Stage-Matrix or Leslie Population Models

Rather than model an entire population as a whole

- Stage-matrix models divide the population into various classes or subsets to obtain a more detailed description of the population.

- In the models that we will examine, the classes will usually be determined by age: age classes.

- The survival rates for various age classes are usually quite different. (In wild populations, the survival rate of juveniles is often very low, while adult survival rates are much higher.)

- We will focus on females only (because they control reproduction) and we will generally assume that the number of males is approximately the number of females (or that they are at least proportional).

EXAMPLE 5.3.1 (A Simple Bird Population). The model assumptions are

- Females only

- Two age classes $\begin{cases} \text{juveniles} < 1 \text{ yr old} \\ \text{adults} \geq 1 \text{ yr old} \end{cases}$

- The population in year k is $\mathbf{x}_k = \begin{bmatrix} j_k \\ a_k \end{bmatrix} = \begin{cases} \text{juveniles at start of year } k \\ \text{adults at start of year k} \end{cases}$

- For each and every year we assume that the **survival rates** and **fecundity rates** are the same:
  - some juveniles survive to become adults (say $\frac{1}{8}$): "juvenile survival rate."
  - some adults survive remain adults (say $\frac{1}{2}$): "adult survival rate."
  - adult females lay eggs and produce new juveniles (say 5/yr): "fecundity rate."

This means in year $k+1$

$$\mathbf{x}_{k+1} = \begin{bmatrix} j_{k+1} \\ a_{k+1} \end{bmatrix} = \begin{bmatrix} 5a_k \\ \frac{1}{8}j_k + \frac{1}{2}a_k \end{bmatrix} = \begin{bmatrix} 0 & 5 \\ \frac{1}{8} & \frac{1}{2} \end{bmatrix} \begin{bmatrix} j_k \\ a_k \end{bmatrix} = A\mathbf{x}_k = A(A\mathbf{x}_{k-1}) = A^2\mathbf{x}_{k-1} = \cdots = A^k\mathbf{x}_0,$$

Here you can see why diagonalization will be useful to calculate these matrix products.

where $\mathbf{x}_0$ is the initial population. Notice the similarity with Markov chain models. The difference this time is that A is not a stochastic matrix.

YOU TRY IT 5.1. Suppose that the initial population is $\mathbf{x}_0 = \begin{bmatrix} 5 \\ 5 \end{bmatrix}$. What does this mean? Use `Maple` to create the matrix A above and determine $\mathbf{x}_1$, $\mathbf{x}_5$, and $\mathbf{x}_{20}$. Then check your answers on the next page.

Yr	Juveniles	Adults	Population	Pop(n)/Pop($n-1$)	$\mathbf{x}_k/\|\|\mathbf{x}_{k-1}\|\|_1$
0	5	5	10		(0.5000, 0.5000)
1	25	3.125	28.125	2.8125	(0.8889, 0.1111)
2	15.625	4.6875	20.3125	0.722222222	(0.7692, 0.2308)
3	23.4375	4.296875	27.734375	1.365384615	(0.8451, 0.1549)
4	21.484375	5.078125	26.5625	0.957746479	(0.8088, 0.1912)
5	25.390625	5.224609375	30.61523438	1.15257353	(0.8293, 0.1707)
6	26.12304688	5.786132812	31.90917969	1.042264753	(0.8187, 0.1813)
7	28.93066406	6.158447266	35.08911133	1.0996557	(0.8245, 0.1755)
8	30.79223633	6.695556641	37.48779297	1.068359715	(0.8214, 0.1786)
9	33.4777832	7.196807861	40.67459106	1.085008955	(0.8231, 0.1769)
10	35.98403931	7.783126831	43.76716614	1.076032112	(0.8222, 0.1778)
11	38.91563416	8.389568329	47.30520248	1.080837684	(0.8227, 0.1773)
12	41.94784164	9.059238434	51.00708008	1.07825519	(0.8224, 0.1776)
13	45.29619217	9.773099422	55.06929159	1.07964015	(0.8225, 0.1775)
14	48.86549711	10.54857373	59.41407084	1.078896589	(0.8225, 0.1775)
15	52.74286866	11.38247401	64.12534267	1.079295557	(0.8225, 0.1775)
16	56.91237003	12.28409559	69.19646561	1.079081417	(0.8225, 0.1775)
17	61.42047793	13.25609405	74.67657197	1.079196333	(0.8225, 0.1775)
18	66.28047023	14.30560676	80.58607699	1.079134658	(0.8225, 0.1775)
19	71.52803382	15.43786216	86.96589598	1.079167757	(0.8225, 0.1775)
20	77.1893108	16.65993531	93.84924611	1.079149994	(0.8225, 0.1775)

Problems

1. (*a*) What's happening to the population as time increases?

(*b*) What's happening to the percentage of juveniles and adults in the population?

(*c*) What's happening to the population growth rate?

(*d*) Try the `Maple`command below and examine its output.

$$lambda, v := evalf\left(Eigenvectors\left(A\right)\right) \qquad \overbrace{\begin{bmatrix} 1.079156198 \\ -0.5791561975 \end{bmatrix}}^{\text{eigenvalues } \lambda}, \overbrace{\begin{bmatrix} 4.633249579 & -8.633249580 \\ 1.0 & 1.0 \end{bmatrix}}^{\text{corresponding eigenvectors } \mathbf{v}}$$

The **dominant eigenvalue** (largest magnitude) is $\lambda_1 = 1.079156198$ and the other eigenvalue is $\lambda_2 = -0.5791561975$. Define $\mathbf{x}$ to be the eigenvector corresponding to the dominant eigenvalue and extract it from v above:

$$x := v[1..,1] \qquad \begin{bmatrix} 4.633249579 \\ 1.0 \end{bmatrix}$$

(*e*) Use the following command to obtain the corresponding normalized eigenvector for the dominant eigenvalue is

$$\frac{1}{VectorNorm(x,1)}\,x \qquad \begin{bmatrix} 0.822482568005810988 \\ 0.177517432199999992 \end{bmatrix}$$

☞ The normalized eigenvector for the dominant eigenvalue gives the proportion of the age class in the long run population.

Case Study: Dynamical Systems and Spotted Owls

In this case study, eigenvalues and eigenvectors are used to study the change in a population over time. The population of Northern spotted owls, *Strix occidentalis caurina*, is divided into three age classes: juvenile (up to 1 year old), subadult (1 to 2 years old), and adult (over 2 years old). The population is examined at yearly intervals. Since it is assumed that the number of male and female owls is equal, only female owls are counted in the analysis. If there are j_k juvenile females, s_k subadult females, and a_k adult females at year k, then [R. Lamberson *et al*] found that the population of owls could be modelled by a system of equations.

In the model, juveniles and subadults do not produce offspring, but each adult female produces (on average) 0.33 juvenile females per year. This means that the number of juveniles j_{k+1} in year $k+1$ equals $0.33a_k$, or 0.33 times the number of adults in the previous year. (0.33 measures the *fecundity* of the adult females.) The other equations in the system below show *survival*. In this model, 18% of the juvenile females survive to become subadults (the rest die), 71% of the subadults survive to become adults (the others die), and 94% of the adults survive each year. Note that the model assumes that the fecundity and survival rates remain constant through time.

$$\begin{array}{rcrcrcl} 0j_k & + & 0s_k & + & 0.33a_k & = & j_{k+1} \\ .18j_k & + & 0s_k & + & 0a_k & = & s_{k+1} \\ 0j_k & + & .71s_k & + & 0.94a_k & = & a_{k+1} \end{array}$$

This can be rewritten in matrix form as

$$\begin{bmatrix} 0 & 0 & .33 \\ .18 & 0 & 0 \\ 0 & .71 & .94 \end{bmatrix} \begin{bmatrix} j_k \\ s_k \\ a_k \end{bmatrix} = \begin{bmatrix} j_{k+1} \\ s_{k+1} \\ a_{k+1} \end{bmatrix}.$$

If we let $A = \begin{bmatrix} 0 & 0 & .33 \\ .18 & 0 & 0 \\ 0 & .71 & .94 \end{bmatrix}$ and $\mathbf{x}_k = \begin{bmatrix} j_k \\ s_k \\ a_k \end{bmatrix}$, then the population model has the form

$$\mathbf{x}_{k+1} = A\mathbf{x}_k = A^k\mathbf{x}_0 \tag{5.1}$$

and is the **stage-matrix model** for the owl population. The first column (row) of the matrix A corresponds to juveniles, the second to subadults, and the third to adults. As noted above the entries in the first row of A describe the fecundity of the population; here only adult females produce juveniles. The entries in the other rows indicate survival. In this model, juveniles and subadults either survive and enter the next age class or die. Only adults, if they survive, stay in their current class. Note: *the model assumes that the fecundity and survival rates remain constant through time.*

The main goal is to examine the long-term dynamics of the population: Does the population become extinct or does it increase? To answer this question, we examine the eigenvalues of the matrix A using `Maple`.

Problems

2. Create the transition matrix for the spotted owl population. *Note:* Use fractions to make subsequent calculations more exact.

3. (*a*) To determine the eigenvalues of A use the *Eigenvalues* command and *evalf* to get decimal output.

(*b*) You should find $\lambda_1 = .9836$, $\lambda_2 = -.0218 + .2059i$, and $\lambda_3 = -.0218 - .2059i$. Two of the eigenvalues are complex numbers!

Interpretation. Jack's Theorem says that since the eigenvalues are distinct, the corresponding eigenvectors $\mathbf{v}_1$, $\mathbf{v}_2$, and $\mathbf{v}_3$ are independent and form a basis of $\mathbb{C}^3$ (it's ok to think $\mathbb{R}^3$). Consequently the initial vector $\mathbf{x}_0$ (whatever it happens to be) can be expressed as a linear combination of the basis vectors

$$\mathbf{x}_0 = c_1\mathbf{v}_1 + c_2\mathbf{v}_2 + c_3\mathbf{v}_3.$$

Using basic properties of eigenvectors (including a homework problem on the next assignment) it follows that

$$\mathbf{x}_k = A^k\mathbf{x}_0 = c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + c_3(\lambda_3)^k\mathbf{v}_3$$

and is called the **eigenvector decomposition** of $\mathbf{x}_k$. (See page 302 of your text.)

Next, we examine the magnitude[1] (norm) of each eigenvalue. To find the magnitudes (norms) of the eigenvalues use a loop and the *abs* command in `Maple`:

[1] The norm of the complex number $a+bi$ is $|a+bi| = \sqrt{a^2+b^2}$ just like the distance to the origin in $\mathbb{R}^2$.

```
> for i from 1 by 1 to 3 do abs(lambda[i]) end do;
```

0.9835927397
0.2070688348
0.2070688348

Each eigenvalue has magnitude less than 1, so $\lim_{k\to\infty} \lambda_i^k = 0$. Since $\mathbf{x}_k = c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + c_3(\lambda_3)^k\mathbf{v}_3$, we see that

$$\lim_{k\to\infty} \mathbf{x}_k = \lim_{k\to\infty} [c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + c_3(\lambda_3)^k\mathbf{v}_3] = \mathbf{0} + \mathbf{0} + \mathbf{0} = \mathbf{0}.$$

In other words, the population is becoming extinct *no matter what the initial population* $\mathbf{x}_0$ *is*.

The number of greatest importance to this analysis is the **dominant** eigenvalue $\lambda_1 = .9836$, the eigenvalue of greatest magnitude. If λ_1 happened to be greater than 1, the population would have increased steadily.

Problems

4. (*a*) **Modifying the Example.** Suppose the survival rate for juveniles were somehow increased to 50%. What would the new stage matrix be? Enter it into `Maple`.

(*b*) Use the *Eigenvectors* command (see Problem 1 (d)) to list both the eigenvalues and their corresponding eigenvectors in columns. Check that the eigenvalues of this new matrix are $\lambda_1 = 1.0469$, $\lambda_2 = -.0534 + .3302i$, and $\lambda_3 = -.0534 - .3302i$.

(*c*) Use a loop to determine the dominant eigenvector.

(*d*) If $\mathbf{v}_1$, $\mathbf{v}_2$, and $\mathbf{v}_3$ now denote eigenvectors of this new matrix, there is a new eigenvector decomposition for $\mathbf{x}_k$:

$$\mathbf{x}_k = c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + c_3(\lambda_3)^k\mathbf{v}_3.$$

Since the magnitudes of λ_2 and λ_3 are still less than 1, as $k \to \infty$, the second and third vectors tend to the zero vector, but the first does not. This time

$$\lim_{k\to\infty} \mathbf{x}_k = \lim_{k\to\infty} [c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + c_3(\lambda_3)^k\mathbf{v}_3] = c_1(\lambda_1)^k\mathbf{v}_1 + \mathbf{0} + \mathbf{0} = \lim_{k\to\infty} c_1(1.0469)^k\mathbf{v}_1 = \begin{bmatrix}\infty\\\infty\\\infty\end{bmatrix}.$$

The owl population is increasing exponentially at an annual growth rate of 1.0469, i.e., the population is increasing by 4.69% per year *no matter what the initial population* $\mathbf{x}_0$ *is*.

(*e*) Let $\mathbf{x}$ be the eigenvector corresponding to the dominant eigenvalue. Use `Maple` to determine the long run behavior. Interpret this vector. What does it say about the long run age-class proportions of the population?

$$\frac{1}{VectorNorm(x,1)}\,x$$

Summary of Key Points

1. The equation $\mathbf{x}_{k+1} = A\mathbf{x}_k = A^k\mathbf{x}_0$ is a stage-matrix model of the population. A is an $n \times n$ matrix, where the population has been divided into n classes or stages.
2. The eigenvalues of A are calculated and listed in descending order of magnitude: $|\lambda_1| \geq |\lambda_2| \geq |\lambda_3| \geq \cdots \geq |\lambda_n|$. If $|\lambda_1|$ is strictly greater than $|\lambda_2|$, we call λ_1 the **dominant eigenvalue**.
3. If A is diagonalizable, for example, if A has n distinct (possibly complex) eigenvalues, then $\mathbf{x}_k$ can be expressed (decomposed) in terms of its eigenvalues and corresponding eigenvectors:
$$\mathbf{x}_k = c_1(\lambda_1)^k\mathbf{v}_1 + c_2(\lambda_2)^k\mathbf{v}_2 + \cdots + c_n(\lambda_3)^k\mathbf{v}_n.$$
4. If $|\lambda_1| < 1$, then the population will decrease to extinction, no matter what the initial population.
5. If λ_1 is a real number greater than 1 and all the other eigenvalues are less than 1 in magnitude, then the population is increasing exponentially (no matter what the initial population). In this case the unit eigenvector $\frac{1}{||\mathbf{v}_1||_1}\mathbf{v}_1$ gives the percentages found in each class in the long-run population distribution.

Sustainable Harvesting

If a population is increasing, one might be interested in harvesting a portion of the population for some purpose. An issue of major interest in this case is how much of the population might be harvested while maintaining the population at a constant level. This is surely an important issue in the forestry and fishing industries. Classes are not distinguished in the harvest, although this could be added to the model with only slightly more difficulty. If a fraction h of the population is harvested each year, where $0 \leq h < 1$, the population model becomes

$$\mathbf{x}_{k+1} = A\mathbf{x}_k - hA\mathbf{x}_k.$$

It is desired to find h so that the population at year $k+1$ equals that of year k. Letting $\mathbf{x}$ be this common population vector, then an h is sought with

$$\mathbf{x} = A\mathbf{x} - hA\mathbf{x} = (1-h)A\mathbf{x}.$$

Since this equation may be rewritten as

$$A\mathbf{x} = \frac{1}{1-h}\mathbf{x},$$

the number $\frac{1}{1-h}$ must be an eigenvalue of A. Since $h < 1$, then $\frac{1}{1-h} > 1$. If λ_1 is the only eigenvalue of A with magnitude larger than 1, it follows that we have

$$\frac{1}{1-h} = \lambda_1 \qquad \text{or} \qquad h = \frac{\lambda_1 - 1}{\lambda_1}.$$

In the increasing owl population above, $\lambda_1 = 1.0469$. Even though it is difficult to imagine why owls would be harvested, the appropriate calculation shows that

$$h = \frac{\lambda_1 - 1}{\lambda_1} = \frac{.0469}{1.0469} \approx 0.0447.$$

Thus, 4.47% of the population could be harvested each year and the population would remain constant.

Homework and Stage-Matrix Questions: Due Monday

1. Complete the second half of the proof of (rewrite or copy)

THEOREM 5.3.2 (The Diagonalization Theorem). An $n \times n$ matrix A is diagonalizable if and only if A has n independent eigenvectors $\{\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n\}$. In fact, if $P = [\mathbf{v}_1\, \mathbf{v}_2\, \ldots\, \mathbf{v}_n]$ and

$$D = \begin{bmatrix} \lambda_1 & 0 & \cdots & 0 \\ 0 & \lambda_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \lambda_n \end{bmatrix}$$

is the diagonal matrix whose diagonal entries are the eigenvalues corresponding to $\{\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n\}$, then $A = PDP^{-1}$.

Proof. $\Leftarrow$ Given A has n independent eigenvectors $\{\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n\}$ corresponding to $\lambda_1, \ldots, \lambda_n$ (λ's are not necessarily, distinct by the way). Let $P = [\mathbf{v}_1\, \mathbf{v}_2\, \ldots\, \mathbf{v}_n]$. By the Connections Theorem, P is ______________________________. Let

$$D = \begin{bmatrix} \lambda_1 & 0 & \cdots & 0 \\ 0 & \lambda_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \lambda_n \end{bmatrix}$$

Because $\{\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n\}$ are ______________________________________.

$$AP = [\qquad\qquad\qquad\qquad\qquad\qquad] = [\lambda_1\mathbf{v}_1\, \ldots\, \lambda_n\mathbf{v}_n] = PD$$

Since $AP = PD$, it follows that $A =$ _______________. So A is ______________________________.

□

2. Page 286–287: Just find P and D if possible: #8, 10, and 12. Note for #12 you are given the eigenvalues.

3. Here's an easy problem: Without doing any calculation give an eigenvalue of $A = \begin{bmatrix} 1 & 2 & 3 \\ 1 & 2 & 3 \\ 1 & 2 & 3 \end{bmatrix}$. Hint: Connections Extension to Eigenvalues.

4. Suppose that an $n \times n$ matrix A has eigenvector $\mathbf{v}_1$ corresponding to eigenvalue λ_1. On the last assignment, you proved that $A^2\mathbf{v}_1 = \lambda_1^2\mathbf{v}$.

   (*a*) Assume that for some positive integer k, you know $A^k\mathbf{v}_1 = \lambda_1^k\mathbf{v}_1$. Prove that $A^{k+1}\mathbf{v}_1 = \lambda_1^{k+1}\mathbf{v}_1$. Hint: Think of A^{k+1} as AA^k.

Comment: Here's what the previous part means. Since we know that A has eigenvector $\mathbf{v}_1$ corresponding to eigenvalue λ_1, we know that $A^1\mathbf{v}_1 = \lambda_1^1\mathbf{v}_1$. By part (a) with $k = 1$, we now know that $A^{k+1}\mathbf{v}_1 = A^{1+1}\mathbf{v}_1 = A^2\mathbf{v}_1 = \lambda_1^2\mathbf{v}_1$. By part (a) again with $k = 2$, we now know that $A^{k+1}\mathbf{v}_1 = A^{2+1}\mathbf{v}_1 = A^3\mathbf{v}_1 = \lambda_1^3\mathbf{v}_1$. By part (a) with $k = 3$, we now know that $A^{k+1}\mathbf{v}_1 = A^{3+1}\mathbf{v}_1 = A^4\mathbf{v}_1 = \lambda_1^4\mathbf{v}_1$, and so on. So we have shown

THEOREM 5.3.3. Suppose that a square matrix A has eigenvector $\mathbf{v}_1$ corresponding to eigenvalue λ_1. Then for any positive integer n, $A^n\mathbf{v}_1 = \lambda_1^n\mathbf{v}_1$

   (*b*) Suppose that an $n \times n$ matrix A has eigenvector $\mathbf{v}_1$ corresponding to λ_1. Let c be any scalar. Using the theorem above and basic matrix algebra, prove: For any positive integer n, $A^n(c\mathbf{v}_1) = c\lambda_1^n\mathbf{v}$. (This is a quick proof.)

   (*c*) Ok, now go a step further. Suppose that an $n \times n$ matrix A has eigenvectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_p$ with corresponding eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_p$. If the vector $\mathbf{x}$ can be expressed as $\mathbf{x} = c_1\mathbf{v}_1 + c_2\mathbf{v}_2 + \cdots + c_p\mathbf{v}_p$, then use your result above and matrix algebra to show

$$A^n\mathbf{x} = c_1\lambda_1^n\mathbf{v}_1 + c_2\lambda_2^n\mathbf{v}_2 + \cdots + c_p\lambda_p^n\mathbf{v}_p$$

5. Carefully read Theorem 5.7(b) on page 285. Now do Exercises 24 and 26 on page 287.

6. Review the definition of **diagonalizable** (see page 282 or your notes). Prove the following: If A is an $n \times n$ diagonalizable matrix, then A^T is diagonalizable. Hint: Carefully use transpose algebra and at the end rename $(P^T)^{-1}$ as Q.

Complete these `Maple` problems with your partner: One good copy.

1. These data come from Levi Arthur's (H '05) final project for Math 214 and pertain to the white-tailed deer, *Odocoileus virginianus*, population in New York. It has three age-classe: fawns, subadults, and does (adult females).

   Each adult female gives birth on average to 0.52 female fawns per year
   55% of female fawns survive to become subadults
   60% of female subadult deer survive to become adults
   90% of female adult deer survive to become adults

   (*a*) Determine the stage-matrix for this problem.

   (*b*) Show that the deer population is increasing.

   (*c*) Determine the percentage of each class in the long-run population.

   (*d*) Assume you work for the NY State Department of Environmental Conservation. Determine the sustainable harvest rate (read the handout) for white-tailed deer in New York. (By the way, this 'harvesting' rate applies to all age classes.)

2. This modeling technique may also be applied to plants. Instead of age classes, classes based on the size of plant are used. Instead of fecundity, the growth of the plant is called sprout production. In Reference 1, a population of a common shrub called the speckled alder, *Alnus incana ssp. rugosa*, was grouped into five size classes based on stem diameter: less than .1 cm, .1–.9 cm, 1–1.9 cm, 2–2.9 cm, and 3–3.9 cm. The number of stems with diameter of more than 4 cm was too small to allow meaningful measurement. The following

matrix was derived for this situation:

$$\begin{bmatrix} .78 & .02 & .06 & .10 & .14 \\ .12 & .76 & 0 & 0 & 0 \\ 0 & .12 & .86 & 0 & 0 \\ 0 & 0 & .14 & .58 & 0 \\ 0 & 0 & 0 & .38 & .83 \end{bmatrix}.$$

(*a*) Interpret biologically what each entry in the first row of this matrix means.

(*b*) Interpret biologically what .58 in row 4, column 4 means.

(*c*) Determine whether the alder shoot 'population' is becoming 'extinct' in this model. If the population is not becoming extinct, determine the percentage of each class in the long-run population.

3. (*a*) **Extra Credit for Homework Grade** (Due Tuesday at 5:00 pm). Return to Problem 1 above. Suppose that you work for the NY State Department of Environmental Conservation. By issuing hunting permits for does (adult females) your department can lower the survival rate of adult females below the current 90%. What survival rate r would you need to achieve to produce a situation where the population is stable, that is the dominant eigenvalue is $\lambda_1 = 1$? You can solve this using trial and error by trying various values for r in the stage-matrix for deer and finding the eigenvalues. Your answer for r should give an eigenvalue correct to three decimal places, that is, λ_1 should be between 0.9995 and 1.0005.

(*b*) What would be the long-run population distribution in this case?

(*c*) Further Bonus: Determine r using a method other than trial and error. It is easy if you think about it in the correct way.

Background on the Northern Spotted Owl

Present Status: The spotted owl has been a focal point of the Pacific Northwest forest debate since it was Federally listed as a threatened species in July of 1990 due to extensive loss of habitat in old-growth and late-successional forest.[2] The survival of the owl in the Pacific Northwest and northern California depends on maintaining adequate, well-distributed nesting, roosting, and foraging (NRF) habitat throughout the species' range. Because of the owl's dependency on old-growth and late-successional forests in much of its range, loss of these forest habitats due to timber harvest activities threaten the future of the northern spotted owl.

[2] See `http://www.fws.gov/oregonfwo/articles.cfm?id=149489595`

General Habitat: Northern spotted owls generally have large home ranges and use large tracts of land containing significant acreage of older forest to meet their biological needs. Northern spotted owl habitat consists of four components: (1) Nesting, (2) roosting, (3) foraging, and (4) dispersal. The attributes of superior nesting and roosting habitat typically include a moderate to high canopy closure (60 to 80 percent closure); a multi-layered, multi-species canopy with large overstory trees; a high incidence of large trees with various deformities (e.g., large cavities, broken tops, mistletoe infections, and debris accumulations); large accumulations of fallen trees and other debris; and sufficient open space below the canopy for owls to fly.

Spotted owls use a wider array of forest types for foraging, including more open and fragmented habitat. Habitat that meets the spotted owl's need for nesting and roosting also provides foraging habitat. However, some habitat that supports foraging may be inadequate for nesting and roosting. In much of the species' northern range, large, dense forests are also chosen as foraging habitat, probably because they provide relatively high densities of favored prey, the northern flying squirrel, *Glaucomys sabrinus*, as well as cover from predators. Because much of the flying squirrel's diet is fungal material, old decadent forests provide superior foraging habitat for owls. In southern, lower-elevation portions of the owl's range, the species often forages along the edges of dense forests and in more open forests, preying on the dusky-footed woodrat, *Neotoma fuscipes*.

Although habitat that allows spotted owls to disperse may be unsuitable for nesting, roosting, or foraging, it provides an important linkage among blocks of nesting habitat both locally and over the range of the northern spotted owl. This linkage is essential to the conservation of the spotted owl. Dispersal habitat, at a minimum, consists of forest stands with adequate tree size and canopy closure to provide some degree of protection to spotted owls from avian predators and to allow the owls to forage at least occasionally. Suitable and dispersal habitat vary by province and are described separately under the discussion of each province in the following section.

Reasons for Decline: The northern spotted owl is threatened throughout its range by the loss and adverse modification of suitable habitat as the result of timber harvesting and exacerbated by catastrophic events such as fire, volcanic eruption, and wind storms.

References

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Usher, M. B. 1972. Developments in the Leslie Matrix Model. In *Mathematical Models in Ecology*, 29–60. Oxford: Blackwells.

Math 204: Final Exam Problems

Guidelines: You **must** work with one partner on these three problems. Work from groups of more or less than two will not be accepted. **You must not consult with anyone other than your partner and me. This is an exam.** Hand in one solution set for both of you. You will need to use `Maple` for most (all) of these problems. Make sure to **include explanatory text** using Text formatting in `Maple`. Use 10 point font size. If you can print on both sides of the page, great. Your work must be **stapled**. Your `Maple` output should be neat. Solutions with extraneous or error-laden printouts will be severely graded. If you need help, see me.

Problems

1. The most recent spotted owl data available [Lamberson] yield the following entries for the stage matrix. Notice that a few subadults produce offspring (akin to teenage pregnancy in humans.) Using these data, determine whether the owl population is becoming extinct. If the population is not becoming extinct, determine the percentage of each class in the long-run population.

Juvenile Survival	.33
Subadult Survival	.85
Adult Survival	.85
Subadult Fecundity	.125
Adult Fecundity	.26

2. (*a*) In the 1930s (before its virtual extinction and a great change in its survival rates) a researcher studied the blue whale, *Balaenoptera musculus*, population and obtained these data below. Due to the long gestation period, mating habits, and migration of the blue whale, a female can produce a calf only once in a two-year period. Thus the age classes for the whale are assumed to be: less than 2 years, 2 or 3 years, 4 or 5 years, 6 or 7 years, 8 or 9 years, 10 or 11 years, and 12 or more years. If the stage-matrix for the model is given below, determine whether the blue whale population is becoming extinct. If the population is not becoming extinct, determine the percentage of each class in the long-run population. [Caution: Look carefully at your `Maple` calculation. It may be helpful to widen your window or decrease the font size to see all the output.]

$$\begin{bmatrix} 0 & 0 & .19 & .44 & .50 & .50 & .45 \\ .77 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & .77 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & .77 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & .77 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .77 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & .77 & .78 \end{bmatrix}.$$

(*b*) If the population is not becoming extinct, estimate what percent of the whale population could be harvested every year by indigenous populations while keeping the whale population constant.

3. Darwin's idea of 'the survival of the fittest' was an underlying principle in his theory of natural selection in biology and the first two problems show how that plays out. Capitalists also argue that the market place is an arena where only the fittest (that is, those with a competitive advantage) survive. One very competitive arena is the quest for TV ratings or market share. Market shares are directly tied to the prices that networks can charge advertisers. The arena of "network news" is as competitive as any. The three major network anchors are all competing for viewers in exactly the same time slot. The following gives some idea of how networks might use Markov chains to predict future ratings. Suppose surveys indicate that:

- Of those who watch ABC one night, 70% are likely to watch ABC the next night, 30% switch to CBS, and 0% switch to NBC.
- Of those who watch CBS one night, 50% are likely to watch CBS the next night, 40% switch to ABC, and 10% switch to NBC.

- Of those who watch NBC one night, 60% are likely to watch NBC the next night, 30% switch to CBS, and 10% switch to ABC.

  (*a*) Describe this situation in terms of a 3×3 transition matrix for a Markov Chain model.

  (*b*) Determine whether the matrix is regular.

  (*c*) Find the steady state vector for the system.

  (*d*) Which network comes out on top in the long run?