

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.

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

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 $\mathbf{x}_k = \begin{bmatrix} j_k \\ s_k \\ a_k \end{bmatrix}$, then the population model has the form

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

and is called the **stage-matrix model** for the owl population.¹ 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**. Create the transition matrix for the spotted owl population. *Note:* Using fractions makes subsequent calculations more exact.

$$A := \begin{bmatrix} 0 & 0 & \frac{33}{100} \\ \frac{9}{50} & 0 & 0 \\ 0 & \frac{71}{100} & \frac{47}{50} \end{bmatrix}$$

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

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> lambda:=evalf(Eigenvalues(A))
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$$\lambda := \begin{bmatrix} 0.9835927397 \\ -0.0217963700 + 0.2059184805 i \\ -0.0217963700 - 0.2059184805 i \end{bmatrix}$$

¹Note the similarity to a Markov chain, the difference being that the matrix A is not stochastic.

So $\lambda_1 = .9836$, $\lambda_2 = -.0218 + .2059i$, and $\lambda_3 = -.0218 - .2059i$. 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 (see Problem 1) the vector \mathbf{x}_k may be expressed as a linear combination of the basis vectors

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

and is called the **eigenvector decomposition** of \mathbf{x}_k . (See page 343 of your text.)

Next, we examine the magnitude² (norm) of each eigenvalue. To find the magnitudes (norms) of the eigenvalues use a loop and the *abs* command in Maple:

```
> 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 $\lim_{k \rightarrow \infty} \lambda_i^k = 0$. 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

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

In other words, the population is becoming extinct.

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

Modifying the Example. If the survival rate for juveniles were somehow increased to 50%, the new matrix would be

$$A = \begin{bmatrix} 0 & 0 & .33 \\ .50 & 0 & 0 \\ 0 & .71 & .94 \end{bmatrix}$$

The eigenvalues of this matrix are $\lambda_1 = 1.0469$, $\lambda_2 = -.0534 + .3302i$, and $\lambda_3 = -.0534 - .3302i$. 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 $k \rightarrow \infty$, the second and third vectors tend to the zero vector, but the first does not. This time

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

The owl population is increasing exponentially at a growth rate of 1.0469, i.e., the population is increasing by 4.69% per year. The Maple *Eigenvectors* command lists both the eigenvalues and their corresponding eigenvectors in columns. For example the command *evalf(Eigenvectors(A))* produces the output

$$\begin{bmatrix} 1.046890636 \\ -0.0534453182 + 0.3302217500 i \\ -0.0534453182 - 0.3302217500 i \end{bmatrix}, \begin{bmatrix} 0.3152191725 & -0.1576095864 - 0.9738198815 i & -0.1576095864 + 0.9738198815 i \\ 0.1505501919 & -1.399218758 + 0.4651010563 i & -1.399218758 - 0.4651010563 i \\ 1.0 & 1.0 & 1.0 \end{bmatrix}$$

While the vector \mathbf{v}_1 (in the first column of the matrix above) is not a steady-state vector (the population is growing), it does tell us the long-run distribution of the owls in the various age classes. As with steady-states, we normalize the eigenvector by dividing by the absolute value of the sum of its components. We mentioned earlier that this is called the **1-norm** of the vector and is denoted by $\|\mathbf{v}_1\|_1$. So $\frac{1}{\|\mathbf{v}_1\|_1} \mathbf{v}_1$ gives the long-term distribution of the owls by life stages. Here are the Maple commands for this (note you can cut and paste the individual entries for \mathbf{v}_1 from the earlier Maple output).

$$\frac{1}{\text{VectorNorm}(v_1, 1)} v_1 \quad \begin{bmatrix} 0.215053732361338429 \\ 0.102710696240441213 \\ 0.682235571700000043 \end{bmatrix}$$

This means that the female population will be 21.50% juveniles, 10.27% subadults, and 68.22% adults. This analysis may be used on other animal or plant species, as shown in the questions below.

²The 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 .