .

- b. Show the same as above for the 4×4 \mathbf{P} matrix [equations (7.43) or (7.138)] with

$\lambda_1 = 1, \lambda_2 = \varepsilon, \lambda_3 = \varepsilon', \lambda_4 = \frac{1}{4}$ (7.144) for full-sib mating by setting \mathbf{P} equal to $\mathbf{K}\boldsymbol{\lambda}\mathbf{K}^{-1}$ where $\mathbf{K} = (\mathbf{c}_3 \ \mathbf{c}_1 \ \mathbf{c}_4 \ \mathbf{c}_2)$

[see equation (7.174)]. You will need to use equations (7.145) to (7.150). Assuming that you associate \mathbf{K} and $\boldsymbol{\lambda}$, or perform that operation first, it is possibly most convenient to express $\mathbf{K}\boldsymbol{\lambda}$ in the following form [to reduce the algebra in the subsequent matrix multiplication $(\mathbf{K}\boldsymbol{\lambda})\mathbf{K}^{-1}$]:

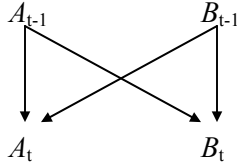
$$\mathbf{K}\boldsymbol{\lambda} = \begin{bmatrix} 0 & 1 & 0 & 0 \\ \frac{1+2\varepsilon'}{4} & 1 & -\frac{1}{4} & \frac{1+2\varepsilon}{4} \\ \varepsilon' & 1 & \frac{1}{4} & \varepsilon \\ 1 & 1 & 1 & 1 \end{bmatrix}$$

- c. State the general conclusion from what you have learned in parts (a) and (b).

Exercise 7.9.

a. In Example 4.10 we calculated the eight probabilities $\delta_{\ddot{X}\ddot{Y}}, \Delta_{\ddot{X}\cdot\ddot{Y}}, \Delta_{\ddot{X}+\ddot{Y}}, \gamma_{\ddot{X}Y}, \gamma_{X\ddot{Y}}, F_{\ddot{X}}, F_{\ddot{Y}}, \theta_{XY}$ (generation 1) as functions of the corresponding probabilities $\delta_{\ddot{S}\ddot{T}}, \Delta_{\ddot{S}\cdot\ddot{T}}, \Delta_{\ddot{S}+\ddot{T}}, \gamma_{\ddot{S}T}, \gamma_{S\ddot{T}}, F_{\ddot{S}}, F_{\ddot{T}}, \theta_{ST}$ (generation 0) (see Fig. 4.25, p. 4.108). Then in Example 4.11, p 4.109, we calculated the probabilities $\delta_{\ddot{X}\ddot{Y}}, \Delta_{\ddot{X}\cdot\ddot{Y}}, \Delta_{\ddot{X}+\ddot{Y}}, \gamma_{\ddot{X}Y}, \gamma_{X\ddot{Y}}, F_{\ddot{X}}, F_{\ddot{Y}}, \theta_{XY}$ (generation 2) as functions of the corresponding probabilities (generation 1) which were equal to the probabilities labeled for individuals X and Y in Fig. 4.25 (see Fig. 4.26, p. 4.109).

Let us consider the full-sib pedigree (as labeled in Fig. 6.3, p. 6.19), namely,



Then the above probabilities in any generation are designated by use of the letters A and B , and the generation number t , i.e., $\delta_{\ddot{A}\ddot{B}t}, \Delta_{\ddot{A}\cdot\ddot{B}t}, \dots, \theta_{ABt}$. In addition, we place these probabilities for generation t in a vector $\mathbf{f}_1^{(t)}$ as follows: (Hint: you may find that you need to redefine the vector by adding some constant element to the vector.)

$$\mathbf{f}_1^{(t)} = \begin{bmatrix} \delta_{\ddot{A}\ddot{B}t} \\ \Delta_{\ddot{A}\cdot\ddot{B}t} \\ \Delta_{\ddot{A}+\ddot{B}t} \\ \gamma_{\ddot{A}Bt} \\ \gamma_{AB\ddot{t}} \\ F_{\ddot{A}t} \\ F_{\ddot{B}t} \\ \theta_{ABt} \end{bmatrix}$$

Find the matrix \mathbf{A}_1 such that $\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)}$. (Note that the elements in the vector \mathbf{f}_1 in any generation do not sum to one. Also note that the columns for this matrix \mathbf{A}_1 do not sum to 1, as would be required for the reformulation of equation (7.32) in the form $\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)}$, namely,

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

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

However, in the present formulation $\mathbf{f}_1^{(t)} = \mathbf{A}_1 \mathbf{f}_1^{(t-1)}$, the rows do sum to one.)

b. Suppose that we define the vector $\mathbf{f}_2^{(t)}$ to be composed of the coefficients of identity Δ_i , $i = 1, \dots, 9$, namely,

$$\mathbf{f}_2^{(t)} = \begin{bmatrix} \Delta_1 \\ \Delta_2 \\ \Delta_3 \\ \Delta_4 \\ \Delta_5 \\ \Delta_6 \\ \Delta_7 \\ \Delta_8 \\ \Delta_9 \end{bmatrix}$$

- i. First, find the matrix \mathbf{T} which transforms the probabilities $\delta_{\dot{A}\dot{B}}, \Delta_{\dot{A}\dot{B}}, \dots, \theta_{AB}$ in any generation to $\Delta_1, \Delta_2, \dots, \Delta_9$, i.e., $\mathbf{f}_2^{(t)} = \mathbf{T}\mathbf{f}_1^{(t)}$.
- ii. Then what is the matrix \mathbf{A}_2 equal to in terms of \mathbf{T} and other matrices which you may choose to define such that $\mathbf{f}_2^{(t)} = \mathbf{A}_2\mathbf{f}_2^{(t-1)}$?

Exercise 7.10.

Briefly explain the spectral decomposition method of obtaining the t th power of the \mathbf{P} matrix. Clearly identify what features or properties exist that permit the simplification in obtaining the power of a matrix.

Exercise 7.11.

In Chapter 6, Section 6.3.4.2, pp. 6.53 to 6.54, the mating of the younger parent to the offspring is described. Work out the transition matrix \mathbf{P} for this kind of inbreeding system, assuming only two alleles.

Exercise 7.12. Enumerate the mating types in the case of an X-linked locus with an arbitrary number of alleles. Give examples in terms of genotypes of the kinds of crosses composing each mating type.

Exercise 7.13.

- a. Consider a cross between two homozygous lines, parent 1 with genotype $AABB$ and parent 2 with genotype $aabb$, when the two loci are unlinked ($\rho_1 = 0.5$). Answer all questions by elementary principles in general genetics and probability.
 - i. What are the frequencies of the nine genotypes in the F_2 generation or random-mating population?
 - ii. In the F_3 generation assuming self-fertilization?
 - iii. From basic probability principles, give the general expression for the frequency of each of the nine genotypes in any F_{2+t} generation.
 - iv. What are the frequencies of the genotypes when the population is fully inbred?
- b. Consider the same cross as above, except suppose that the two loci are linked ($\rho_1 < 0.5$).
 - i. What are the frequencies of the 10 genotypes in the F_2 generation or random-mating population?
 - ii. Give the 10×10 transition \mathbf{P} matrix. Arrange the order of the rows and columns so that they correspond to the following order of the genotypes: $AABB, AAbb, aaBB, aabb, AABb, AaBB, Aabb, aAbB, AB/ab, Ab/aB$.
 - iii. Suppose $\rho_1 = 0.2$. Calculate the F_2 frequencies from b(i), and the elements in the \mathbf{P} matrix. Then calculate the frequencies of the 10 genotypes in the F_3 generation, using the \mathbf{P} matrix.

Exercise 7.14. Discuss the phenomenon of genotypic disequilibrium as distinct from linkage disequilibrium.

Exercise 7.15.

What is the meaning of genotypic disequilibrium? Discuss the conditions under which it occurs?

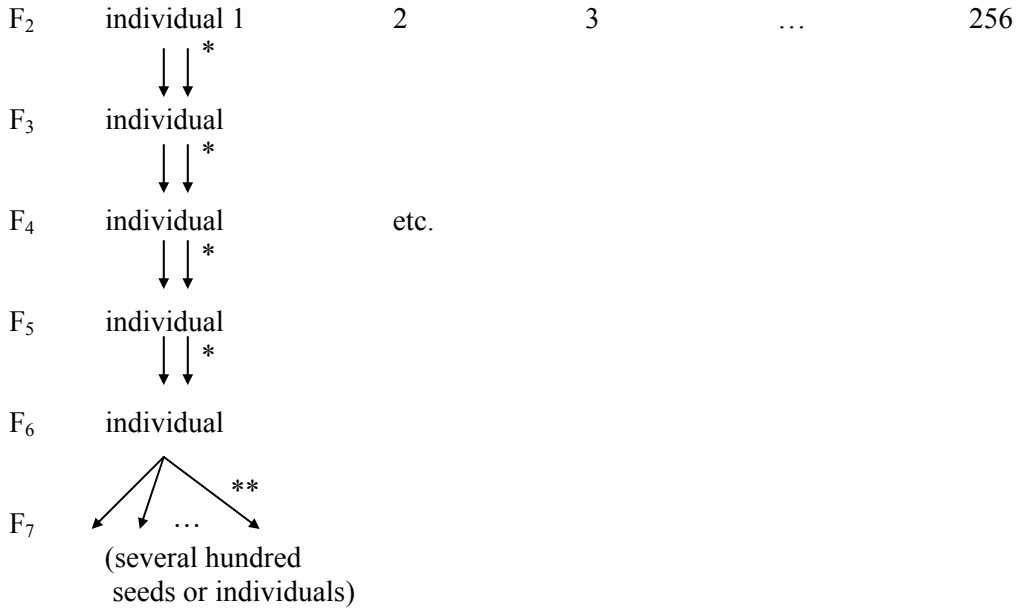
Exercise 7.16. Describe the nature of the phenomenon known as genotypic disequilibrium? It occurs under what conditions?

Exercise 7.17. In Chapter 7, we collapsed the two different homozygous kinds of matings in self-fertilization into one mating type [see equation (7.26)], so that we dealt with only a 2×2 transition matrix. Instead of doing that, keep the two different homozygotes separate, so that one has a 3×3 transition matrix.

- a. Give the 3×3 transition matrix.
- b. Find the eigenvalues.
- c. Find the corresponding right-hand eigenvectors for the 3×3 transition matrix.
- d. Find the corresponding left-hand eigenvectors for the 3×3 transition matrix.
- e. Calculate the spectral matrices.
- f. Find the fifth power of the transition matrix by use of the spectral matrices.
- g. Find the fifth power of the transition matrix by the partitioning method.
- h. Given that $p_{AA} = 0.38$, $p_{Aa} = 0.51$, and $p_{aa} = 0.11$ in generation 0, find their frequencies in generation 5.
 - i. If you want the frequencies of the two homozygous mating kinds, is it essential to use this expanded form of a 3×3 matrix compared to a 2×2 matrix? Discuss.

Exercise 7.18. Breeders of self-fertilizing species often make a cross between two fully homozygous parents, self the F_1 individual, create an F_2 population of several hundred individuals, advance each F_2 individual by single-seed descent for several generations, and then increase the seed supply by saving all the selfed seed (usually several hundred seeds) from the last single individual in the descending series of selfed individuals. Breeders obtain many relatively homozygous lines or so-called random recombinant inbred lines. The single-seed descent method is the idealized population described in Section 6.1 for $N = 1$, except for a redesignation of the generations. The F_2 population is regarded as the random-mating base population and every F_2 individual is assumed to be unrelated and noninbred, i.e., $\theta_{F_2} = F_{F_2} = 0$, even though we know in reality it is equal to $1/2$.

To be specific we assume the following pedigree for every F_2 individual. We assume 256 F_2 individuals.



*double arrow denotes selfing

**a single arrow denotes a double arrow or selfing

The collection of several hundred seeds or individuals would be designated an F_6 -derived F_7 recombinant inbred line. It is designated F_6 -derived because it is the last common ancestor, and is designated F_7 because that is the generation of the seed or the individual plants from the F_6 individual.

- What is the inbreeding coefficient of a random individual in the F_7 generation?
- If a particular locus is segregating in the cross, what is the frequency of heterozygotes in the F_7 generation in the whole population consisting of all 256 recombinant inbred lines?
- What is the expected frequency of recombinant inbred lines still segregating for that particular locus? What is the expected frequency of lines homozygous for either allele at that particular locus?
- Considering all loci in the genome, which were originally segregating in the cross, what proportion of loci in a random individual in the F_7 generation would be expected to be homozygous? Linkage does not affect this.
- Of all those loci segregating in the cross, what is the expected frequency of those loci still heterozygous in a random individual in the F_7 generation?