CHAPTER 2

Linear Models of Structured Populations

In the previous chapter we first discussed the linear difference equation model $P_{t+1} = \lambda P_t$ which results in exponential growth or decay. After criticizing this model for not being realistic enough, we looked at non-linear models that could result in quite complicated dynamics.

However, there is another way our models in the last chapter were simplistic — they treated all individuals in a population identically. In most populations, there are actually many subgroups whose vital behavior can be quite different. For instance, in humans, the death rate for infants is often higher than for older children. Also, children before the age of puberty contribute nothing to the birth rate. Even among adults, death rates are not constant, but tend to rise with advancing age.

In non-human populations, the differences can be more extreme. Insects go through a number of distinct life stages, such as egg, larva, pupa, and adult. Death rates may vary greatly across these different stages, and only adults are capable of reproducing. Plants also may have various stages they pass through, such as dormant seed, seedling, non-flowering, and flowering. How can a mathematical model take into account the subgroup structure that we would expect to play a large role in determining the overall growth or decline of such populations?

To create such *structured models*, we will focus on linear models. Even without resorting to non-linear formulas, we can gain insight into how populations with distinct age groups, or developmental stages, can behave. Ultimately we'll see that the behavior of these new linear models is quite similar to the exponential growth and decay of the linear model in the last chapter, with some important and interesting twists.

1. Linear Models and Matrix Algebra

The main modeling idea we'll use is simple. Rather than lumping the size of the entire population we are tracking into one quantity, with no regard for age or developmental stage, we consider several different quantities, such as the number of adults and the number of young. However, we limit ourselves to using very simple equations.

EXAMPLE. Suppose we consider a hypothetical insect with three life stages: egg, larva, and adult. Our insect is such that individuals progress from egg to larva over one time step, and from larva to adult over another. Finally, adults lay eggs and die in one more time step. To formalize this let

$$E_t = \text{the number of eggs at time } t,$$
$$L_t = \text{the number of larvae at time } t,$$
$$A_t = \text{the number of adults at time } t.$$

Suppose we collect data and find that only 4% of the eggs survive to become larvae, only 39% of the larvae make it to adulthood, and adults on average produce 73 eggs each. This can be expressed by the three equations

$$E_{t+1} = 73A_t,$$
$$L_{t+1} = .04E_t,$$
$$A_{t+1} = .39L_t.$$

This system of three difference equations is a model of the insect population. Note that since the equations involve no terms more complicated than those that appear in the equation of a line, it is justifiable to refer to this as a linear model. Also note that if we wish to use this model to predict future populations, we need three initial values, E_0, L_0, and A_0, one for each stage class. Since the three equations are *coupled* (because the population of one developmental stage appears in the formula giving the future population of a different stage), this system of difference equations is slightly more complicated than the linear models in the last chapter.

▶ The above example could actually be studied by the model

$$A_{t+3} = (.39)(.04)(73)A_t = 1.1388A_t,$$

where A_t is the number of adults. Explain why.

Of course, if we realize that $A_{t+3} = 1.1388A_t$ describes our population, then we immediately know that the population will grow exponentially, by a factor of 1.1388 for each 3 time steps.

EXAMPLE. Consider the example above, but suppose that rather than dying, 65% of the adults alive at any time survive for an additional time step. Then the model becomes

$$E_{t+1} = 73A_t,$$
$$L_{t+1} = .04E_t,$$
$$A_{t+1} = .39L_t + .65A_t.$$

Again, we call this a linear model since all terms are of degree one. Because of our modification, however, it is no longer clear how to express the population's growth in terms of a single equation. It should be intuitively clear that the change in our model should result in an even more rapidly growing population than before. The adults who survive longer can produce more eggs, producing even more adults that survive longer, and so on. However, the new growth rate is by no means obvious.

EXAMPLE. Suppose we are interested in a forest that is composed of two species of tree, with A_t and B_t denoting the number of each species in the forest in year t. When a tree dies, a new tree grows in its place, but the new tree might be of either species. To be concrete, suppose the species A trees are relatively long lived, with only 1% dying in any given year. On the other hand, 5% of the species B trees die. Because they are rapid growers, the B trees, however, are more likely to succeed in winning a vacant spot left by a dead tree; 75% of all vacant spots go to species B trees, while only 25% go to species A trees. All this can be expressed by

$$A_{t+1} = (.99 + (.25)(.01))A_t + (.25)(.05)B_t,$$
(1)
$$B_{t+1} = (.75)(.01)A_t + (.95 + (.75)(.05))B_t.$$

▶ Explain the source of each of the terms in these equations.

After simplifying, the model is a system of two linear difference equations

$$A_{t+1} = .9925A_t + .0125B_t,$$
$$B_{t+1} = .0075A_t + .9875B_t.$$

Unlike in the previous two examples, there is no obvious guess as to how populations modeled by these equations will behave.

In order to try to get numerical insight, suppose that we begin with a population of $A_0 = 10$ and $B_0 = 990$. These initial population values might describe the forest if most of the A trees were selectively logged in the past.

What will happen to the populations over time? A computer calculation shows the results in Table 1.

Year	A_t	B_t
0	10	990
1	22.30	977.70
2	34.35	965.65
3	46.17	953.83
4	57.74	942.26
5	69.09	930.91
⋮	⋮	⋮
10	122.50	877.50
⋮	⋮	⋮
50	401.04	598.96
⋮	⋮	⋮
100	543.44	456.56
⋮	⋮	⋮
500	624.97	375.03
⋮	⋮	⋮
1000	625	375
⋮	⋮	⋮

TABLE 1. Forest model simulation

This table shows rather interesting behavior; it appears that the forest approaches an equilibrium, with 625 trees of species A and 375 of species B. In fact, as you can see in Figure 1, if we had started with any other non-negative choices of A_0 and B_0, numerical calculations would have shown a similar movement toward exactly the same ratio $\frac{625}{375} = \frac{5}{3}$ of A trees to B trees. That the forest would even approach a stable distribution of the two species of trees is not obvious from our equations. It's even less clear why the stable distribution is in this $\frac{5}{3}$ ratio. To begin to understand the behavior of models such as the one above, we need to develop some more mathematical tools.

Vectors and matrices. The most convenient mathematical language to express models of the type above is that of linear algebra. It involves several types of mathematical objects that may be new to you.

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FIGURE 1. Two forest model simulations

DEFINITION. A <u>vector</u> <u>in</u> $\mathbb{R}^n$ is a list of n real numbers, usually written as a column.

EXAMPLE. $\begin{pmatrix} 10 \\ 990 \end{pmatrix}$ and $\begin{pmatrix} 625 \\ 375 \end{pmatrix}$ are both vectors in $\mathbb{R}^2$, while $\begin{pmatrix} 1 \\ -2 \\ 3 \end{pmatrix}$ is a vector in $\mathbb{R}^3$.

Vectors are usually denoted by small boldface letters, so for instance, we might use $\mathbf{x}_t = \begin{pmatrix} A_t \\ B_t \end{pmatrix}$ to denote the tree distribution in year t in our last example, so that $\mathbf{x}_3 = \begin{pmatrix} 46.17 \\ 953.83 \end{pmatrix}$. As you can see, much space is being wasted on this page by insisting that vectors be written in columns. To remedy this, we'll write things like $\mathbf{x}_3 = (46.17, 953.83)$ from now on, but we'll always expect you to act as if we'd written the numbers in a column.

DEFINITION. An <u>$m \times n$</u> <u>matrix</u> is a two-dimensional rectangular array of real numbers, with m rows and n columns.

EXAMPLE. $\begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$ is a 2×2 matrix and $\begin{pmatrix} 1 & -2 & 3 & -4 \\ 5 & -6 & -7 & 8 \\ -9 & 10 & -11 & 12 \end{pmatrix}$ is a 3×4 matrix.

If a matrix has the same number of rows as columns, it is said to be *square*. Note that there isn't really any important difference between a vector in $\mathbb{R}^n$ and a $n \times 1$ matrix; they are written in an identical manner.

Matrices (the plural of 'matrix') are usually denoted by capital letters, such as A, M, or P. For instance we might say

$$P = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$$

is the *projection*, or *transition*, matrix for our forest model above, since the entries in it are the numbers used to project future tree populations.

We'll now rewrite the forest model

$$A_{t+1} = .9925A_t + .0125B_t$$
(2)
$$B_{t+1} = .0075A_t + .9875B_t$$

in matrix notation as

(3)
$$\begin{pmatrix} A_{t+1} \\ B_{t+1} \end{pmatrix} = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix} \begin{pmatrix} A_t \\ B_t \end{pmatrix}$$

or $\mathbf{x}_{t+1} = P\mathbf{x}_t$. We've really gotten a bit ahead of ourselves here in our zeal to express the model in the simple form $\mathbf{x}_{t+1} = P\mathbf{x}_t$, which looks so much like the linear models we considered in the last chapter. What we've neglected to do is to make sure we know what we mean by writing $P\mathbf{x}_t$, a matrix times a vector.

We will define $P\mathbf{x}_t$ to be whatever is necessary so that equation (3) means the same thing as equations (2). In other words, we need

$$\begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix} \begin{pmatrix} A_t \\ B_t \end{pmatrix} = \begin{pmatrix} .9925 A_t + .0125 B_t \\ .0075 A_t + .9875 B_t \end{pmatrix}$$

This leads us to define multiplication by:

DEFINITION. The product of a 2×2 matrix and a vector in $\mathbb{R}^2$ is defined by

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} ax + by \\ cx + dy \end{pmatrix}.$$

Rather than try to remember this formula, it's better to remember the process by which we multiply: Entries in the first row of the matrix are multiplied by the corresponding entries in the column vector and then all these products are added. This gives us the top entry in the product. The bottom entry is obtained the same way but using the bottom row of the matrix.

If we have a larger matrix than a 2×2, we proceed analogously. Notice that to do this each row of the matrix must have as many entries as the column vector. That means that if we have a vector in $\mathbb{R}^n$ and we try to multiply it on the left by a matrix, the matrix must have n entries in each row, and hence have n columns. Since we'll be dealing primarily with square matrices, we'll generally use $n \times n$ matrices to multiple vectors in $\mathbb{R}^n$.

EXAMPLE.

$$\begin{pmatrix} 1 & -2 & 3 \\ -4 & 5 & -6 \\ 7 & -8 & 9 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ -1 \end{pmatrix} = \begin{pmatrix} 1 \cdot 1 - 2 \cdot 0 + 3 \cdot -1 \\ -4 \cdot 1 + 5 \cdot 0 - 6 \cdot -1 \\ 7 \cdot 1 - 8 \cdot 0 + 9 \cdot -1 \end{pmatrix} = \begin{pmatrix} -2 \\ 2 \\ -2 \end{pmatrix}$$

Think again of our forest with the two species of trees. Suppose the description above of the way the forest composition changes is what happens only in a wet year, so we rename the projection matrix

$$W = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}.$$

If in dry years we suppose species B dies at a greater rate, then a projection matrix for those years might be

$$D = \begin{pmatrix} .9925 & .0975 \\ .0075 & .9025 \end{pmatrix}.$$

▶ What is it about this matrix that suggests B trees have a higher mortality in dry years than in wet years?

In fact, all we've changed here is that the likelihood of a B tree dying in a dry year is now .39. All the other parameters are just as they were in equations (1).

▶ Verify that if the probability of a B tree dying is changed to .39, then the matrix D above results.

Suppose our initial populations are given by $\mathbf{x}_0 = (10, 990)$ as before. Then if the first year is dry,

$$\mathbf{x}_1 = D\mathbf{x}_0 = \begin{pmatrix} .9925 & .0975 \\ .0075 & .9025 \end{pmatrix} \begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} .9925 \cdot 10 + .0975 \cdot 990 \\ .0075 \cdot 10 + .9025 \cdot 990 \end{pmatrix} = \begin{pmatrix} 106.45 \\ 893.55 \end{pmatrix}.$$

Now suppose we have a dry year followed by a wet year; how should the populations change? Since we know $\mathbf{x}_1 = D\mathbf{x}_0$ and $\mathbf{x}_2 = W\mathbf{x}_1$, we see $\mathbf{x}_2 = W(D\mathbf{x}_0)$, which we could compute relatively easily by matrix multiplication:

$$\mathbf{x}_2 = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix} \begin{pmatrix} 106.45 \\ 893.55 \end{pmatrix} \approx \begin{pmatrix} 116.82 \\ 883.18 \end{pmatrix}.$$

A more interesting question is can we find a *single* matrix that will tell us the cumulative effect on populations of a dry year followed by a wet year? While $\mathbf{x}_2 = W(D\mathbf{x}_0)$, is there a matrix B so that $\mathbf{x}_2 = B\mathbf{x}_0$?

What we'd like to do is simply move some parentheses in the equation $\mathbf{x}_2 = W(D\mathbf{x}_0)$, writing it as $\mathbf{x}_2 = (WD)\mathbf{x}_0$, and say the matrix that does what we want is WD. The problem with this is that we don't yet know how we could multiply the two matrices W and D to get a new matrix WD.

What should this matrix WD look like? Rather than worry about the particular numbers involved in our concrete example, let

$$D = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad W = \begin{pmatrix} e & f \\ g & h \end{pmatrix}, \quad \mathbf{x}_t = \begin{pmatrix} x_t \\ y_t \end{pmatrix}.$$

So

$$x_1 = ax_0 + by_0, \qquad\qquad x_2 = ex_1 + fy_1$$
$$y_1 = cx_0 + dy_0, \qquad\qquad y_2 = gx_1 + hy_1.$$

By substituting the left two equations into the right ones, we get

$$x_2 = e(ax_0 + by_0) + f(cx_0 + dy_0)$$
$$y_2 = g(ax_0 + by_0) + h(cx_0 + dy_0),$$

or after rearranging,

$$x_2 = (ea + fc)x_0 + (eb + fd)y_0$$
$$y_2 = (ga + hc)x_0 + (gb + hd)y_0.$$

In matrix form this becomes

$$\mathbf{x}_2 = \begin{pmatrix} ea + fc & eb + fd \\ ga + hc & gb + hd \end{pmatrix} \mathbf{x}_0.$$

This indicates how we should define the product of two matrices; we want

$$WD = \begin{pmatrix} e & f \\ g & h \end{pmatrix} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} ea + fc & eb + fd \\ ga + hc & gb + hd \end{pmatrix}.$$

Notice the first column of our product on the right comes from multiplying W times the first column of D (treated as a vector), and the second column of the product comes from multiplying W times the second column of D.

DEFINITION. The product of two matrices is a new matrix, whose columns are found by multiplying the matrix on the left times each of the columns of the matrix on the right.

This means that in order to multiply two matrices, if the one on the right has n entries in each column, the one on the left must have n entries in each row.

EXAMPLE.

$$\begin{pmatrix} 1 & 3 \\ -1 & 2 \end{pmatrix} \begin{pmatrix} 2 & 1 \\ -2 & 1 \end{pmatrix} = \begin{pmatrix} 1 \cdot 2 + 3 \cdot -2 & 1 \cdot 1 + 3 \cdot 1 \\ -1 \cdot 2 + 2 \cdot -2 & -1 \cdot 1 + 2 \cdot 1 \end{pmatrix} = \begin{pmatrix} -4 & 4 \\ -6 & 1 \end{pmatrix}.$$

An interesting thing happens if we multiply the above two matrices again, but with them written in the opposite order — we get a different result.

EXAMPLE.

$$\begin{pmatrix} 2 & 1 \\ -2 & 1 \end{pmatrix} \begin{pmatrix} 1 & 3 \\ -1 & 2 \end{pmatrix} = \begin{pmatrix} 2 \cdot 1 + 1 \cdot -1 & 2 \cdot 3 + 1 \cdot 2 \\ -2 \cdot 1 + 1 \cdot -1 & -2 \cdot 3 + 1 \cdot 2 \end{pmatrix} = \begin{pmatrix} 1 & 8 \\ -3 & -4 \end{pmatrix}.$$

Warning: For most matrices A and B, $AB \neq BA$. Matrix multiplication is not commutative. The order within a product matters.

▶ Biologically, would you expect the effect on a forest of a dry year followed by a wet year to be exactly the same as that of a wet year followed by a dry year? What does this have to do with the warning?

EXAMPLE. Note that while a product like $\begin{pmatrix} .2 & .7 \\ 0 & .4 \end{pmatrix} \begin{pmatrix} 3.2 \\ 1.1 \end{pmatrix}$ makes sense, if the vector is placed on the left as $\begin{pmatrix} 3.2 \\ 1.1 \end{pmatrix} \begin{pmatrix} .2 & .7 \\ 0 & .4 \end{pmatrix}$, then the product doesn't make sense anymore. Since there is only one entry in each row of $\begin{pmatrix} 3.2 \\ 1.1 \end{pmatrix}$, while $\begin{pmatrix} .2 & .7 \\ 0 & .4 \end{pmatrix}$ has two entries in each column, the definition of matrix multiplication cannot be used. Because we are writing our vectors as columns, this means we must always put matrices to the left of vectors in products.

The fact that for matrices multiplication is not commutative — that order matters in a product — is a significant difference from the algebra of ordinary numbers. It's very important to always be aware of this when using matrices.

Fortunately, although we won't carefully show it here, matrix multiplication is associative: when multiplying three matrices, it is always true that $(AB)C = A(BC)$. You can regroup products however you wish, as long as you don't change the order. (A hint at why this turns out to be true: we defined the product of two matrices so that $A(BC) = (AB)C$ would hold in the special case when C is a vector. It only takes a little more thought to see that the definition then forces the same equality to be true when C is any matrix.)

Of course, it takes some practice to get comfortable with the algebra of matrices, but that's what the exercises are for. Most people use computers for performing matrix calculations, especially when the sizes of the matrices are large. Once you understand how to perform the work, the whole process becomes very tedious to do by hand. Nonetheless, you have to be able to do simple hand calculations to develop the understanding to use a computer effectively.

There are a few other terms and rules that are used in manipulating vectors and matrices.

Since we have names (vectors and matrices) for arrays of numbers, it's convenient to have a name for single numbers as well.

DEFINITION. A <u>scalar</u> is a single number.

DEFINITION. To multiply a vector or a matrix by a scalar, multiply every entry by that scalar.

EXAMPLE. $3 \begin{pmatrix} 1 \\ 2 \\ 3 \end{pmatrix} = \begin{pmatrix} 3 \\ 6 \\ 9 \end{pmatrix}$ and $-.2 \begin{pmatrix} 1 & -1 \\ 2 & 1 \end{pmatrix} = \begin{pmatrix} -.2 & .2 \\ -.4 & -.2 \end{pmatrix}.$

DEFINITION. To add two vectors together or to add two matrices together, add corresponding entries. The things being added must be the same size.

EXAMPLE. $\begin{pmatrix} 1 \\ 2 \end{pmatrix} + \begin{pmatrix} -1 \\ 4 \end{pmatrix} = \begin{pmatrix} 0 \\ 6 \end{pmatrix}$ and $\begin{pmatrix} 1 & -1 \\ 2 & 1 \end{pmatrix} + \begin{pmatrix} 0 & 1 \\ -1 & 2 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 1 & 3 \end{pmatrix}.$

DEFINITION. A vector whose entries are all zero is called a <u>zero</u> <u>vector</u>, and is denoted by $\mathbf{0}$.

Vectors and matrices also obey several distributive laws of multiplication over addition such as

$$A(B + C) = AB + AC, \quad (B + C)A = BA + CA, \text{ and } A(\mathbf{x} + \mathbf{y}) = A\mathbf{x} + A\mathbf{y}.$$

Finally, we note that while matrices in products do not usually commute, it is valid to interchange the order of a matrix and a scalar; for instance $A c\mathbf{x} = cA\mathbf{x}$.

Problems:

1. Without a computer, find the products

   a. $\begin{pmatrix} 2 & -3 \\ 1 & 7 \end{pmatrix} \begin{pmatrix} 3 \\ 2 \end{pmatrix}$

   b. $\begin{pmatrix} 1 & 3 & -2 \\ 4 & -3 & 1 \\ 0 & 1 & -4 \end{pmatrix} \begin{pmatrix} 3 \\ 2 \\ 5 \end{pmatrix}$

   c. $\begin{pmatrix} 2 & -3 \\ 1 & 7 \end{pmatrix} \begin{pmatrix} 3 & 2 \\ 2 & 4 \end{pmatrix}$

   d. $\begin{pmatrix} 1 & 3 & -2 \\ 4 & -3 & 1 \\ 0 & 1 & -4 \end{pmatrix} \begin{pmatrix} 3 & 1 & 0 \\ 2 & -1 & 3 \\ 5 & 0 & 1 \end{pmatrix}$

2. Explain why the product $\begin{pmatrix} 3 \\ 2 \end{pmatrix} \begin{pmatrix} 2 & -3 \\ 1 & 7 \end{pmatrix}$ cannot be calculated.

3. For $A = \begin{pmatrix} 1 & 2 \\ -1 & 1 \end{pmatrix}$, $B = \begin{pmatrix} 3 & -1 \\ -2 & 2 \end{pmatrix}$, and $C = \begin{pmatrix} -1 & 1 \\ -3 & 4 \end{pmatrix}$, find the following without a computer. Then check your answers with MATLAB. Matrices are entered as `A=[1,2;-1,1]`.

   a. $A + B$
   b. AB
   c. BA
   d. $A^2 = AA$
   e. $2A$
   f. Show $(A + B)C = AC + BC$.

4. For $A = \begin{pmatrix} 1 & 0 & -1 \\ 2 & 1 & 0 \\ -1 & 1 & -2 \end{pmatrix}$, $B = \begin{pmatrix} 3 & 2 & -1 \\ -2 & 0 & 2 \\ 0 & -1 & 1 \end{pmatrix}$, and $C = \begin{pmatrix} 1 & 0 & 2 \\ -2 & 1 & 1 \\ 3 & -1 & 1 \end{pmatrix}$, find the following without a computer. Then check your answers with MAT-LAB.

   a. $A + B$
   b. AB

    c. BA

    d. $A^2 = AA$

    e. 2A

    f. Show $C(A + B) = CA + CB$.

5. For $A = \begin{pmatrix} r & s \\ t & u \end{pmatrix}$ and $\mathbf{x} = \begin{pmatrix} x \\ y \end{pmatrix}$ and c a scalar, show $A(c\mathbf{x}) = c(A\mathbf{x})$ by computing each side.

6. For the matrix P in the text that models a forest succession, compute P^2, P^3, P^{500}. What is the biological meaning of each of these matrices? What is significant about the entries you see in P^{500}? (Use MATLAB for calculations.)

7. For the matrix P in the text that models a forest succession, produce a plot of the number of trees of each type over many years assuming $\mathbf{x}_0 = (10, 990)$. Use the MATLAB commands

```
P=[.9925 .0125; .0075 .9875]
x=[10; 990]
pops=[x]
x=P*x
pops=[pops x]
x=P*x
pops=[pops x]
x=P*x
pops=[pops x]
       ⋮
plot(pops')
```

Repeat this process several more times using different initial vectors with entries adding to 1000. Do all initial vectors ultimately lead to the same forest composition?

8. The first example of this section describes an insect model given by

$$E_{t+1} = 73A_t,$$
$$L_{t+1} = .04E_t,$$
$$A_{t+1} = .39L_t.$$

    a. Express this model as $\mathbf{x}_{t+1} = P\mathbf{x}_t$ using a 3×3 matrix P. What is $\mathbf{x}_t$?

    b. Compute P^2 and P^3 without the aid of a computer. What is the biological meaning of these matrices?

    c. Your computation of P^3 should remind you of the equation

$$A_{t+3} = (.39)(.04)(73)A_t = 1.1388A_t$$

in the text. Explain the connection.

9. The second example of this section describes an insect model given by

$$E_{t+1} = 73A_t,$$
$$L_{t+1} = .04E_t,$$
$$A_{t+1} = .39L_t + .65A_t.$$

    a. Express this model using a 3×3 matrix P.

    b. Compute P^2 and P^3 without the aid of a computer.

c. Beginning with initial populations of $(E_0, L_0, A_0) = (10, 10, 10)$, produce a plot of the population sizes over time using a computer. You can modify the commands in Problem 7 to do this with MATLAB.

2. Projection Matrices for Structured Models

Although linear models have many applications beyond understanding population growth, there are several common applications of them in modeling populations. In this setting, the projection matrices often have a rather distinct form, since there are natural ways of breaking the population into subgroups by age or developmental stage.

The Leslie Model: In some species the amount of reproduction varies greatly with the age of individuals. For instance, consider two different human populations that have the same total size. If one is comprised primarily of those over 50 in age, while the other has mostly individuals in their 20s, we would expect quite different population growth from them. Clearly the age-structure of the population matters.

Humans progress through a relatively long period before puberty when no reproduction occurs. After puberty, various social factors discourage or encourage childbearing at certain ages. Finally, menopause limits reproduction by older women.

To capture the effects on population growth, we might begin modeling a human population by creating five age classes with:

$$x_1(t) = \text{number of individuals age 0 through 14 at time } t,$$
$$x_2(t) = \text{number of individuals age 15 through 29 at time } t,$$
$$x_3(t) = \text{number of individuals age 30 through 44 at time } t,$$
$$x_4(t) = \text{number of individuals age 45 through 59 at time } t,$$
$$x_5(t) = \text{number of individuals age 60 through 75 at time } t.$$

While this formulation makes the unrealistic assumption that no one survives past age 75, that shortcoming could of course be remedied by creating additional age classes. Using a time step of 15 years, we can describe the population through equations like:

$$
\begin{aligned}
x_1(t+1) &= f_1 x_1(t) && + f_2 x_2(t) && + f_3 x_3(t) && + f_4 x_4(t) && + f_5 x_5(t) \\
x_2(t+1) &= \tau_{1,2} x_1(t) \\
x_3(t+1) &= && \tau_{2,3} x_2(t) \\
x_4(t+1) &= && && \tau_{3,4} x_3(t) \\
x_5(t+1) &= && && && \tau_{4,5} x_4(t)
\end{aligned}
$$

Here f_i denotes a birth rate (over a 15 year period) for parents in the ith age class, and $\tau_{i,i+1}$ denotes a survival rate for those in the ith age class passing into the $(i+1)$th. Since a single set of parents may be in different age groups, we should attribute half of their offspring to each in choosing values for f_i.

In matrix notation, the model is simply $\mathbf{x}_{t+1} = P\mathbf{x}_t$ where

$$\mathbf{x}_t = (x_1(t), x_2(t), x_3(t), x_4(t), x_5(t))$$

is the column vector of subpopulation sizes at time t and

$$
P = \begin{pmatrix}
f_1 & f_2 & f_3 & f_4 & f_5 \\
\tau_{1,2} & 0 & 0 & 0 & 0 \\
0 & \tau_{2,3} & 0 & 0 & 0 \\
0 & 0 & \tau_{3,4} & 0 & 0 \\
0 & 0 & 0 & \tau_{4,5} & 0
\end{pmatrix}
$$

is the projection matrix.

We might expect f_1 to be smaller than f_2, since fewer 0–15-year-olds are likely to give birth than 15–30-year-olds. However, remember that in the course of a time step the 0–15-year-olds age by 15 years, so the birth rate to such parents is probably not as small as you might have thought. It is also possible that some of the f_i are zero; for instance the very old may not reproduce.

▶ If data were collected, which of the numbers f_i do you think would be largest? which would be smallest? How might this vary depending on which particular human population was being modeled?

▶ What might be reasonable values for the $\tau_{i,i+1}$? Which are likely to be largest? smallest?

Of course we might improve our model by using more age classes of smaller duration, say 5 years or even 1 year, and adding additional age classes for those over 75. For humans, age classes of 15 years are too long for much accuracy. Demographers often use 5 year classes and track individuals to age 85, which results in a 17×17 matrix.

With an improved model, our matrix would be larger, but it would still have the same form: the top row would have fecundity information, the *subdiagonal* would have survival information, and the rest of the matrix would have entries of 0. A model whose projection matrix has this form is called a *Leslie* model.

EXAMPLE. A Leslie model describing the U.S. population in 1964 was formulated in [**KM67**]. Tracking only females, and hence ignoring the births of any males in the computation of birth rates, it used 10 age groups of five-year durations, and a time step of 5 years. The top row of the matrix was

(.0000, .0010, .0878, .3487, .4761, .3377, .1833, .0761, .0174, .0010),

while the subdiagonal was

(.9966, .9983, .9979, .9968, .9961, .9947, .9923, .9987, .9831).

▶ What is the meaning of the fact that the first subdiagonal entry is smaller than the second? What are possible explanations for this?

▶ Why might the seventh subdiagonal entry be smaller than those to either side of it? What age group of females is this number describing?

▶ Why might it be reasonable to only include females up to age 50 in this model?

The Usher Model: An Usher model is a slight variation on a Leslie model in which there may be non-zero entries on the diagonal. For example, return to the 5×5 matrix model of humans above, and continue to use 15-year-long age classes, but make the time step only five years in duration. Then while some of the individuals in a class will move up to the next class after a time step, many will stay where they are. This results in a matrix like

$$\begin{pmatrix} f_1 + \tau_{1,1} & f_2 & f_3 & f_4 & f_5 \\ \tau_{1,2} & \tau_{2,2} & 0 & 0 & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} & 0 & 0 \\ 0 & 0 & \tau_{3,4} & \tau_{4,4} & 0 \\ 0 & 0 & 0 & \tau_{4,5} & \tau_{5,5} \end{pmatrix},$$

with the parameters $\tau_{i,i}$ describing the fraction of the ith age class that remains in that class in passage to the next time step. Note that the values of the entries $\tau_{i,i+1}$ and f_i will be different from what they were in the Leslie version above, since the time step size has been changed.

Perhaps a more natural example of an Usher model is one based on the developmental stages an organism passes through in its lifetime. For instance for a mammal such as a whale that takes several years to reach sexual maturity, and may also live past an age where it breeds, a 3-stage model might be used, with immature, breeding, and post-breeding classes. The Usher matrix

$$\begin{pmatrix} \tau_{1,1} & f_2 & 0 \\ \tau_{1,2} & \tau_{2,2} & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} \end{pmatrix}$$

could describe such a population.

▶ Why is there only one non-zero f_i in this matrix?

Other Structured Population Models: While Leslie and Usher models are natural and common ones for describing populations, mathematically there is little special about the particular matrix forms they use. If a species can be better modeled by a different matrix model, then there is no reason not to.

As an example consider a plant which takes several years to mature to a flowering stage, and which does not flower every year after reaching maturity. In addition, seeds may lie dormant for several years before germinating.

The life cycle of this plant could be modeled using time steps of a year and the classes

$$x_1(t) = \text{number of ungerminated seeds at time } t,$$
$$x_2(t) = \text{number of sexually immature plants at time } t,$$
$$x_3(t) = \text{number of mature plants flowering at time } t,$$
$$x_4(t) = \text{number of mature plants not flowering at time } t,$$

With $\mathbf{x}(t) = (x_1(t), x_2(t), x_3(t), x_4(t))$, the projection matrix for the model might have the form

$$\begin{pmatrix} \tau_{1,1} & 0 & f_{3,1} & 0 \\ \tau_{1,2} & \tau_{2,2} & f_{3,2} & 0 \\ 0 & \tau_{2,3} & \tau_{3,3} & \tau_{4,3} \\ 0 & 0 & \tau_{3,4} & \tau_{4,4} \end{pmatrix}.$$

Here the parameter $\tau_{4,3}$ describes mature plants that did not flower in one season passing into the flowering class for the next. In addition, there are two parameters describing fertility — $f_{3,1}$ describes the production of seeds that do not germinate immediately, while $f_{3,2}$ describes the production of seedlings through new seeds that germinate by the next time step.

▶ Which parameter describes the seeds produced in previous years which again do not germinate, but may germinate in the future?

EXAMPLE. For this plant model with the particular parameter choices given by

(4)
$$\begin{pmatrix} .02 & 0 & 11.9 & 0 \\ .05 & .12 & 5.7 & 0 \\ 0 & .14 & .21 & .32 \\ 0 & 0 & .43 & .11 \end{pmatrix},$$

and an initial population vector of $\mathbf{x}_0 = (0, 50, 50, 0)$, the populations over the next 12 time steps are shown in Figure 2. We see a clear growth trend in the sizes of

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FIGURE 2. Simulation of plant model; at right side of graphs classes are in order 1,2,3,4 from top

all the classes, with some overlying oscillations for at least the first few time steps. Moreover, there is a roughly constant ratio between the sizes of the classes after a few steps.

The behavior exhibited in Figure 2 is typical of Leslie and Usher models as well, regardless of the number of classes involved. Generally there is a dominant trend of growth or decay, though smaller scale fluctuations are often also present. The dominant trend appears similar to the exponential growth or decay of the Malthusian model. However, the class structure of the model produces more intricate behavior as well.

The forest model of Section 1 is another example of a linear model that is neither Leslie nor Usher. Since it tracks two types of tree, rather than an organism going through its life cycle, the projection matrix has a rather different form. In fact, it's an example of a *Markov* model, which we'll develop further in Chapter 4. We saw, however, in Figure 1 that this model also showed a long term trend, toward an equilibrium. We'll develop means of extracting information on the main trends produced by any linear model in the next section.

In modeling real populations' life stages, the decision to use a Leslie model, an Usher model, or a unnamed variant, must take into account a number of factors. An understanding of the life cycle of the organism may make a natural choice of classes clear. However, the difficulty of finding good estimates of the parameters could also dictate choices, since if more classes are used, then more parameters appear in the model. Using very small age groups or many different stages should, in theory, produce a more accurate model. However, it also requires more detailed surveying to obtain reasonably accurate parameter values.

The identity matrix and matrix inverses. Having looked in more detail at the types of matrices used in linear population models, let's return to developing some mathematical tools for understanding them.

Suppose a linear population model uses only two classes, and hence has a 2×2 projection matrix P. If the population at time 1 is given by the vector $\mathbf{x}_1$, then computing the populations at the next time step just requires a multiplication

$$\mathbf{x}_2 = P\mathbf{x}_1.$$

But imagine that we are interested in deducing the populations at the previous time step. If we know $\mathbf{x}_1$ and P, how can we find $\mathbf{x}_0$? In other words, can we

project populations *backward* in time if we only have a matrix P describing how they change *forward* in time?

If P were a scalar instead of a matrix, we'd know how to do this. We'd take the equation $\mathbf{x}_1 = P\mathbf{x}_0$ and 'divide' each side by P to solve for $\mathbf{x}_0$. Unfortunately it's not clear what 'dividing by a matrix' means.

A slightly better way to think of it is as follows: Can we take the equation $\mathbf{x}_1 = P\mathbf{x}_0$ and multiply each side by some matrix in order to remove the P from the right hand side? Suppose we try this and pick some 2×2 matrix Q so that $\mathbf{x}_1 = P\mathbf{x}_0$ becomes $Q\mathbf{x}_1 = QP\mathbf{x}_0$. If our goal was to get rid of the P, we need QP to disappear from the equation. Unfortunately, QP will be a 2×2 matrix and there's no way around that. However, there is a special 2×2 matrix that would be good enough for our purposes.

DEFINITION. The 2×2 identity matrix is

$$I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

The $n \times n$ identity matrix is a square matrix whose entries are all 0, except for 1's on the main diagonal.

Notice that

$$I \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} x \\ y \end{pmatrix},$$

so that I behaves like the number 1 in ordinary algebra with scalars. Multiplying any vector times I leaves the vector unchanged. You should check that $AI = A$ and $IA = A$ for any matrix A as well.

Returning to our attempt to project a population backward in time, we had $Q\mathbf{x}_1 = QP\mathbf{x}_0$ so that if we can just pick Q so that $QP = I$, the equation becomes

$$Q\mathbf{x}_1 = I\mathbf{x}_0 = \mathbf{x}_0.$$

In other words, we'll have managed to solve for $\mathbf{x}_0$ by calculating $Q\mathbf{x}_1$.

DEFINITION. If P and Q are both $n \times n$ square matrices with $QP = I$, then we say that Q is the inverse of P. We will then use the notation $Q = P^{-1}$.

While we won't prove it here, it is possible to show that for square matrices, if $QP = I$, then $PQ = I$ as well. So if Q is the inverse of P, then P is the inverse of Q.

Before we try to calculate the inverse of a matrix, we should ask ourselves if one really has to exist. For instance

$$\begin{pmatrix} -2 & 1 \\ 1.5 & -.5 \end{pmatrix} \begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix},$$

so

$$\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}^{-1} = \begin{pmatrix} -2 & 1 \\ 1.5 & -.5 \end{pmatrix}.$$

On the other hand, if $A = \begin{pmatrix} 0 & -2 \\ 0 & -3 \end{pmatrix}$ then A doesn't have an inverse. To see this think about

$$\begin{pmatrix} * & * \\ * & * \end{pmatrix} \begin{pmatrix} 0 & -2 \\ 0 & -3 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

You simply can't fill in the entries in the top row of the matrix on the left so that the upper left entry in the product is 1. Because of the column of 0's in A, the upper left entry in the product will always be 0 as well.

While this example has shown there are some matrices without inverses, trying to find the inverse of a generic 2×2 matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ will give us more insight into the problem. We will make guesses as to how to fill out the unknown matrix in the equation

$$\begin{pmatrix} * & * \\ * & * \end{pmatrix} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Focusing on the upper right entry in the product first, we can easily get a zero there by putting d and $-b$ in the top row of the empty matrix. To get a zero in the bottom left entry of the product, we can put $-c$ and a in the bottom row. This leaves us with

$$\begin{pmatrix} d & -b \\ -c & a \end{pmatrix} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} ad - bc & 0 \\ 0 & ad - bc \end{pmatrix}.$$

To make sure we get 1's on the diagonal, we just need to divide every entry in the matrix on the left by $ad - bc$ so

$$\begin{pmatrix} \frac{d}{ad-bc} & \frac{-b}{ad-bc} \\ \frac{-c}{ad-bc} & \frac{a}{ad-bc} \end{pmatrix} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

The number $ad - bc$ is given a special name:

DEFINITION. The <u>determinant</u> of a 2×2 matrix $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ is the scalar $ad - bc$. It is denoted by $\det A$ or $|A|$.

Our formula for the inverse of a 2×2 matrix becomes:

If $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, then $A^{-1} = \frac{1}{\det A} \begin{pmatrix} d & -b \\ -c & a \end{pmatrix}$.

EXAMPLE.

$$\begin{pmatrix} 3 & -1 \\ 2 & 1 \end{pmatrix}^{-1} = \frac{1}{3 \cdot 1 + -2 \cdot -1} \begin{pmatrix} 1 & 1 \\ -2 & 3 \end{pmatrix} = \begin{pmatrix} .2 & .2 \\ -.4 & .6 \end{pmatrix}.$$

Since not every matrix has an inverse, we can't have really found a formula for the inverse of all 2×2 matrices. Something must go wrong occasionally. Looking at the formula, we see that it doesn't make sense if $\det A = 0$. In fact, though we won't prove it, if $\det A = 0$ then A has no inverse. In other words, to find the inverse of a 2×2 matrix, we can just try to use the formula. If the formula doesn't make sense, then the matrix has no inverse. We summarize this with

THEOREM. A square matrix has an inverse if, and only if, its determinant is non-zero.

EXAMPLE. $\begin{pmatrix} 1 & -2 \\ -2 & 4 \end{pmatrix}$ has no inverse since its determinant is $1 \cdot 4 + 2 \cdot -2 = 0$.

For a matrix that is 3×3 or larger, calculating the determinant or inverse (if it exists) is harder. While there are formulas for the determinant and inverse of any square matrix, they are too complicated to be very useful. Inverses are usually calculated through a different approach, called the Gauss-Jordan method, which is

taught in linear algebra courses. In this text, for matrices larger than 2×2 we rely on software such as MATLAB to do the calculations for us.

It's important to remember, though, that not every matrix will have an inverse. If you attempt to calculate one when none exists, MATLAB will let you know. Fortunately, most square matrices do in fact have inverses, for any reasonable interpretation of the word 'most.' For this reason matrices without inverses are said to be *singular*.

Let's return to our original motivation for developing the matrix inverse.

EXAMPLE. For the forest model of Section 1, suppose at time 1 the populations were $\mathbf{x}_1 = (500, 500)$. What must they have been at time 0?

To answer this, since $\mathbf{x}_1 = P\mathbf{x}_0$, we multiple by P^{-1} to find

$$\mathbf{x}_0 = P^{-1}\mathbf{x}_1$$

$$= \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}^{-1} \begin{pmatrix} 500 \\ 500 \end{pmatrix}$$

$$= \frac{1}{(.9925)(.9875) - (.0075)(.0125)} \begin{pmatrix} .9875 & -.0125 \\ -.0075 & .9925 \end{pmatrix} \begin{pmatrix} 500 \\ 500 \end{pmatrix}$$

$$= \frac{1}{.98} \begin{pmatrix} 487.5 \\ 492.5 \end{pmatrix} \approx \begin{pmatrix} 497.449 \\ 502.551 \end{pmatrix}$$

Problems:

1. The first section of this chapter began with two examples of insect population models. Is either of these a Leslie model? Is either of these an Usher model? Explain why by describing the form of the projection matrices for them.

2. In MATLAB, create the Leslie matrix for the 1964 U.S. population model of [**KM67**] described in the text with the commands
   ```
   sd=[.9966,.9983,.9979,.9968,.9961,.9947,.9923,.9987,.9831]
   P=diag(sd,-1)
   P(1,:)=[.0000,.0010,.0878,.3487,.4761,...
           .3377,.1833,.0761,.0174,.0010]
   ```
   For several choices of initial populations, produce graphs of the population over the next 10 time steps. Describe your observations.

3. Without using a computer, find the determinants and inverses of
   $$\begin{pmatrix} 1 & 2 \\ 2 & 3 \end{pmatrix}, \begin{pmatrix} 2 & -1 \\ 2 & 3 \end{pmatrix}, \begin{pmatrix} .7 & .3 \\ -1.4 & -.6 \end{pmatrix},$$
   provided they exist. Then check your answers with a computer. (The MATLAB commands to find the inverse and determinant of a matrix A are `inv(A)` and `det(A)`.)

4. Use a computer to find the determinants and inverses of the matrices
   $$\begin{pmatrix} 1 & 0 & -1 \\ 2 & 1 & 0 \\ -1 & 1 & -2 \end{pmatrix}, \begin{pmatrix} 3 & 2 & -1 \\ -2 & 0 & 2 \\ 0 & -1 & 1 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 2 \\ -2 & 1 & 1 \\ 3 & -1 & 1 \end{pmatrix},$$

provided they exist. Check to see that the computed inverse times the original
matrix really gives the identity matrix.

5. A simple Usher model of a certain organism tracks immature and mature
classes, and is given by the matrix $P = \begin{pmatrix} .2 & 3 \\ .3 & .5 \end{pmatrix}$.

   a. On average, how many births are attributed to each adult in a time step?

   b. What percentage of adults die in each time step?

   c. Assuming no immature individuals are able to reproduce in a time step,
   what is the meaning of the upper left entry in P?

   d. What is the meaning of the lower left entry in P?

6. For the model of the last problem,

   a. Find P^{-1}.

   b. If $\mathbf{x}_1 = (1100, 450)$, find $\mathbf{x}_0$ and $\mathbf{x}_2$.

7. Suppose a structured population model has projection matrix A, which has an
inverse.

   a. What is the meaning of the matrix A^{100}? If a population vector is multiplied
   by it, what is produced? If a population vector is multiplied by $(A^{100})^{-1}$, what
   is produced?

   b. What is the meaning of the matrix $(A^{-1})^{100}$? If a population vector is
   multiplied by it, what is produced?

   c. Based on your answers to (a) and (b), explain why $(A^n)^{-1} = (A^{-1})^n$ for
   any positive integer n. This matrix is often denoted by A^{-n}.

8. A model given in [**Cul85**], based on data collected in [**NK76**], describes a
certain coyote population. Three stage classes – pup, yearling, and adult – are
used while the matrix

$$P = \begin{pmatrix} .11 & .15 & .15 \\ .3 & 0 & 0 \\ 0 & .6 & .6 \end{pmatrix}$$

describes changes over a time step of one year. Explain what each entry in
this matrix is saying about the population. Be careful in trying to explain the
meaning of the .11 in the upper left corner.

9. a. Show that $A\mathbf{x} = A\mathbf{y}$ does not necessarily mean $\mathbf{x} = \mathbf{y}$ by calculating $A\mathbf{x}$
   and $A\mathbf{y}$ for $A = \begin{pmatrix} 2 & 1 \\ 6 & 3 \end{pmatrix}$, $\mathbf{x} = \begin{pmatrix} 5 \\ 7 \end{pmatrix}$, and $\mathbf{y} = \begin{pmatrix} 6 \\ 5 \end{pmatrix}$.

   b. Explain why if $A\mathbf{x} = A\mathbf{y}$ and A^{-1} exists, then $\mathbf{x} = \mathbf{y}$

10. Unlike scalars, for matrices usually $(AB)^{-1} \neq A^{-1}B^{-1}$. Instead, as long as the
inverses exist, $(AB)^{-1} = B^{-1}A^{-1}$.

   a. For $A = \begin{pmatrix} 2 & 1 \\ 1 & 1 \end{pmatrix}$ and $B = \begin{pmatrix} 1 & 2 \\ 3 & 5 \end{pmatrix}$, without using a computer compute
   $(AB)^{-1}$, $A^{-1}B^{-1}$, and $B^{-1}A^{-1}$ to verify these statements.

   b. Pick any two other invertible 2×2 matrices C and D and verify that
   $(CD)^{-1} = D^{-1}C^{-1}$.

   c. Pick two invertible 3×3 matrices E and F and use a computer to verify
   that $(EF)^{-1} = F^{-1}E^{-1}$.

11. The formula $(AB)^{-1} = B^{-1}A^{-1}$ can be explained several ways.

   a. Explain why $(B^{-1}A^{-1})(AB) = I$. Why does this show $(AB)^{-1} = B^{-1}A^{-1}$?

   b. Suppose, as in the first section of this chapter, that D is a projection matrix
   for a forest population in a dry year, and W is a projection matrix for a wet

year. Then if the first year is dry and the second wet, $\mathbf{x}_2 = WD\mathbf{x}_0$. How could you find $\mathbf{x}_1$ from $\mathbf{x}_2$? How could you find $\mathbf{x}_0$ from $\mathbf{x}_1$? Combine these to explain how you could find $\mathbf{x}_0$ from $\mathbf{x}_2$. How does this show $(WD)^{-1} = D^{-1}W^{-1}$?

12. A forest is composed of two species of trees, A and B. Each year $\frac{1}{3}$ of the trees of species A are replaced by trees of species B, while $\frac{1}{4}$ of the trees of species B are replaced by trees of species A. The remaining trees either survive or are replaced by trees of their own species.

a. Letting A_t and B_t denote the number of trees of each type in year t, give equations for A_{t+1} and B_{t+1} in terms of A_t and B_t.

b. Write the equations of part (a) as a single matrix equation.

c. Use (b) to get a formula for A_{t+2} and B_{t+2} in terms of A_t and B_t.

d. Use (b) to get a formula for A_{t-1} and B_{t-1} in terms of A_t and B_t.

e. Suppose $A_0 = 100$ and $B_0 = 100$. By hand calculate A_t and B_t for $t = 1, 2$, and 3. Use MATLAB to check your work and extend the calculation through $t = 10$. What is happening to the populations?

f. Choose several different values of A_0 and B_0 and use MATLAB to track how the populations change over time. How do your results compare to those of part (e)?

3. Eigenvectors and Eigenvalues

Let's return to the forest model introduced in Section 1 of this chapter. Recall that we tracked two types of trees in a forest by

$$\mathbf{x}_{t+1} = P\mathbf{x}_t, \text{ with } P = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}.$$

The vector $\mathbf{v}_1 = (625, 375)$, which gave the population values that the forest approached in our numerical investigation, has the significant property that $P\mathbf{v}_1 = \mathbf{v}_1$. (Make sure you check this.) Using the language of Chapter 1, we'd call $\mathbf{v}_1$ an equilibrium vector for our model.

Actually, there is another vector that is almost as well behaved as $\mathbf{v}_1$ for this particular model. If $\mathbf{v}_2 = (1, -1)$ then $P\mathbf{v}_2 = .98\mathbf{v}_2$. (Check this too.) While $\mathbf{v}_2$ isn't an equilibrium, it does exhibit rather simple behavior when multiplied by P — the effect of multiplying $\mathbf{v}_2$ by P is exactly the same as multiplying it by the scalar .98.

DEFINITION. If A is an $n \times n$ matrix, $\mathbf{v}$ a non-zero vector in $\mathbb{R}^n$, and λ a scalar such that $A\mathbf{v} = \lambda\mathbf{v}$, then we say that $\mathbf{v}$ is an <u>eigenvector</u> of A with <u>eigenvalue</u> λ.

We require that eigenvectors not be the zero vector, since $A\mathbf{0} = \mathbf{0} = \lambda\mathbf{0}$ for *all* real numbers λ. As long as an eigenvector $\mathbf{v} \neq \mathbf{0}$, there can be only one eigenvalue associated to it.

Using this terminology, the matrix P above has eigenvector $(625, 375)$ with eigenvalue 1, and eigenvector $(1, -1)$ with eigenvalue .98.

Notice however that like $(625, 375)$, the vectors $(5, 3)$, $(-10, -6)$, and $(15, 9)$ are also eigenvectors of P with eigenvalue 1. However, since all of these vectors are scalar multiples of one another this may not seem too surprising. This is explained by:

THEOREM. If $\mathbf{v}$ is an eigenvector of A with eigenvalue λ, then for any scalar c, $c\mathbf{v}$ is also an eigenvector of A with the same eigenvalue λ.

Proof: If $A\mathbf{v} = \lambda\mathbf{v}$, then $A(c\mathbf{v}) = c(A\mathbf{v}) = c(\lambda\mathbf{v}) = \lambda(c\mathbf{v})$.

The practical consequence of this is that while people might speak of $(5, 3)$ as 'the' eigenvector of P with eigenvalue 1, for instance, they don't really mean there is only one such eigenvector. Any non-zero scalar multiple of $(5, 3)$ is also an eigenvector.

Understanding eigenvectors is a crucial to understanding linear models. As a first step to seeing why this is so, consider what happens when the initial values of a linear model are given by an eigenvector. Consider a model $\mathbf{x}_{t+1} = A\mathbf{x}_t$ where we know that $A\mathbf{v} = \lambda\mathbf{v}$. Then if $\mathbf{x}_0 = \mathbf{v}$ we produce Table 2.

The entries in Table 2 lead to the formula $\mathbf{x}_t = \lambda^t\mathbf{v}$. This means that when the initial vector is an eigenvector, we can give a simple formula for all future values. Note that this formula involves a scalar exponential, just like the corresponding formula for the linear model of Chapter 1. The only difference is that this exponential multiplies the eigenvector of initial population values, rather then the single initial population value used in Chapter 1.

t	$\mathbf{x}_t$
0	$\mathbf{v}$
1	$A\mathbf{v} = \lambda\mathbf{v}$
2	$A\lambda\mathbf{v} = \lambda^2\mathbf{v}$
3	$A\lambda^2\mathbf{v} = \lambda^3\mathbf{v}$
$\vdots$	$\vdots$

TABLE 2. Linear model simulation with eigenvector as initial values

EXAMPLE. If the forest model with $P = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$ has initial vector $\mathbf{x}_0 = (1, -1)$, then $\mathbf{x}_t = .98^t(1, -1) = (.98^t(1), .98^t(-1))$. Thus as time increases the entries of $\mathbf{x}_t$ will both decay (rather slowly) to 0.

There are at least two questions that you might be wondering about: 1) Since populations can't be negative, why is an eigenvector with a negative entry relevant to understanding this biological model? 2) How was the eigenvector $(1, -1)$ found? We'll address the first of these questions next, and defer the second to the next section.

The use of eigenvectors. For the forest model $P = \begin{pmatrix} .9925 & .0125 \\ .0075 & .9875 \end{pmatrix}$ we have the two eigenvector equations

$$P \begin{pmatrix} 5 \\ 3 \end{pmatrix} = 1 \begin{pmatrix} 5 \\ 3 \end{pmatrix}, \quad P \begin{pmatrix} 1 \\ -1 \end{pmatrix} = .98 \begin{pmatrix} 1 \\ -1 \end{pmatrix}.$$

If we begin with an initial population that is not one of these eigenvectors, how can we use the eigenvectors to understand what will happen?

The key idea is to try to write our initial population vector in terms of eigenvectors. Specifically, given an initial population vector $\mathbf{x}_0 = (A_0, B_0)$ we look for two scalars c_1 and c_2 with

$$\begin{pmatrix} A_0 \\ B_0 \end{pmatrix} = c_1 \begin{pmatrix} 5 \\ 3 \end{pmatrix} + c_2 \begin{pmatrix} 1 \\ -1 \end{pmatrix}.$$

Equivalently, we need to solve

$$\begin{pmatrix} A_0 \\ B_0 \end{pmatrix} = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix}.$$

Notice that the matrix appearing in this equation has the eigenvectors of A as its columns. Now this equation can be solved provided that the matrix has an inverse. We've shown the 2×2 version of the following theorem.

THEOREM. Suppose A is an $n \times n$ matrix with n eigenvectors which form the columns of a matrix S. If S has an inverse, then any vector can be written as a sum of eigenvectors.

EXAMPLE. When we investigated the forest model numerically, we used the initial population vector $\mathbf{x}_0 = (10, 990)$. The eigenvector matrix is $S = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix}$.

To solve $\begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} 5 & 1 \\ 3 & -1 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix}$, we compute $S^{-1} = \frac{1}{-8} \begin{pmatrix} -1 & -1 \\ -3 & 5 \end{pmatrix}$, so

$$\begin{pmatrix} c_1 \\ c_2 \end{pmatrix} = \frac{1}{-8} \begin{pmatrix} -1 & -1 \\ -3 & 5 \end{pmatrix} \begin{pmatrix} 10 \\ 990 \end{pmatrix} = \begin{pmatrix} 125 \\ -615 \end{pmatrix}.$$

Thus

$$\begin{pmatrix} 10 \\ 990 \end{pmatrix} = 125 \begin{pmatrix} 5 \\ 3 \end{pmatrix} - 615 \begin{pmatrix} 1 \\ -1 \end{pmatrix}.$$

Technical remark: Not every matrix has eigenvectors that can be used as columns to form an invertible matrix. However, it is possible to prove that if a matrix doesn't have eigenvectors with this property, then by changing the entries an 'arbitrarily small' amount, you can get a matrix that does. Moreover, 'most' matrices do have this property — if you pick a matrix at random it is essentially guaranteed to have the property. The consequences of these facts for applying the theory of eigenvectors to biological models is that there is no need to really worry about not having nice enough eigenvectors.

Now that we understand how to express initial values in terms of eigenvectors, how do we use that expression? Let's suppose A is $n \times n$, with n eigenvectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n$, whose corresponding eigenvalues are $\lambda_1, \lambda_2, \ldots, \lambda_n$. We express our initial vector $\mathbf{x}_0$ as

$$\mathbf{x}_0 = c_1 \mathbf{v}_1 + c_2 \mathbf{v}_2 + \cdots + c_n \mathbf{v}_n,$$

so then

$$\begin{aligned} \mathbf{x}_1 = A\mathbf{x}_0 &= A(c_1 \mathbf{v}_1 + c_2 \mathbf{v}_2 + \cdots + c_n \mathbf{v}_n) \\ &= Ac_1 \mathbf{v}_1 + Ac_2 \mathbf{v}_2 + \cdots + Ac_n \mathbf{v}_n. \end{aligned}$$

But each term in this last expression is simply A applied to an eigenvector, so we see

$$\mathbf{x}_1 = c_1 \lambda_1 \mathbf{v}_1 + c_2 \lambda_2 \mathbf{v}_2 + \cdots + c_n \lambda_n \mathbf{v}_n.$$

But then

$$\begin{aligned} \mathbf{x}_2 = A\mathbf{x}_1 &= A(c_1 \lambda_1 \mathbf{v}_1 + c_2 \lambda_2 \mathbf{v}_2 + \cdots + c_n \lambda_n \mathbf{v}_n) \\ &= Ac_1 \lambda_1 \mathbf{v}_1 + Ac_2 \lambda_2 \mathbf{v}_2 + \cdots + Ac_n \lambda_n \mathbf{v}_n, \end{aligned}$$

and since each term is again A times an eigenvector,

$$\mathbf{x}_2 = c_1 \lambda_1^2 \mathbf{v}_1 + c_2 \lambda_2^2 \mathbf{v}_2 + \cdots + c_n \lambda_n^2 \mathbf{v}_n.$$

Continuing to apply A, we obtain the formula

$$\mathbf{x}_t = c_1 \lambda_1^t \mathbf{v}_1 + c_2 \lambda_2^t \mathbf{v}_2 + \cdots + c_n \lambda_n^t \mathbf{v}_n.$$

Understanding the eigenvectors has allowed us to find a formula for the values of $\mathbf{x}_t$ at any time. Notice the similarity of this formula to the corresponding one for the Malthusian model of Chapter 1. While there are a number of terms added together, each one has a simple exponential form that is already familiar.

EXAMPLE. For the populations used in the numerical investigation of the forest model we've already seen $\mathbf{x}_0 = \begin{pmatrix} 10 \\ 990 \end{pmatrix} = 125 \begin{pmatrix} 5 \\ 3 \end{pmatrix} - 615 \begin{pmatrix} 1 \\ -1 \end{pmatrix}$. This means

$$\mathbf{x}_t = 1^t(125) \begin{pmatrix} 5 \\ 3 \end{pmatrix} + .98^t(-615) \begin{pmatrix} 1 \\ -1 \end{pmatrix} =$$

$$\begin{pmatrix} 1^t(125)(5) + .98^t(-615)(1) \\ 1^t(125)(3) + .98^t(-615)(-1) \end{pmatrix} = \begin{pmatrix} 625 - (615).98^t \\ 375 + (615).98^t \end{pmatrix}.$$

We've thus found a formula giving all the entries in Table 1 that were originally produced by numerical investigation. Try picking a few values of t and seeing that you get the same values as appear in the table. Notice also that the formulas make clear that the populations will approach $(625, 375)$ as t grows.

Why does this all work? As far as an eigenvector is concerned, multiplication by the matrix is the same as multiplying by a scalar (the eigenvalue). Thus initial values given by eigenvectors will produce fully understandable behavior (exponential growth or decay). If we decompose any initial vector into eigenvectors, we can understand the model's effect on the initial vector through its effect on the eigenvectors.

Asymptotic behavior. Given a linear model $\mathbf{x}_{t+1} = A\mathbf{x}_t$ with initial vector $\mathbf{x}_0$, we now know how to find an explicit formula for $\mathbf{x}_t$: If $\lambda_1, \lambda_2, \ldots, \lambda_n$ are eigenvalues of A with $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n$ the corresponding eigenvectors, then writing $\mathbf{x}_0$ in terms of the eigenvectors

$$\mathbf{x}_0 = c_1\mathbf{v}_1 + c_2\mathbf{v}_2 + \cdots + c_n\mathbf{v}_n$$

means

(5) $$\mathbf{x}_t = c_1\lambda_1^t\mathbf{v}_1 + c_2\lambda_2^t\mathbf{v}_2 + \cdots + c_n\lambda_n^t\mathbf{v}_n.$$

This formula for $\mathbf{x}_t$ immediately gives us qualitative information on the model. Suppose, for example, that all the λ_i satisfy $|\lambda_i| < 1$; then as higher powers of the λ_i will shrink to 0, the populations $\mathbf{x}_t$ will also decline to $\mathbf{0}$ as t increases. On the other hand, if for at least one i we have $\lambda_i > 1$ (and the corresponding $c_i \neq 0$), then $\mathbf{x}_t$ should have a component of exponential growth. We also see that a negative value for λ_i should produce some form of oscillatory behavior, as its powers alternate in sign. Viewing the formula this way shows that the eigenvalues are really the key to the qualitative behavior of the model.

DEFINITION. An eigenvalue of A that is largest in absolute value is called a <u>dominant</u> <u>eigenvalue</u> of A. An eigenvector corresponding to it is called a <u>dominant eigenvector</u>.

Notice that we didn't say 'the' dominant eigenvalue in the definition, since it may be that several eigenvalues have the same absolute value. If there is an eigenvalue whose absolute value is strictly larger than all the others (e.g., $|\lambda_1| > |\lambda_i|$ for $i = 2, 3, \ldots, n$), we say it is *strictly* dominant.

Numbering the eigenvalues so that λ_1 is a dominant one, then equation (5) can be rewritten as

(6) $$\mathbf{x}_t = \lambda_1^t \left(c_1\mathbf{v}_1 + c_2 \left(\frac{\lambda_2}{\lambda_1} \right)^t \mathbf{v}_2 + \cdots + c_n \left(\frac{\lambda_n}{\lambda_1} \right)^t \mathbf{v}_n \right).$$

Assuming λ_1 is strictly dominant, then $\left|\frac{\lambda_i}{\lambda_1}\right| < 1$ for $i = 2, 3, \ldots, n$, so as t increases all the terms in the parentheses will decay exponentially, except for the first. Discarding the decaying terms shows the behavior of $\mathbf{x}_t$ is approximated by

$$\mathbf{x}_t \approx \lambda_1^t c_1 \mathbf{v}_1.$$

Overall, then, the model displays roughly exponential growth or decay, depending on the value of λ_1. For example, the model producing Figure 2 must have had a dominant eigenvalue that was larger than 1, since the graph shows exponential growth.

The dominant eigenvalue describes the main component of the model's behavior. For a linear population model, the dominant eigenvalue is often called the *intrinsic growth rate* of the population, and it is the single most important number describing how the population changes over time. It is an example of a summary statistic, since it extracts the most important feature from all the entries in the matrix.

Equation (6) can tell us more, though. Dividing each side by λ_1^t it becomes

$$\frac{1}{\lambda_1^t} \mathbf{x}_t = c_1 \mathbf{v}_1 + c_2 \left(\frac{\lambda_2}{\lambda_1}\right)^t \mathbf{v}_2 + \cdots + c_n \left(\frac{\lambda_n}{\lambda_1}\right)^t \mathbf{v}_n.$$

As $t \to \infty$, we see $\frac{1}{\lambda_1^t} \mathbf{x}_t \to c_1 \mathbf{v}_1$. In words, once we counteract the growth the model predicts for $\mathbf{x}_t$, the vector will simply approach a multiple of the dominant eigenvector. Therefore, for large t, the entries of $\mathbf{x}_t$ should be in roughly the same proportions to one another as the entries of $\mathbf{v}_1$. We see this in Figure 2, after the first few time steps have passed.

For a population model, the dominant eigenvector is hence often referred to as the *stable age distribution* or *stable stage distribution*, since it gives us the proportions of the population that should appear in each age or stage class, once we account for the growth trend.

Up to this point we've avoided commenting on the significance of the coefficients c_i in equations (5) and (6). Recall that they were found by letting $\mathbf{c} = (c_1, c_2, \ldots, c_n)$ and solving $\mathbf{x}_0 = S\mathbf{c}$, where S is a matrix with the eigenvectors as its columns. This means that if we change $\mathbf{x}_0$, we change the values of the c_i's. It's only through the c_i's that the initial vector $\mathbf{x}_0$ enters into formulas (5) and (6).

Even though it was not pointed out above, the discussion of the growth rate and stable distribution actually required an assumption that $c_1 \neq 0$. If we slough over this point, we reach the rather significant conclusion that the main features of the qualitative behavior of the model — the intrinsic growth rate and the stable age distribution — are independent of the initial vector. The dominant eigenvector and eigenvalue alone tell us the most important features of the model. This result is sometimes called the *Strong Ergodic Theorem* for linear models, or, in the context of population models, the *Fundamental Theorem of Demography*.

While certain choices of $\mathbf{x}_0$ might cause $c_1 = 0$, that happens rarely; for most choices of $\mathbf{x}_0$, we expect $c_1 \neq 0$. For many types of models it can even be proved $c_1 \neq 0$ for all biologically-meaningful choices of $\mathbf{x}_0$.

EXAMPLE. Consider an Usher model for a population with two stage classes given by the matrix

$$P = \begin{pmatrix} 0 & 2 \\ .5 & .1 \end{pmatrix}.$$

Because we have only two classes, we can make some reasonable guesses as to how the population should change. Note each adult produces two offspring, but only half of these make it to adulthood. If the lower right hand entry were not .1, we might expect a stable population size, but the small fraction of adults surviving for more than one time step, and therefore reproducing again, should result in a growing population. Because the fraction of adults surviving for an additional time step is small, the population will probably grow slowly.

Now using a computer to calculate eigenvectors and eigenvalues gives us

$$P \begin{pmatrix} .8852 \\ .4653 \end{pmatrix} = 1.0512 \begin{pmatrix} .8852 \\ .4653 \end{pmatrix}, \quad P \begin{pmatrix} .9031 \\ -.4295 \end{pmatrix} = -.9512 \begin{pmatrix} .9031 \\ -.4295 \end{pmatrix}.$$

This means that if we write our initial population (which hasn't been given here!) as

$$\mathbf{x}_0 = c_1 \begin{pmatrix} .8852 \\ .4653 \end{pmatrix} + c_2 \begin{pmatrix} .9031 \\ -.4295 \end{pmatrix},$$

for some numbers c_1 and c_2, then future populations are given by

$$\mathbf{x}_t = c_1 (1.0512)^t \begin{pmatrix} .8852 \\ .4653 \end{pmatrix} + c_2 (-.9512)^t \begin{pmatrix} .9031 \\ -.4295 \end{pmatrix}.$$

The first term here will produce slow growth, while the second term will decline in size. Notice that the sign of the eigenvalue in the second term will cause the numbers in that term to oscillate between negative and positive values as they approach zero. This means that if we pick any initial population, calculate future populations, and graph them, we should expect a slow exponential growth trend, with a decaying oscillation superimposed on it. You can see this for two choices of initial population vectors in Figure 3.

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FIGURE 3. Two simulations of a linear model; note similar qualitative features despite different initial values

The stable stage distribution for the model is given by $\mathbf{v}_1 = (.8852, .4653)$. Even though the population continues to grow, after enough time has elapsed we should see the populations in the two classes in proportion approximately $\frac{.8852}{.4653} = 1.9024$. That is, for every adult there will be about 1.9 immature individuals.

Many theorems have been proved about the particular types of matrices appearing in Leslie and Usher models. One of these is:

THEOREM. A Leslie model in which two consecutive age classes are fertile (*i.e.*, both $f_i > 0$ and $f_{i+1} > 0$) will have a positive real strictly dominant eigenvalue, and hence a stable age distribution.

While such theorems are useful for making general statements about the way populations must behave, when it comes to any particular model it is always necessary to actually find the eigenvectors and eigenvalues.

Complex numbers. As you'll see when you compute eigenvectors and eigenvalues, the above examples are a little misleading since eigenvectors and eigenvalues often involve complex numbers. Despite this, the discussion of asymptotic behavior is still valid, provided we explain how to measure the size of complex numbers.

DEFINITION. The <u>absolute</u> <u>value</u> of a complex number $a + ib$ is $|a + ib| = \sqrt{a^2 + b^2}$.

Notice that if $b = 0$ then $|a + i0| = \sqrt{a^2} = |a|$ is the usual meaning of absolute value for real numbers. Also $|a + ib| \geq 0$, and $|a + ib| = 0$ only when $a + ib = 0$, as we'd like for something that purports to measure the size of a number. Less obvious properties are:

THEOREM. For real numbers $a, b, c, d,$
a) $|(a + bi)(c + di)| = |a + bi||c + di|$
b) $|(a + bi)^n| = |a + bi|^n$
c) $\left| \dfrac{a + ib}{c + id} \right| = \dfrac{|a + ib|}{|c + id|}$

Notice that all three of these statements are familiar to you in the special case when $b = 0$ and $d = 0$, when the absolute value simply means the one you are familiar with for real numbers.

The proof of statement (a) appears as an exercise, and just requires multiplying out each side. Statement (b) is shown by just applying (a) repeatedly, since $(a + bi)^n = (a + bi)^{n-1}(a + bi)$. Statement (c) also follows from (a), if you first multiply the equation in (c) through by $|c + di|$ to clear the denominator.

To see how the discussion of the asymptotic behavior of a linear model is affected by complex eigenvalues, look back at equation (6). Even if some of the eigenvalues λ_i are complex, if λ_1 is strictly dominant so $|\lambda_1| > |\lambda_i|$ for $i = 2, 3, \ldots, n$, then by part (c) of the theorem, $\left| \frac{\lambda_i}{\lambda_1} \right| < 1$ as before, and so $\left| \frac{\lambda_i}{\lambda_1} \right|^t$ approaches 0 as t increases. By part (b) of the theorem, this would mean $\left| \left(\frac{\lambda_i}{\lambda_1} \right)^t \right|$ approaches 0, and so we must have that $\left(\frac{\lambda_i}{\lambda_1} \right)^t$ approaches 0. Just as before, we see that all the terms inside the parentheses in equation (6), except for the first, vanish as t increases. Our earlier argument is still valid even if some eigenvalues are complex.

Though the appearance of complex eigenvalues can be confusing at first, once you understand how to measure their size with the absolute value, they do not create any difficulties for analyzing a model. Their presence will usually result in irregular-looking oscillations as part of the model's behavior, just as negative eigenvalues cause oscillations. For population models a strictly dominant eigenvalue will always turn out to be real.

Problems:

1. Use MATLAB to investigate the model $P = \begin{pmatrix} 0 & 2 \\ .5 & .1 \end{pmatrix}$ discussed in the text. Show that for a variety of choices of initial populations, the model behaves exactly as one would predict from knowing only the two eigenvalues.

2. The MATLAB command `[S D]=eig(A)` computes the eigenvectors and eigenvalues of a matrix `A`. The columns of `S` will be the eigenvectors and the corresponding diagonal entries of `D` their eigenvalues.
   Use MATLAB to compute the eigenvectors and eigenvalues for the matrix P in the text for the forest succession model. Are they the 'same' ones given in the text? Explain.

3. Use MATLAB to compute the eigenvalues of the matrix given in equation (4) of Section 2 describing a plant model. Explain how the eigenvalues are related to the graph in Figure 2.

4. Consider the plant model of equation (4) of Section 2, as well as another plant model obtained by replacing all entries in the first row and column of that matrix with 0's.
   a. In biological terms, what is the meaning of replacing the specified entries with 0's?
   b. Compute the dominant eigenvalue for each model. Is there much difference in the intrinsic growth rate? Did the intrinsic growth rate change the way you thought it would? Explain.
   c. If the ungerminated seeds have little affect on the intrinsic growth rate of this plant, why might they still be biologically advantageous to the species?

5. Consider the Leslie model with $P = \begin{pmatrix} .3 & 2 \\ .4 & 0 \end{pmatrix}$.
   a. By thinking about the biological meaning of each entry in this matrix, do you think it describes a growing or declining population? Would you guess the population size would change rapidly or slowly?
   b. Compute eigenvectors and eigenvalues of the model with MATLAB.
   c. What is the intrinsic growth rate? the stable stage distribution?
   d. Express the initial vector $\mathbf{x}_0 = (5, 5)$ as a sum of the eigenvectors.
   e. Use your answer in (d) to give a formula for the population vector $\mathbf{x}_t$.

6. Repeat the last problem for the Usher model $P = \begin{pmatrix} 0 & 0 & 73 \\ .04 & 0 & 0 \\ 0 & .39 & .65 \end{pmatrix}$ with $\mathbf{x}_0 = (100, 10, 1)$.

7. Find the growth rate and stable stage distribution of the coyote model whose matrix is
$$P = \begin{pmatrix} .11 & .15 & .15 \\ .3 & 0 & 0 \\ 0 & .6 & .6 \end{pmatrix}.$$
Will the population grow or decline? quickly or slowly?

8. Find the intrinsic growth rate and stable age distribution for the U.S. population model described in the text and Problem 2 of Section 2. Recalling that the time step for this model was five years, how would you express the intrinsic growth rate on a yearly basis?

9. Suppose a simple population is broken up into immature and mature developmental classes. Only one-sixth of the immature individuals make it to maturity at each time step (with the rest dying). A typical mature individual gives birth

to five young at each time step. Finally, three-quarters of the adults die (after producing young) at each time step, while the rest survive.

a. Model this situation using a matrix. Is this a Leslie or an Usher model, or neither?

b. Compute eigenvectors and eigenvalues of the projection matrix using MAT-LAB.

c. What is the intrinsic growth rate? the stable stage distribution?

10. Show that the absolute value for complex numbers satisfies

$$|a + bi||c + di| = |(a + bi)(c + di)|.$$

Projects:

1. Consider a specific Leslie model with two age groups. After interpreting each matrix entry in biological terms, investigate the behavior of your model numerically using MATLAB for a variety of initial populations, including the eigenvectors of the matrix. Explain how the eigenvalues and eigenvectors are reflected in the behaviors you see when you plot the populations over time. Repeat for several other matrices.

   Suggestions:
   • Begin with the Leslie model

   $$\begin{pmatrix} \frac{1}{8} & 6 \\ \frac{1}{5} & 0 \end{pmatrix},$$

   using a MATLAB command sequence like:
   ```
   P=[1/8 6; 1/5 0]
   x=[10; 990]
   xhistory=x
   x=P*x, xhistory=[xhistory x]
   x=P*x, xhistory=[xhistory x]
   x=P*x, xhistory=[xhistory x]
   ⋮
   plot(xhistory')
   ```
   • For a variety of choices of the initial populations, describe what appears to be happening to the populations over time. Do the number of individuals in each group get bigger or smaller? Do they oscillate? Compute the ratio of immature individuals to adults at various times. How does this ratio change? Repeat this work with several different choices of an initial vector. Qualitatively describe all the behaviors you see.
   • Compute the eigenvectors and eigenvalues of A by entering `[S,D]=eig(A)`. Use the first eigenvector as your initial vector by letting `x=S(:,1)` and repeat the work above, including producing a plot. Do this again using the second eigenvector with `x= (:,2)`. Describe the behavior of the model with these choices on initial vectors. How is the behavior different? How is it the same? How are the eigenvalues responsible for these behaviors?