

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. To begin, recall the example of the spotted owl given in the Introduction to Chapter 5.

The population of spotted owls 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. (see Reference 3) found that the population of owls could be modelled by the equation

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

Let $\mathbf{x}_k = (j_k, s_k, a_k)$, and note that the population model has the form $\mathbf{x}_{k+1} = A\mathbf{x}_k$, which is a difference equation. This model is called the **stage-matrix model** for a population. The entries in the matrix A have important meanings. The entries in the first row describe the **fecundity** of the population. Thus in the model above juveniles and subadults do not produce offspring, but each adult female produces (on the average) .33 juvenile females per year. The other entries in the matrix show **survival**. In this model, 18% of the juvenile females survive to become subadults, 71% of the subadults survive to become adults, and 94% of the adults survive each year. Note that the measures of fecundity and survival remain constant through time.

The goal is to determine the long-term dynamics of the population: whether the population is becoming extinct or is increasing. To answer these questions, examine the eigenvalues of the matrix A ($\lambda_1 = .98$, $\lambda_2 = -.02 + .21i$, $\lambda_3 = -.02 - .21i$). If the corresponding eigenvectors are labelled \mathbf{v}_1 , \mathbf{v}_2 , and \mathbf{v}_3 , the vector \mathbf{x}_k may be expressed as

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

This expression of \mathbf{x}_k is called the **eigenvector decomposition** of \mathbf{x}_k (see page 337 of the text). Since each eigenvalue has magnitude less than 1, \mathbf{x}_k is approaching the zero vector as k increases: the population is becoming extinct. Notice that the number of greatest importance to this analysis is $\lambda_1 = .98$, the eigenvalue of greatest magnitude. If λ_1 happened to be greater than 1, the population would instead be increasing steadily.

For example, consider Example 7 on page 351. If the survival rate for juveniles were somehow increased to 30%, the new matrix A would be

$$\begin{bmatrix} 0 & 0 & .33 \\ .30 & 0 & 0 \\ 0 & .71 & .94 \end{bmatrix}$$

The eigenvalues of this matrix are $\lambda_1 = 1.01$, $\lambda_2 = -.03 + .26i$, $\lambda_3 = -.03 - .26i$. 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 :

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

As $k \rightarrow \infty$ the second and third vectors tend to the zero vector, but the first does not. Thus \mathbf{x}_k is approaching $c_1(1.01)^k \mathbf{v}_1$ as $k \rightarrow \infty$. So the population of owls would be increasing exponentially at a growth rate of 1.01; the population would be increasing by 1% per year. The eigenvector \mathbf{v}_1 gives the long-term distribution of the owls by life stages. In this case \mathbf{v}_1 is approximately (10, 3, 31), so for every 31 adult females, there will be 10 juvenile females and 3 subadult females. The vector \mathbf{v}_1 could be further rescaled so that its entries sum to 1, namely: (.227, .068, .705). The entries in this vector show the fraction of the owl population in each class; for example, 22.7% of the owls would be juveniles.

This analysis may be used on other animal and plant species as shown in the questions below. For convenience, here is a summary of results drawn from Chapter 5.

1. The difference equation $\mathbf{x}_{k+1} = A\mathbf{x}_k$ is used to model the population in question; 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: $|\lambda_1| \geq |\lambda_2| \geq \dots \geq |\lambda_n|$.
3. If A is diagonalizable or if A has distinct (possibly complex) eigenvalues, then \mathbf{x}_k can be expressed in terms of its eigenvalues and corresponding eigenvectors:

$$\mathbf{x}_k = c_1(\lambda_1)^k \mathbf{v}_1 + c_2(\lambda_2)^k \mathbf{v}_2 + \dots + c_n(\lambda_n)^k \mathbf{v}_n$$

4. If $|\lambda_1| < 1$, then the population is decreasing to extinction.
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. As noted on page 351, in this case the eigenvector \mathbf{v}_1 gives the stable distribution of the population between classes, and yields the percentages found in each class if scaled so that its entries sum to 1.

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, where $0 \leq h < 1$, each year, 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 $h < 1$, $\frac{1}{1-h} > 1$. If λ_1 is the only eigenvalue of A in magnitude larger than 1, it follows that

$$\frac{1}{1 - h} = \lambda_1, \quad \text{or} \quad h = \frac{\lambda_1 - 1}{\lambda_1}$$

In the increasing owl population above, $\lambda_1 = 1.01$. Even though it is difficult to imagine *why* owls would be harvested, the appropriate calculation shows that $h = \frac{.01}{1.01} \approx .0099$. Thus .99% of the population could be harvested each year and the population would remain constant.

Questions:

1. The most recent spotted owl data available (Reference 4) gives the following entries for the matrix A :

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

Using this data, determine the long-range population of the Northern spotted owl. Are prospects for the owl better or worse than given in the data in the example above?

2. In the 1930's (before its virtual extinction and a great change in its survival rates) a researcher studied the blue whale population (see References 2, 5 and 6 for this data). 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 were 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. The matrix for the model is given by

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

Determine whether the blue whale population is becoming extinct in this model. If the population is not becoming extinct, determine the percentage of each class in the stable population.

3. This modelling 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:

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

Determine whether the population of alder is becoming extinct in this model. If the population is not becoming extinct, determine the percentage of each class in the stable population.

4. Suppose that the alders are altered in the previous problem, increasing the numbers of plants which are produced. Let the first row of the matrix be changed to

$$[.78 \quad .06 \quad .18 \quad .30 \quad .42]$$

Determine whether the population of alder is becoming extinct in this model. If the population is not becoming extinct, determine the percentage of each class in the stable population and also find the percentage of the alders which could be harvested each year while keeping the population constant.

5. Using the blue whale data from Question 2, estimate what percent of the whale population could be harvested every year while keeping the whale population constant.

References:

1. Huenneke, L. F. and Marks, P. L. "Stem Dynamics of the Shrub *Alnus Incana* SSP. *Rugosa*: Transition Models." *Ecology* **68** (1987), 1234-1242.
2. Jeffers, John N. R. *An Introduction to Systems Analysis: with Ecological Applications*. London: Edward Arnold, 1978.
3. Lamberson, R. H. et al. "A Dynamic Analysis of the Viability of the Northern Spotted Owl in a Fragmented Forest Environment." *Conservation Biology* **6**(1992), 505-512.
4. Lamberson, R. H. Private communication, 1999.
5. Laws, R. M. "Some Effects of Whaling on the Southern Stocks of Baleen Whales." In *The Exploitation of Natural Animal Populations*, 242-259. Oxford: Blackwells, 1962.
6. Usher, M. B. "Developments in the Leslie Matrix Model." In *Mathematical Models in Ecology*, 29-60. Oxford: Blackwells, 1972.