11.17

GENETICS

In this section we investigate the propagation of an inherited trait in successive generations by computing powers of a matrix.

Prerequisites: Eigenvalues and Eigenvectors
Diagonalization of a Matrix
Intuitive Understanding of Limits

Inheritance Traits

In this section we examine the inheritance of traits in animals or plants. The inherited trait under consideration is assumed to be governed by a set of two genes, which we designate by A and a. Under ***autosomal inheritance*** each individual in the population of either gender possesses two of these genes, the possible pairings being designated AA, Aa, and aa. This pair of genes is called the individual's ***genotype***, and it determines how the trait controlled by the genes is manifested in the individual. For example, in snapdragons a set of two genes determines the color of the flower. Genotype AA produces red flowers, genotype Aa produces pink flowers, and genotype aa produces white flowers. In humans, eye coloration is controlled through autosomal inheritance. Genotypes AA and Aa have brown eyes, and genotype aa has blue eyes. In this case we say that gene A ***dominates*** gene a, or that gene a is ***recessive*** to gene A, because genotype Aa has the same outward trait as genotype AA.

In addition to autosomal inheritance we will also discuss ***X-linked inheritance***. In this type of inheritance, the male of the species possesses only one of the two possible genes (A or a), and the female possesses a pair of the two genes (AA, Aa, or aa). In humans, color blindness, hereditary baldness, hemophilia, and muscular dystrophy, to name a few, are traits controlled by X-linked inheritance.

Below we explain the manner in which the genes of the parents are passed on to their offspring for the two types of inheritance. We construct matrix models that give the probable genotypes of the offspring in terms of the genotypes of the parents, and we use these matrix models to follow the genotype distribution of a population through successive generations.

Autosomal Inheritance

In autosomal inheritance an individual inherits one gene from each of its parents' pairs of genes to form its own particular pair. As far as we know, it is a matter of chance which of the two genes a parent passes on to the offspring. Thus, if one parent is of genotype Aa, it is equally likely that the offspring will inherit the A gene or the a gene from that parent. If one parent is of genotype aa and the other parent is of genotype Aa, the offspring will always receive an a gene from the aa parent and will receive either an A gene or an a gene, with equal probability, from the Aa parent. Consequently, each of the offspring has equal probability of being genotype aa or Aa. In Table 1 we list the probabilities of the possible genotypes of the offspring for all possible combinations of the genotypes of the parents.

Table 1

Genotype of Offspring	**Genotypes of Parents**					
	$AA-AA$	$AA-Aa$	$AA-aa$	$Aa-Aa$	$Aa-aa$	$aa-aa$
AA	1	$\frac{1}{2}$	0	$\frac{1}{4}$	0	0

Genotype of Offspring	Genotypes of Parents					
	$AA-AA$	$AA-Aa$	$AA-aa$	$Aa-Aa$	$Aa-aa$	$aa-aa$
Aa	0	$\frac{1}{2}$	1	$\frac{1}{2}$	$\frac{1}{2}$	0
aa	0	0	0	$\frac{1}{4}$	$\frac{1}{2}$	1

EXAMPLE 1 Distribution of Genotypes in a Population

Suppose that a farmer has a large population of plants consisting of some distribution of all three possible genotypes AA, Aa, and aa. The farmer desires to undertake a breeding program in which each plant in the population is always fertilized with a plant of genotype AA and is then replaced by one of its offspring. We want to derive an expression for the distribution of the three possible genotypes in the population after any number of generations.

For $n = 0$, 1, 2, … , let us set

a_n = fraction of plants of genotype AA in *n*th generation
b_n = fraction of plants of genotype Aa in *n*th generation
c_n = fraction of plants of genotype aa in *n*th generation

Thus a_0, b_0, and c_0 specify the initial distribution of the genotypes. We also have that

$$a_n + b_n + c_n = 1 \qquad \text{for } n = 0, 1, 2, \ldots$$

From Table 1 we can determine the genotype distribution of each generation from the genotype distribution of the preceding generation by the following equations:

$$\begin{aligned} a_n &= a_{n-1} + \tfrac{1}{2}b_{n-1} \\ b_n &= c_{n-1} + \tfrac{1}{2}b_{n-1} \qquad n = 1, 2, \ldots \\ c_n &= 0 \end{aligned} \tag{1}$$

For example, the first of these three equations states that all the offspring of a plant of genotype AA will be of genotype AA under this breeding program and that half of the offspring of a plant of genotype Aa will be of genotype AA.

Equations 1 can be written in matrix notation as

$$\mathbf{x}^{(n)} = M\mathbf{x}^{(n-1)}, \qquad n = 1, 2, \ldots \tag{2}$$

where

$$\mathbf{x}^{(n)} = \begin{bmatrix} a_n \\ b_n \\ c_n \end{bmatrix}, \qquad \mathbf{x}^{(n-1)} = \begin{bmatrix} a_{n-1} \\ b_{n-1} \\ c_{n-1} \end{bmatrix}, \qquad \text{and} \qquad M = \begin{bmatrix} 1 & \frac{1}{2} & 0 \\ 0 & \frac{1}{2} & 1 \\ 0 & 0 & 0 \end{bmatrix}$$

Note that the three columns of the matrix *M* are the same as the first three columns of Table 1.

From Equation 2 it follows that

$$\mathbf{x}^{(n)} = M\mathbf{x}^{(n-1)} = M^2\mathbf{x}^{(n-2)} = \cdots = M^n\mathbf{x}^{(0)} \tag{3}$$

Consequently, if we can find an explicit expression for M^n, we can use 3 to obtain an explicit expression for $\mathbf{x}^{(n)}$. To find an explicit expression for M^n, we first diagonalize *M*. That is, we find an invertible matrix *P* and a diagonal matrix *D* such that

$$M = PDP^{-1} \tag{4}$$

With such a diagonalization, we then have (see Exercise 1)

$$M^n = PD^nP^{-1} \qquad \text{for } n = 1, 2, \ldots$$

where

$$D^n = \begin{bmatrix} \lambda_1 & 0 & 0 & \ldots & 0 \\ 0 & \lambda_2 & 0 & \ldots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \ldots & \lambda_k \end{bmatrix}^n = \begin{bmatrix} \lambda_1^n & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2^n & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \cdots & \lambda_k^n \end{bmatrix}$$

The diagonalization of *M* is accomplished by finding its eigenvalues and corresponding eigenvectors. These are as follows (verify):

$$\text{Eigenvalues:} \qquad \lambda_1 = 1, \qquad \lambda_2 = \frac{1}{2}, \qquad \lambda_3 = 0$$

$$\text{Corresponding eigenvectors: } \mathbf{v}_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \qquad \mathbf{v}_2 = \begin{bmatrix} 1 \\ -1 \\ 0 \end{bmatrix}, \qquad \mathbf{v}_3 \begin{bmatrix} 1 \\ -2 \\ 1 \end{bmatrix}$$

Thus, in Equation 4 we have

$$D = \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

and

$$P = [\mathbf{v}_1 | \mathbf{v}_2 | \mathbf{v}_3] = \begin{bmatrix} 1 & 1 & 1 \\ 0 & -1 & -2 \\ 0 & 0 & 1 \end{bmatrix}$$

Therefore,

$$\mathbf{x}^{(n)} = PD^nP^{-1}\mathbf{x}^{(0)} = \begin{bmatrix} 1 & 1 & 1 \\ 0 & -1 & -2 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & \left(\frac{1}{2}\right)^n & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} 1 & 1 & 1 \\ 0 & -1 & -2 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} a_0 \\ b_0 \\ c_0 \end{bmatrix}$$

or

$$\mathbf{x}^{(n)} = \begin{bmatrix} a_n \\ b_n \\ c_n \end{bmatrix} = \begin{bmatrix} 1 & 1 - \left(\frac{1}{2}\right)^n & 1 - \left(\frac{1}{2}\right)^{n-1} \\ 0 & \left(\frac{1}{2}\right)^n & \left(\frac{1}{2}\right)^{n-1} \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} a_0 \\ b_0 \\ c_0 \end{bmatrix}$$

$$= \begin{bmatrix} a_0 + b_0 + c_0 - \left(\frac{1}{2}\right)^n b_0 - \left(\frac{1}{2}\right)^{n-1} c_0 \\ \left(\frac{1}{2}\right)^n b_0 + \left(\frac{1}{2}\right)^{n-1} c_0 \\ 0 \end{bmatrix}$$

Using the fact that $a_0 + b_0 + c_0 = 1$, we thus have

$$
\begin{aligned}
a_n &= 1 - \left(\frac{1}{2}\right)^n b_0 - \left(\frac{1}{2}\right)^{n-1} c_0 \\
b_n &= \left(\frac{1}{2}\right)^n b_0 + \left(\frac{1}{2}\right)^{n-1} c_0 \qquad n = 1, 2, \ldots \\
c_n &= 0
\end{aligned}
\tag{5}
$$

These are explicit formulas for the fractions of the three genotypes in the *n*th generation of plants in terms of the initial genotype fractions.

Because $\left(\frac{1}{2}\right)^n$ tends to zero as *n* approaches infinity, it follows from these equations that

$$
\begin{aligned}
a_n &\longrightarrow 1 \\
b_n &\longrightarrow 0 \\
c_n &= 0
\end{aligned}
$$

as *n* approaches infinity. That is, in the limit all plants in the population will be genotype AA.

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EXAMPLE 2 Modifying Example 1

We can modify Example 1 so that instead of each plant being fertilized with one of genotype AA, each plant is fertilized with a plant of its own genotype. Using the same notation as in Example 1, we then find

$$\mathbf{x}^{(n)} = M^n \mathbf{x}^{(0)}$$

where

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

The columns of this new matrix *M* are the same as the columns of Table 1 corresponding to parents with genotypes $AA - AA$, $Aa - Aa$, and $aa - aa$.

The eigenvalues of *M* are (verify)

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

The eigenvalue $\lambda_1 = 1$ has multiplicity two and its corresponding eigenspace is two-dimensional. Picking two linearly independent eigenvectors $\mathbf{v}_1$ and $\mathbf{v}_2$ in that eigenspace, and a single eigenvector $\mathbf{v}_3$ for the simple eigenvalue $\lambda_3 = \frac{1}{2}$, we have (verify)

$$\mathbf{v}_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \qquad \mathbf{v}_2 = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}, \qquad \mathbf{v}_3 = \begin{bmatrix} 1 \\ -2 \\ 1 \end{bmatrix}$$

The calculations for $\mathbf{x}^{(n)}$ are then

$$\mathbf{x}^{(n)} = M^n\mathbf{x}^{(0)} = PD^nP^{-1}\mathbf{x}^{(0)}$$

$$= \begin{bmatrix} 1 & 0 & 1 \\ 0 & 0 & -2 \\ 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & \left(\frac{1}{2}\right)^n \end{bmatrix} \begin{bmatrix} 1 & \frac{1}{2} & 0 \\ 0 & \frac{1}{2} & 1 \\ 0 & -\frac{1}{2} & 0 \end{bmatrix} \begin{bmatrix} a_0 \\ b_0 \\ c_0 \end{bmatrix}$$

$$= \begin{bmatrix} 1 & \frac{1}{2} - \left(\frac{1}{2}\right)^{n+1} & 0 \\ 0 & \left(\frac{1}{2}\right)^n & 0 \\ 0 & \frac{1}{2} - \left(\frac{1}{2}\right)^{n+1} & 1 \end{bmatrix} \begin{bmatrix} a_0 \\ b_0 \\ c_0 \end{bmatrix}$$

Thus,

$$\begin{aligned} a_n &= a_0 + \left[\frac{1}{2} - \left(\frac{1}{2}\right)^{n+1}\right] b_0 \\ b_n &= \left(\frac{1}{2}\right)^n b_0 \qquad\qquad n = 1, 2, \ldots \\ c_n &= c_0 + \left[\frac{1}{2} - \left(\frac{1}{2}\right)^{n+1}\right] b_0 \end{aligned} \tag{6}$$

In the limit, as *n* tends to infinity, $\left(\frac{1}{2}\right)^n \longrightarrow 0$ and $\left(\frac{1}{2}\right)^{n+1} \longrightarrow 0$, so

$$\begin{aligned} a_n &\longrightarrow a_0 + \frac{1}{2}b_0 \\ b_n &\longrightarrow 0 \\ c_n &\longrightarrow c_0 + \frac{1}{2}b_0 \end{aligned}$$

Thus, fertilization of each plant with one of its own genotype produces a population that in the limit contains only genotypes AA and aa.

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Autosomal Recessive Diseases

There are many genetic diseases governed by autosomal inheritance in which a normal gene *A* dominates an abnormal gene *a*. Genotype AA is a normal individual; genotype Aa is a carrier of the disease but is not afflicted with the disease; and genotype aa is afflicted with the disease. In humans such genetic diseases are often associated with a particular racial group—for instance, cystic fibrosis (predominant among Caucasians), sickle-cell anemia (predominant among blacks), Cooley's anemia (predominant among people of Mediterranean origin), and Tay-Sachs disease (predominant among Eastern European Jews).

Suppose that an animal breeder has a population of animals that carries an autosomal recessive disease. Suppose further that those animals afflicted with the disease do not survive to maturity. One possible way to control such a disease is for the breeder to always mate a female, regardless of her genotype, with a normal male. In this way, all future offspring will either have a normal father and a normal mother ($AA-AA$ matings) or a normal father and a carrier mother ($AA-Aa$ matings). There can be no $AA-aa$ matings since animals of genotype aa do not survive to maturity. Under this type of mating program no future offspring will be afflicted with the disease, although there will still be carriers in future generations. Let us now determine the fraction of carriers in future generations. We set

$$\mathbf{x}^{(n)} = \begin{bmatrix} a_n \\ b_n \end{bmatrix}, \qquad n = 1, 2, \ldots$$

where

a_n = fraction of population of genotype AA in *n*th generation
b_n = fraction of population of genotype Aa (carriers) in *n*th generation

Because each offspring has at least one normal parent, we may consider the controlled mating program as one of continual mating with genotype AA, as in Example 1. Thus, the transition of genotype distributions from one generation to the next is governed by the equation

$$\mathbf{x}^{(n)} = M\mathbf{x}^{(n-1)}, \qquad n = 1, 2, \ldots$$

where

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

Because we know the initial distribution $\mathbf{x}^{(0)}$, the distribution of genotypes in the *n*th generation is thus given by

$$\mathbf{x}^{(n)} = M^n\mathbf{x}^{(0)}, \qquad n = 1, 2, \ldots$$

The diagonalization of *M* is easily carried out (see Exercise 4) and leads to

$$\mathbf{x}^{(n)} = PD^nP^{-1}\mathbf{x}^{(0)} = \begin{bmatrix} 1 & 1 \\ 0 & -1 \end{bmatrix}\begin{bmatrix} 1 & 0 \\ 0 & \left(\frac{1}{2}\right)^n \end{bmatrix}\begin{bmatrix} 1 & 1 \\ 0 & -1 \end{bmatrix}\begin{bmatrix} a_0 \\ b_0 \end{bmatrix}$$

$$= \begin{bmatrix} 1 & 1 - \left(\frac{1}{2}\right)^n \\ 0 & \left(\frac{1}{2}\right)^n \end{bmatrix}\begin{bmatrix} a_0 \\ b_0 \end{bmatrix} = \begin{bmatrix} a_0 + b_0 - \left(\frac{1}{2}\right)^n b_0 \\ \left(\frac{1}{2}\right)^n b_0 \end{bmatrix}$$

Because $a_0 + b_0 = 1$, we have

$$\left.\begin{aligned} a_n &= 1 - \left(\frac{1}{2}\right)^n b_0 \\ b_n &= \left(\frac{1}{2}\right)^n b_0 \end{aligned}\right\} \quad n = 1, 2, \ldots \tag{7}$$

Thus, as *n* tends to infinity, we have

$$\begin{aligned} a_n &\longrightarrow 1 \\ b_n &\longrightarrow 0 \end{aligned}$$

so in the limit there will be no carriers in the population.

From 7 we see that

$$b_n = \frac{1}{2}b_{n-1}, \qquad n = 1, 2, \ldots \tag{8}$$

That is, the fraction of carriers in each generation is one-half the fraction of carriers in the preceding generation. It would be of interest also to investigate the propagation of carriers under random mating, when two animals mate without regard to their genotypes. Unfortunately, such random mating leads to nonlinear equations, and the techniques of this section are not applicable. However, by other techniques it can be shown that under random mating, Equation 8 is replaced by

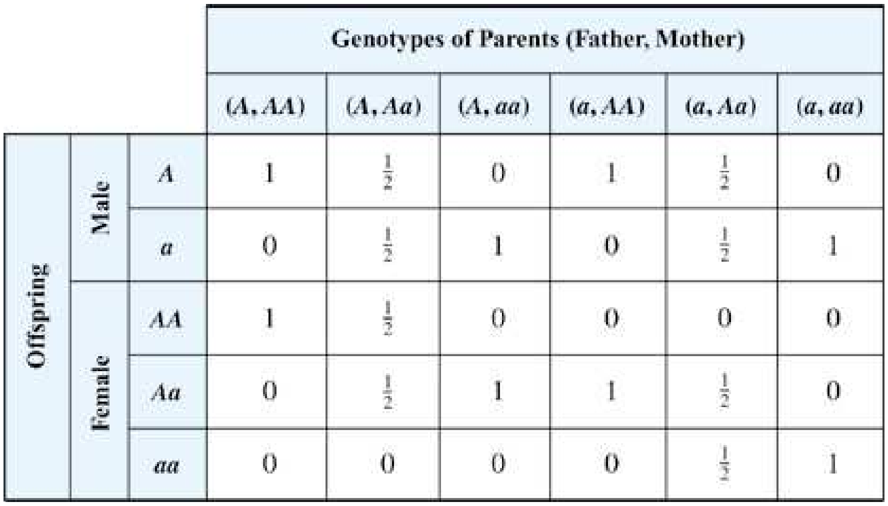
$$b_n = \frac{b_{n-1}}{1 + \frac{1}{2}b_{n-1}}, \qquad n = 1, 2, \ldots \tag{9}$$

As a numerical example, suppose that the breeder starts with a population in which 10% of the animals are carriers. Under the controlled-mating program governed by Equation 8, the percentage of carriers can be reduced to 5% in one generation. But under random mating, Equation 9 predicts that 9.5% of the population will be carriers after one generation ($b_n = 0.95$ if $b_{n-1} = .10$). In addition, under controlled mating no offspring will ever be afflicted with the disease, but with random mating it can be shown that about 1 in 400 offspring will be born with the disease when 10% of the population are carriers.

X-Linked Inheritance

As mentioned in the introduction, in X-linked inheritance the male possesses one gene (A or a) and the female possesses two genes (AA, Aa, or aa). The term *X-linked* is used because such genes are found on the X-chromosome, of which the male has one and the female has two. The inheritance of such genes is as follows: A male offspring receives one of his mother's two genes with equal probability, and a female offspring receives the one gene of her father and one of her mother's two genes with equal probability. Readers familiar with basic probability can verify that this type of inheritance leads to the genotype probabilities in Table 2.

Table 2



			Genotypes of Parents (Father, Mother)					
			(A, AA)	(A, Aa)	(A, aa)	(a, AA)	(a, Aa)	(a, aa)
Offspring	Male	A	1	$\frac{1}{2}$	0	1	$\frac{1}{2}$	0
		a	0	$\frac{1}{2}$	1	0	$\frac{1}{2}$	1
	Female	AA	1	$\frac{1}{2}$	0	0	0	0
		Aa	0	$\frac{1}{2}$	1	1	$\frac{1}{2}$	0
		aa	0	0	0	0	$\frac{1}{2}$	1

We will discuss a program of inbreeding in connection with X-linked inheritance. We begin with a male and female; select two of their offspring at random, one of each gender, and mate them; select two of the resulting offspring and mate them; and so forth. Such inbreeding is commonly performed with animals. (Among humans, such brother-sister marriages were used by the rulers of ancient Egypt to keep the royal line pure.)

The original male-female pair can be one of the six types, corresponding to the six columns of Table 2:

$$(A, AA), \quad (A, Aa), \quad (A, aa), \quad (a, AA), \quad (a, Aa), \quad (a, aa)$$

The sibling pairs mated in each successive generation have certain probabilities of being one of these six types. To compute these probabilities, for $n = 0$, 1, 2, …, let us set

a_n = probability sibling-pair mated in nth generation is type (A, AA)
b_n = probability sibling-pair mated in nth generation is type (A, Aa)
c_n = probability sibling-pair mated in nth generation is type (A, aa)
d_n = probability sibling-pair mated in nth generation is type (a, AA)
e_n = probability sibling-pair mated in nth generation is type (a, Aa)
f_n = probability sibling-pair mated in nth generation is type (a, aa)

With these probabilities we form a column vector

$$\mathbf{x}^{(n)} = \begin{bmatrix} a_n \\ b_n \\ c_n \\ d_n \\ e_n \\ f_n \end{bmatrix}, \qquad n = 0, 1, 2, \ldots$$

From Table 2 it follows that

$$\mathbf{x}^{(n)} = M\mathbf{x}^{(n-1)}, \qquad n = 1, 2, \ldots \tag{10}$$

where

$$M = \begin{array}{ccccccc} (A,AA) & (A,Aa) & (A,aa) & (a,AA) & (a,Aa) & (a,aa) & \\ 1 & \frac{1}{4} & 0 & 0 & 0 & 0 & (A,AA) \\ 0 & \frac{1}{4} & 0 & 1 & \frac{1}{4} & 0 & (A,Aa) \\ 0 & 0 & 0 & 0 & \frac{1}{4} & 0 & (A,aa) \\ 0 & \frac{1}{4} & 0 & 0 & 0 & 0 & (a,AA) \\ 0 & \frac{1}{4} & 1 & 0 & \frac{1}{4} & 0 & (a,Aa) \\ 0 & 0 & 0 & 0 & \frac{1}{4} & 1 & (a,aa) \end{array}$$

For example, suppose that in the $(n-1)$-st generation, the sibling pair mated is type (A, Aa). Then their male offspring will be genotype *A* or *a* with equal probability, and their female offspring will be genotype AA or Aa with equal probability. Because one of the male offspring and one of the female offspring are chosen at random for mating, the next sibling pair will be one of type (A, AA), (A, Aa), (a, AA), or (a, Aa) with equal probability. Thus, the second column of *M* contains "$\frac{1}{4}$" in each of the four rows corresponding to these four sibling pairs. (See Exercise 9 for the remaining columns.)

As in our previous examples, it follows from 10 that

$$\mathbf{x}^{(n)} = M^n \mathbf{x}^{(0)}, \qquad n = 1, 2, \ldots \tag{11}$$

After lengthy calculations, the eigenvalues and eigenvectors of *M* turn out to be

$$\lambda_1 = 1, \quad \lambda_2 = 1, \quad \lambda_3 = \frac{1}{2}, \quad \lambda_4 = -\frac{1}{2}, \quad \lambda_5 = \frac{1}{4}(1+\sqrt{5}), \quad \lambda_6 = \frac{1}{4}(1-\sqrt{5})$$

$$\mathbf{v}_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \quad \mathbf{v}_2 = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{bmatrix}, \quad \mathbf{v}_3 = \begin{bmatrix} -1 \\ 2 \\ -1 \\ 1 \\ -2 \\ 1 \end{bmatrix}, \quad \mathbf{v}_4 = \begin{bmatrix} 1 \\ -6 \\ -3 \\ 3 \\ 6 \\ -1 \end{bmatrix},$$

$$\mathbf{v}_5 = \begin{bmatrix} \frac{1}{4}(-3-\sqrt{5}) \\ 1 \\ \frac{1}{4}(-1+\sqrt{5}) \\ \frac{1}{4}(-1+\sqrt{5}) \\ 1 \\ \frac{1}{4}(-3-\sqrt{5}) \end{bmatrix}, \quad \mathbf{v}_6 = \begin{bmatrix} \frac{1}{4}(-3+\sqrt{5}) \\ 1 \\ \frac{1}{4}(-1-\sqrt{5}) \\ \frac{1}{4}(-1-\sqrt{5}) \\ 1 \\ \frac{1}{4}(-3+\sqrt{5}) \end{bmatrix}$$

The diagonalization of *M* then leads to

$$\mathbf{x}^{(n)} = PD^nP^{-1}\mathbf{x}^{(0)}, \qquad n = 1, 2, \ldots \tag{12}$$

where

$$P = \begin{bmatrix} 1 & 0 & -1 & 1 & \frac{1}{4}(-3-\sqrt{5}) & \frac{1}{4}(-3+\sqrt{5}) \\ 0 & 0 & 2 & -6 & 1 & 1 \\ 0 & 0 & -1 & -3 & \frac{1}{4}(-1+\sqrt{5}) & \frac{1}{4}(-1-\sqrt{5}) \\ 0 & 0 & 1 & 3 & \frac{1}{4}(-1+\sqrt{5}) & \frac{1}{4}(-1-\sqrt{5}) \\ 0 & 0 & -2 & 6 & 1 & 1 \\ 0 & 1 & 1 & -1 & \frac{1}{4}(-3-\sqrt{5}) & \frac{1}{4}(-3+\sqrt{5}) \end{bmatrix}$$

$$D^n = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & \left(\frac{1}{2}\right)^n & 0 & 0 & 0 \\ 0 & 0 & 0 & \left(-\frac{1}{2}\right)^n & 0 & 0 \\ 0 & 0 & 0 & 0 & \left[\frac{1}{4}(1+\sqrt{5})\right]^n & 0 \\ 0 & 0 & 0 & 0 & 0 & \left[\frac{1}{4}(1-\sqrt{5})\right]^n \end{bmatrix}$$

$$P^{-1} = \begin{bmatrix} 1 & \frac{2}{3} & \frac{1}{3} & \frac{2}{3} & \frac{1}{3} & 0 \\ 0 & \frac{1}{3} & \frac{2}{3} & \frac{1}{3} & \frac{2}{3} & 1 \\ 0 & \frac{1}{8} & -\frac{1}{4} & \frac{1}{4} & -\frac{1}{8} & 0 \\ 0 & -\frac{1}{24} & -\frac{1}{12} & \frac{1}{12} & \frac{1}{24} & 0 \\ 0 & \frac{1}{20}(5+\sqrt{5}) & \frac{1}{5}\sqrt{5} & \frac{1}{5}\sqrt{5} & \frac{1}{20}(5+\sqrt{5}) & 0 \\ 0 & \frac{1}{20}(5-\sqrt{5}) & -\frac{1}{5}\sqrt{5} & -\frac{1}{5}\sqrt{5} & \frac{1}{20}(5-\sqrt{5}) & 0 \end{bmatrix}$$

We will not write out the matrix product in 12, as it is rather unwieldy. However, if a specific vector $\mathbf{x}^{(0)}$ is given, the calculation for $\mathbf{x}^{(n)}$ is not too cumbersome (see Exercise 6).

Because the absolute values of the last four diagonal entries of *D* are less than 1, we see that as *n* tends to infinity,

$$D^n \to \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

And so, from Equation 12,

$$\mathbf{x}^{(n)} \to P \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} P^{-1}\mathbf{x}^{(0)}$$

Performing the matrix multiplication on the right, we obtain (verify)

$$\mathbf{x}^{(n)} \to \begin{bmatrix} a_0+\frac{2}{3}b_0+\frac{1}{3}c_0+\frac{2}{3}d_0+\frac{1}{3}e_0 \\ 0 \\ 0 \\ 0 \\ 0 \\ f_0+\frac{1}{3}b_0+\frac{2}{3}c_0+\frac{1}{3}d_0+\frac{2}{3}e_0 \end{bmatrix} \tag{13}$$

That is, in the limit all sibling pairs will be either type (A, AA) or type (a, aa). For example, if the initial parents are type (A, Aa) (that is, $b_0 = 1$ and $a_0 = c_0 = d_0 = e_0 = f_0 = 0$), then as *n* tends to infinity,

$$\mathbf{x}^{(n)} \to \begin{bmatrix} \frac{2}{3} \\ 0 \\ 0 \\ 0 \\ 0 \\ \frac{1}{3} \end{bmatrix}$$

Thus, in the limit there is probability $\frac{2}{3}$ that the sibling pairs will be (A, AA), and probability $\frac{1}{3}$ that they will be (a, aa).

Exercise Set 11.17

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1. Show that if $M = PDP^{-1}$, then $M^n = PD^nP^{-1}$ for $n = 1, 2, \ldots$.

2. In Example 1 suppose that the plants are always fertilized with a plant of genotype Aa rather than one of genotype AA. Derive formulas for the fractions of the plants of genotypes AA, Aa, and aa in the *n*th generation. Also, find the limiting genotype distribution as *n* tends to infinity.

3. In Example 1 suppose that the initial plants are fertilized with genotype AA, the first generation is fertilized with genotype Aa, the second generation is fertilized with genotype AA, and this alternating pattern of fertilization is kept up. Find formulas for the fractions of the plants of genotypes AA, Aa, and aa in the *n*th generation.

4. In the section on autosomal recessive diseases, find the eigenvalues and eigenvectors of the matrix *M* and verify Equation 7.

5. Suppose that a breeder has an animal population in which 25% of the population are carriers of an autosomal recessive disease. If the breeder allows the animals to mate irrespective of their genotype, use Equation 9 to calculate the number of generations required for the percentage of carriers to fall from 25% to 10%. If the breeder instead implements the controlled-mating program determined by Equation 8, what will the percentage of carriers be after the same number of generations?

6. In the section on X-linked inheritance, suppose that the initial parents are equally likely to be of any of the six possible genotype parents; that is,

$$\mathbf{x}^{(0)} = \begin{bmatrix} \frac{1}{6} \\ \frac{1}{6} \\ \frac{1}{6} \\ \frac{1}{6} \\ \frac{1}{6} \\ \frac{1}{6} \end{bmatrix}$$

Using Equation 12, calculate $\mathbf{x}^{(n)}$ and also calculate the limit of $\mathbf{x}^{(n)}$ as *n* tends to infinity.

7. From 13 show that under X-linked inheritance with inbreeding, the probability that the limiting sibling pairs will be of type (A, AA) is the same as the proportion of *A* genes in the initial population.

8. In X-linked inheritance suppose that none of the females of genotype Aa survive to maturity. Under inbreeding the possible sibling pairs are then

$$(A, AA), \qquad (A, aa), \qquad (a, AA), \qquad \text{and} \qquad (a, aa)$$

Find the transition matrix that describes how the genotype distribution changes in one generation.

9. Derive the matrix *M* in Equation 10 from Table 2.

Section 11.17

Technology Exercises

The following exercises are designed to be solved using a technology utility. Typically, this will be MATLAB, *Mathematica*, Maple, Derive, or Mathcad, but it may also be some other type of linear algebra software or a scientific calculator with some linear algebra capabilities. For each exercise you will need to read the relevant documentation for the particular utility you are using. The goal of these exercises is to provide you with a basic proficiency with your technology utility. Once you have mastered the techniques in these exercises, you will be able to use your technology utility to solve many of the problems in the regular exercise sets.

T1.

(a) Use a computer to verify that the eigenvalues and eigenvectors of

$$M = \begin{bmatrix} 1 & \frac{1}{4} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 0 & 1 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{4} & 0 \\ 0 & \frac{1}{4} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{4} & 1 & 0 & \frac{1}{4} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{4} & 1 \end{bmatrix}$$

as given in the text are correct.

(b) Starting with $\mathbf{x}^{(n)} = M\mathbf{x}^{(n-1)}$ and the assumption that

$$\lim_{n \longrightarrow \infty} \mathbf{x}^{(n)} = \mathbf{x}$$

exists, we must have

$$\lim_{n \longrightarrow \infty} \mathbf{x}^{(n)} = M \lim_{n \longrightarrow \infty} \mathbf{x}^{(n-1)} \qquad \text{or} \qquad \mathbf{x} = M\mathbf{x}$$

This suggests that ***x*** can be solved directly using the equation $(M - I)\mathbf{x} = \mathbf{0}$. Use a computer to solve the equation $\mathbf{x} = M\mathbf{x}$, where

$$\mathbf{x} = \begin{bmatrix} a \\ b \\ c \\ d \\ e \\ f \end{bmatrix}$$

and $a + b + c + d + e + f = 1$; compare your results to Equation 13. Explain why the solution to $(M - I)\mathbf{x} = \mathbf{0}$ along with $a + b + c + d + e + f = 1$ is not specific enough to determine $\lim_{n \longrightarrow \infty} \mathbf{x}^{(n)}$.

T2.

(a) Given

$$P = \begin{bmatrix} 1 & 0 & -1 & 1 & \frac{1}{4}(-3-\sqrt{5}) & \frac{1}{4}(-3+\sqrt{5}) \\ 0 & 0 & 2 & -6 & 1 & 1 \\ 0 & 0 & -1 & -3 & \frac{1}{4}(-1+\sqrt{5}) & \frac{1}{4}(-1-\sqrt{5}) \\ 0 & 0 & 1 & 3 & \frac{1}{4}(-1+\sqrt{5}) & \frac{1}{4}(-1-\sqrt{5}) \\ 0 & 0 & -2 & 6 & 1 & 1 \\ 0 & 1 & 1 & -1 & \frac{1}{4}(-3-\sqrt{5}) & \frac{1}{4}(-3+\sqrt{5}) \end{bmatrix}$$

from Equation 12 and

$$\lim_{n \to \infty} D^n = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

use a computer to show that

$$\lim_{n\to\infty} M^n = \begin{bmatrix} 1 & \frac{2}{3} & \frac{1}{3} & \frac{2}{3} & \frac{1}{3} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{3} & \frac{2}{3} & \frac{1}{3} & \frac{2}{3} & 1 \end{bmatrix}$$

(b) Use a computer to calculate M^n for $n = 10$, 20, 30, 40, 50, 60, 70, and then compare your results to the limit in part (a).

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