Mathematical Models in Biology ***An Introduction***
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CHAPTER 2

Linear Models of Structured Populations

2.1. Linear Models and Matrix Algebra

2.1.1. a. $\begin{pmatrix} 0 \\ 17 \end{pmatrix} = (0, 17)$

b. $(-1, 11, -18)$

c. $\begin{pmatrix} 0 & -8 \\ 17 & 30 \end{pmatrix}$

d. $\begin{pmatrix} -1 & -2 & 7 \\ 11 & 7 & -8 \\ -18 & -1 & -1 \end{pmatrix}$

2.1.2. The matrix on the left has 1 column, but the matrix on the right has 2 rows. For multiplication to have been possible, these numbers would have had to have been equal.

2.1.3. a. $\begin{pmatrix} 4 & 1 \\ -3 & 3 \end{pmatrix}$

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

c. $\begin{pmatrix} 4 & 5 \\ -4 & -2 \end{pmatrix}$

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

e. $\begin{pmatrix} 2 & 4 \\ -2 & 2 \end{pmatrix}$

f. Both sides equal $\begin{pmatrix} -7 & 8 \\ -6 & 9 \end{pmatrix}$.

2.1.4. a. $\begin{pmatrix} 4 & 2 & -2 \\ 0 & 1 & 2 \\ -1 & 0 & 1 \end{pmatrix}$

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

c. $\begin{pmatrix} 8 & 1 & -1 \\ -4 & 2 & -2 \\ -3 & 0 & -2 \end{pmatrix}$

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

e. $\begin{pmatrix} 2 & 0 & -2 \\ 4 & 2 & 0 \\ -2 & 2 & -4 \end{pmatrix}$

f. Both sides equal $\begin{pmatrix} 2 & 2 & -4 \\ -9 & -3 & 5 \\ 11 & 5 & -9 \end{pmatrix}$

2.1.5. $A(c\mathbf{x}) = \begin{pmatrix} r(cx) + s(cy) \\ t(cx) + u(cy) \end{pmatrix}$, $c(A\mathbf{x}) = \begin{pmatrix} c(rx + sy) \\ c(tx + uy) \end{pmatrix}$

2.1.6. Rounding to 4 decimal digits, $P^2 = \begin{pmatrix} .9852 & .0247 \\ .0148 & .9753 \end{pmatrix}$, $P^3 = \begin{pmatrix} .9779 & .0368 \\ .0221 & .9632 \end{pmatrix}$, $P^{500} = \begin{pmatrix} .6250 & .6250 \\ .3750 & .3750 \end{pmatrix}$. The matrices are the transition matrices for the forest succession model if the time steps were taken to be two years, three years, or five hundred years respectively. Interestingly, the columns of P^{500} are identical and the column entries are in the same ratio as the equilibrium ratio of A trees to B trees that we saw in the text.

2.1.7. All initial vectors with nonnegative entries will tend towards an equilibrium state of $(625, 375)$.

2.1.8. a. The transition matrix is $P = \begin{pmatrix} 0 & 0 & 73 \\ .04 & 0 & 0 \\ 0 & .39 & 0 \end{pmatrix}$ with $\mathbf{x}_t = (E_t, L_t, A_t)$.

b. $P^2 = \begin{pmatrix} 0 & 28.47 & 0 \\ 0 & 0 & 2.92 \\ .0156 & 0 & 0 \end{pmatrix}$, $P^3 = \begin{pmatrix} 1.1388 & 0 & 0 \\ 0 & 1.1388 & 0 \\ 0 & 0 & 1.1388 \end{pmatrix}$. The matrices represent the transition matrices describing what happens to the population classes over two and three time steps.

c. All the diagonal entries of P^3 are 1.1388. In the text, we argued that the adult insect population would grow exponentially by a factor of 1.1388 every three time steps. This diagonal matrix shows that all three classes of insect grow at the same exponential rate over three time steps, and that over three time steps there is no interaction among the three class sizes.

2.1.9. a. The transition matrix is $P = \begin{pmatrix} 0 & 0 & 73 \\ .04 & 0 & 0 \\ 0 & .39 & .65 \end{pmatrix}$ with $\mathbf{x}_t = (E_t, L_t, A_t)$.

b. $P^2 = \begin{pmatrix} 0 & 28.47 & 47.45 \\ 0 & 0 & 2.92 \\ .0156 & .2535 & .4225 \end{pmatrix}$, $P^2 = \begin{pmatrix} 1.1388 & 18.5055 & 30.8425 \\ 0 & 1.1388 & 1.898 \\ .01014 & .164775 & 1.413425 \end{pmatrix}$. Notice that in P^3 there are now non-zero off-diagonal entries (signifying interaction among the sizes of the classes) and that the $(3, 3)$ entry is larger than in the last problem. These are the effects of 65% of the adults living on to the next cycle and reproducing again.

c. All three populations appear to grow roughly exponentially. There is some oscillation in the population values that is particularly noticeable for a small number of iterations. Of course, if 65% of the adults live on into the next time step to produce eggs, the populations should grow even faster than in the previous problem.

2.2. Projection Matrices for Structured Models

2.2.1. The matrix for the first insect model is a Leslie matrix, and the matrix for the more complicated insect model is an Usher matrix, where the addition of .65 in the (3, 3) position is for the 65% of the adult population that live on into the next reproductive cycle. See problems 2.1.8(a) and 2.1.9(a) for the matrices.

2.2.2. Ultimately, all ten classes settle into what appears to be exponential growth, possibly after some initial oscillation. The class of individuals ages 0–4 is the most populous, followed by the class of individuals ages 5–9, etc.

2.2.3. Letting A, B, and C be the matrices in the order given, $\det A = -1$, $A^{-1} = \begin{pmatrix} -3 & 2 \\ 2 & -1 \end{pmatrix}$; $\det B = 8$, $B^{-1} = \begin{pmatrix} 3/8 & 1/8 \\ -1/4 & 1/4 \end{pmatrix}$; $\det C = 0$, so C has no inverse.

2.2.4. Letting A, B, and C be the matrices in the order given, $\det A = -5$, $A^{-1} = \begin{pmatrix} 2/5 & 1/5 & -1/5 \\ -4/5 & 3/5 & 2/5 \\ -3/5 & 1/5 & -1/5 \end{pmatrix}$; $\det B = 8$, $B^{-1} = \begin{pmatrix} 1/4 & -1/8 & 1/2 \\ 1/4 & 3/8 & -1/2 \\ 1/4 & 3/8 & 1/2 \end{pmatrix}$; $\det C = 0$, so C has no inverse.

2.2.5. a. 3

b. 50%

c. 20% of the organisms in the immature class remain in the immature class with each time step.

d. 30% of the organisms in the immature class progress into the adult class with each time step.

2.2.6. a. $P^{-1} = \begin{pmatrix} -.625 & 3.75 \\ .375 & -.25 \end{pmatrix}$

b. $\mathbf{x}_0 = (1000, 300)$, $\mathbf{x}_2 = (1570, 555)$,

2.2.7. a. A^{100} is the transition matrix for the model in which the time steps are one hundred times as large as they were taken for A. For instance, if $\mathbf{x}_n$ is a population vector and $\mathbf{x}_{n+1} = A\mathbf{x}_n$ is the new population after one year, then $\mathbf{x}_{n+100} = A^{100}\mathbf{x}_n$ is the population vector after one hundred years. If, instead, $\mathbf{x}_n$ is multiplied by $(A^{100})^{-1}$, then the resulting vector is $\mathbf{x}_{n-100}$, the population vector for a time one hundred years earlier.

b. $(A^{-1})^{100}$ is the hundredth power of the transition matrix that take you back one time step; thus, this matrix multiplies a population vector to create a population vector for a time one hundred time steps earlier. In other words $(A^{-1})^{100}\mathbf{x}_n = \mathbf{x}_{n-100}$.

c. Both matrices represent the transition matrix for calculating population vectors one hundred time steps earlier. Since there is nothing special about 100, more generally $(A^n)^{-1} = (A^{-1})^n$ since both are used to project populations n time steps into the past.

2.2.8. .11 represents the percentage of pups that remain pups after one year. (Pups can not give birth.) One possible explanation for some pups living but not progressing into the yearling stage after one year is that coyotes are born over several months throughout the year. The .15 entries indicate that on average each yearling and adult gives birth to .15 pups each year. The percentage of pups that progress into the yearling stage is 30% each year, so $1-.11-.30 = 59\%$ of pups die. While 60% of the yearlings progress into the adult stage, the remaining 40% die. Finally, each year 40% of the adult coyotes die, but 60% live on into the next time step.

2.2.9. a. Both $A\mathbf{x}$ and $A\mathbf{y}$ equal $(17, 51)$, though $\mathbf{x} \neq \mathbf{y}$. Notice that A has no inverse.
b. If A^{-1} exists, then $A\mathbf{x} = A\mathbf{y}$ implies $A^{-1}A\mathbf{x} = A^{-1}A\mathbf{y}$ or $\mathbf{x} = \mathbf{y}$.

2.2.10. a. $(AB)^{-1} = B^{-1}A^{-1} = \begin{pmatrix} -7 & 9 \\ 4 & -5 \end{pmatrix}$, $A^{-1}B^{-1} = \begin{pmatrix} -8 & 3 \\ 11 & -4 \end{pmatrix}$.
b. Answers may vary.
c. Answers may vary.

2.2.11. a. By associativity, $(B^{-1}A^{-1})(AB) = B^{-1}(A^{-1}A)B = B^{-1}B = I$. This shows that (AB) has a left inverse, but if a left inverse exists for a square matrix, then it also serves as a right inverse.
b. $\mathbf{x}_1 = W^{-1}\mathbf{x}_2$; $\mathbf{x}_0 = D^{-1}x_1$. Thus, to find $\mathbf{x}_0$ from $\mathbf{x}_2$, it is necessary to multiply first by W^{-1}, and then by D^{-1}: $\mathbf{x}_0 = D^{-1}W^{-1}\mathbf{x}_2$. This shows that the inverse of (WD) is the product $D^{-1}W^{-1}$ by indicating how to obtain $\mathbf{x}_0$ back from $\mathbf{x}_2 = WD\mathbf{x}_0$. Another way to explain this is that if you want to undo the action of a dry year followed by a wet year, you first undo the action of the recent wet year, then undo the action of the initial dry year.

2.2.12. a. $A_{t+1} = 2/3A_t + 1/4B_t$, $B_{t+1} = 1/3A_t + 3/4B_t$
b. $P = \begin{pmatrix} 2/3 & 1/4 \\ 1/3 & 3/4 \end{pmatrix}$, with $\mathbf{x}_t = (A_t, B_t)$.
c. $P^2 = \begin{pmatrix} 19/36 & 17/48 \\ 17/36 & 31/48 \end{pmatrix}$ so using decimal approximations $A_{t+1} = .5278A_t + .3542B_t$, $B_{t+1} = .4722A_t + .6458B_t$.
d. $P^{-1} = \begin{pmatrix} 9/5 & -3/5 \\ -4/5 & 8/5 \end{pmatrix}$ so $A_{t-1} = 1.8A_t - .6B_t$, $B_{t+1} = -.8A_t + 1.6B_t$.
e. The values of the populations are given in the table below. The populations seem to be stabilizing with $A_t \approx 85.7$ and $B_t \approx 114.3$.

t	0	1	2	3	4	5
A_t	100.0000	91.6667	88.1944	86.7477	86.1449	85.8937
B_t	100.0000	108.3333	111.8056	113.2523	113.8551	114.1063

t	6	7	8	9	10
A_t	85.7890	85.7454	85.7273	85.7197	85.7165
B_t	114.2110	114.2546	114.2727	114.2803	114.2835

e. If the initial populations A_0 and B_0 are non-negative and sum to 200, then they tend toward an equilibrium of around $(85.7, 114.3)$.

2.3. Eigenvectors and Eigenvalues

2.3.1. The model does behave as expected, showing slow exponential growth in both classes, with decaying oscillations superposed.

2.3.2. MATLAB finds that the eigenvector corresponding to eigenvalue 1.0512 is $(-.8852, -.4653)$ and the eigenvector corresponding to eigenvalue $-.9512$ is $(-.9031, .4295)$. These are essentially the same eigenvectors that were given in the text, since any scalar multiple of these are also eigenvectors. The text has simply multiplied them by -1. Note that MATLAB calculates eigenvectors (x, y) with $x^2 + y^2 = 1$

2.3.3. The eigenvalues of the plant model are approximately 1.1694, $-.7463$, $-.0738$, and .1107. The dominant eigenvalue is larger than one and the figure shows that the populations grow exponentially, as expected from an eigenvalue analysis. Since two of the eigenvalues are negative but smaller than 1 in absolute