

The Spotted Owls

Be sure to read the example at the introduction to Chapter 5 in the textbook. It gives more general background information for this example. The example leads to a dynamical system which we can understand better using complex eigenvalues.

The life cycle of the spotted owl is divided into 3 stages in this model:

j	“juvenile”
s	“subadult”
a	“adult”

The model, as described, assumes there is an approximately 1:1 ratio between male and female owls and counts only the females. There is a “stage matrix” A that relates the number of owls in each group to the number a year later. The matrix, with entries based on field data, is

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

$$\mathbf{x}_{k+1} = A \cdot \mathbf{x}_k$$

$$\text{where } \begin{cases} j_k = \text{number of juvenile spotted owls at year } k \\ s_k = \text{number of subadult spotted owls at year } k \\ a_k = \text{number of adult spotted owls at year } k \end{cases}$$

so that

$$\begin{aligned} j_{k+1} &= 0.33 a_k \\ s_{k+1} &= 0.18 j_k \quad \text{(60\% leave nest, 30\% of those succeed)} \\ a_{k+1} &= 0.71 s_k + 0.94 a_k \quad \text{(adults live about 20 yrs)} \end{aligned}$$

From Matlab, the eigenvectors are the columns $\mathbf{v}_1, \mathbf{v}_2, \mathbf{v}_3$ of the matrix

$$P = \begin{bmatrix} 0.0848 - 0.6768i & 0.0848 + 0.6768i & 0.3175 \\ -0.5928 - 0.0114i & -0.5928 + 0.0114i & 0.0581 \\ 0.4167 + 0.0976i & 0.4167 - 0.0976i & 0.9465 \end{bmatrix}$$

$$\begin{aligned} \text{and the corresponding eigenvalues are } \lambda_1 &= -0.0218 + 0.2059i \\ \lambda_2 &= -0.0218 - 0.2059i \\ \lambda_3 &= 0.9836 \end{aligned}$$

Of course, a nonzero multiple of an eigenvector \mathbf{v} is still an eigenvector with the same eigenvalue, because a multiple of \mathbf{v} is in the same eigenspace as \mathbf{v} itself. Therefore

$$10000 * \begin{bmatrix} 0.3175 \\ 0.0581 \\ 0.9465 \end{bmatrix} = \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix} \text{ is also an eigenvector with eigenvalue } \lambda_3 \approx 0.9836$$

To get rid of some decimals, we will use this rescaled vector as a replacement for the eigenvector in column 3 of the matrix P .

1) If the owl population begins (say) as $\mathbf{x}_0 = \mathbf{v}_3 = \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix}$, then the populations in successive years are

$$\begin{aligned} \mathbf{x}_1 &= A\mathbf{x}_0 = \lambda_3\mathbf{x}_0 \\ \mathbf{x}_2 &= A(\mathbf{x}_1) = A(A\mathbf{x}_0) = A(\lambda_3\mathbf{x}_0) = \lambda_3 A(\mathbf{x}_0) = \lambda_3^2\mathbf{x}_0 \\ \mathbf{x}_3 &= A(\mathbf{x}_2) = A(A(A\mathbf{x}_0)) = AA^2(\mathbf{x}_0) = A(\lambda_3^2\mathbf{x}_0) = \lambda_3^3 A\mathbf{x}_0 = \lambda_3^3\mathbf{x}_0 \\ \text{and in general, } & \vdots \\ \mathbf{x}_n &= A(\mathbf{x}_{n-1}) = A^n(\mathbf{x}_0) = \dots = \lambda_3^n\mathbf{x}_0 \end{aligned}$$

$$\approx (0.9836)^n \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix} \rightarrow \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \text{ as } n$$

Therefore: for an initial owl population $\mathbf{x}_0 = \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix}$, the model predicts that the population will eventually die out.

2) Suppose the owl population begins at \mathbf{x}_0 . Since we are thinking of \mathbf{x}_0 as a population vector, we assume its entries are nonnegative real numbers (*but from a purely mathematical point of view, all the following calculations work even if \mathbf{x}_0 has negative or any complex entries*).

P has 3 distinct eigenvalues, and the corresponding eigenvectors $\mathbf{v}_1, \mathbf{v}_2, \mathbf{v}_3$ are a basis for \mathbb{C}^3 . Note that we could also check that these vectors are a basis by confirming (via Matlab) that P is invertible.

$$\mathbf{x}_0 = c_1\lambda_1\mathbf{v}_1 + c_2\lambda_2\mathbf{v}_2 + c_3(0.9836) \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix}$$

In this expression the weights c_i might be any complex numbers. But \mathbf{x}_0 is a real vector (it was a given population vector) – so whatever the c_i 's are, the “imaginary parts” of all the entries will cancel out to produce the real vector \mathbf{x}_0 .

And, since A is a real matrix, $\mathbf{x}_1 = A\mathbf{x}_0$, $\mathbf{x}_2 = A\mathbf{x}_1$, ... are also all real.

Just as in the first example, multiplying n times by A leads to the equation

$$\mathbf{x}_n = c_1 \lambda_1^n \mathbf{v}_1 + c_2 \lambda_2^n \mathbf{v}_2 + c_3 (0.9836)^n \begin{bmatrix} 3175 \\ 581 \\ 9465 \end{bmatrix}$$

Recall that if $\lambda = a + bi$ is any complex number, then $|\lambda| = \sqrt{a^2 + b^2}$ is the distance from λ to the origin in the complex plane.

In the case of the eigenvalue λ_1 , $|\lambda_1| = \sqrt{(-0.0218)^2 + (0.2059)^2} \approx 0.2071 < 1$.

Therefore as $n \rightarrow \infty$, $|\lambda_1^n| = |\lambda_1|^n \approx (0.2071)^n \rightarrow 0$. That is, λ_1^n gets closer and closer to the origin: $\lambda_1^n \rightarrow 0$.

Similarly, as $n \rightarrow \infty$, $|\lambda_2^n| = |\lambda_2|^n \approx (0.2071)^n \rightarrow 0$, so $\lambda_2^n \rightarrow 0$.

So \mathbf{x}_n is a sum of three terms each of which tends to 0 as $n \rightarrow \infty$. So once again we conclude again that $\mathbf{x}_n \rightarrow \mathbf{0}$: for the given stage matrix A , the spotted owl population will eventually die out; it doesn't matter what the initial population \mathbf{x}_0 is.

In this dynamical system with the given matrix A , the origin $\mathbf{0}$ is called a universal attractor – that is, $\mathbf{x}_n \rightarrow \mathbf{0}$ for every choice of initial population vector \mathbf{x}_0 . More informally, “no matter where the system starts, the origin attracts the \mathbf{x}_n 's as the dynamical system progresses.”

As the textbook states, the most crucial number in the model is the “0.18” in the original matrix A : the percentage of juvenile owls who (by finding a territory of their own and a mate) manage to pass into the subadult stage. Their success depends, in part, on how much “good territory” is available for the owls.

If the success rate 0.18 for juveniles passing into the subadult stage is improved to (say)

0.50, then the matrix for the dynamical system becomes $\begin{bmatrix} 0 & 0 & .33 \\ .5 & 0 & 0 \\ 0 & .71 & .94 \end{bmatrix}$.

The eigenvalues and corresponding (linearly independent) eigenvectors turn out to be

$$\lambda_1 = -0.0534 + 0.3302i \quad \mathbf{v}_1 = \begin{bmatrix} -0.2090 - 0.4370i \\ -0.5948 + 0.4128i \\ 0.4711 - 0.1384i \end{bmatrix}$$

$$\lambda_2 = \bar{\lambda}_1 = -0.0534 - 0.3302i \quad \mathbf{v}_2 = \begin{bmatrix} -0.2090 + 0.4370i \\ -0.5948 - 0.4128i \\ 0.4711 + 0.1384i \end{bmatrix}$$

$$\lambda_3 = 1.0469 \quad \mathbf{v}_3 = \begin{bmatrix} 2976 \\ 1421 \\ 9441 \end{bmatrix}$$

If we write the initial population vector \mathbf{x}_0 as a linear combination of these,

$$\mathbf{x}_0 = c_1 \lambda_1 \mathbf{v}_1 + c_2 \lambda_2 \mathbf{v}_2 + c_3 (1.0469)^n \begin{bmatrix} 2976 \\ 1421 \\ 9441 \end{bmatrix} \quad (*)$$

Then
$$\mathbf{x}_n = c_1 \lambda_1^n \mathbf{v}_1 + c_2 \lambda_2^n \mathbf{v}_2 + c_3 (1.0469)^n \begin{bmatrix} 2976 \\ 1421 \\ 9441 \end{bmatrix}$$

As before, $|\lambda_1|$ and $|\lambda_2|$ are < 1 so λ_1^n and $\lambda_2^n \rightarrow 0$ as $n \rightarrow \infty$,

so $c_1 \lambda_1^n \mathbf{v}_1 + c_2 \lambda_2^n \mathbf{v}_2 \rightarrow \mathbf{0}$. Therefore, when n is large

$$\mathbf{x}_n \approx c_3 (1.0469)^n \begin{bmatrix} 2976 \\ 1421 \\ 9441 \end{bmatrix} \quad (\text{exp growth}^{***}) \quad (**)$$

This means that if \mathbf{x}_0 was chosen so that $c_3 \neq 0$, the population continues to grow. (*Of course, at some time the population would become so large that the model would break down. For example, there will eventually not be enough "good territory" available to maintain the 50% success rate for owls passing from the juvenile to the subadult stage.*)

Assume that there's enough territory and other resources to allow n to become big enough that the approximation in (**) is a fair statement. From that time on (until the model breaks down):

i) each new population vector \mathbf{x}_{n+1} is approximately 1.0469 times the preceding population vector: a growth rate of about 4.7%/year. (***) λ_3 controls long term growth)

ii) the population vector remains, each year, (approximately) a constant multiple

of $\begin{bmatrix} 2976 \\ 1421 \\ 9441 \end{bmatrix}$. This means the population of juveniles, subadults and adults each

stabilize at a fixed % of the total owl population: for example, the juveniles at

$$\frac{2976}{(2976 + 1421 + 9441)} * 100 \approx 21.5\% \text{ of the population.}$$

To take a specific \mathbf{x}_0 : suppose the matrix given above (with the 50% juvenile --> subadult rate) is accurate for a forested region with no spotted owls and that a population consisting

entirely of 1000 adult owls is introduced: so $\mathbf{x}_0 = \begin{bmatrix} 0 \\ 0 \\ 1000 \end{bmatrix}$

In that case, from Matlab, the coefficients c_1, c_2, c_3 that work in (*), rounded to 4 places, are

$$c_1 = 2.3494 - 1.8713 i$$

$$c_2 = 2.3494 + 1.8713 i$$

$$c_3 = 0.0009$$

Some sample calculations give (*rounded to the nearest owl*)

$$\mathbf{x}_5 = \begin{bmatrix} 330 \\ 156 \\ 1044 \end{bmatrix} \quad \mathbf{x}_{10} = \begin{bmatrix} 413 \\ 198 \\ 1313 \end{bmatrix} \quad \mathbf{x}_{11} = \begin{bmatrix} 433 \\ 207 \\ 1374 \end{bmatrix}$$

$\uparrow \qquad \qquad \qquad \uparrow$
(Approximately what % growth?)

The “moral” is that the eigenvalues and basic eigenvectors control the long term behavior of the system.

Another Example

Suppose we have a linear dynamical system $\mathbf{x}_{k+1} = A\mathbf{x}_k$ where A (for simplicity) is 2×2 and where A is diagonalizable, with eigenvalues λ_1, λ_2 corresponding to eigenbasis vectors $\mathbf{v}_1, \mathbf{v}_2$.

We can write the initial vector $\mathbf{x}_0 = c_1\mathbf{v}_1 + c_2\mathbf{v}_2$, so

$$\mathbf{x}_1 = A\mathbf{x}_0 = c_1A\mathbf{v}_1 + c_2A\mathbf{v}_2 = c_1\lambda_1\mathbf{v}_1 + c_2\lambda_2\mathbf{v}_2$$

$$\mathbf{x}_2 = A\mathbf{x}_1 = c_1\lambda_1A\mathbf{v}_1 + c_2\lambda_2A\mathbf{v}_2 = c_1\lambda_1^2\mathbf{v}_1 + c_2\lambda_2^2\mathbf{v}_2$$

\vdots

$$\mathbf{x}_{k+1} = A\mathbf{x}_k = c_1\lambda_1^kA\mathbf{v}_1 + c_2\lambda_2^kA\mathbf{v}_2 = c_1\lambda_1^{k+1}\mathbf{v}_1 + c_2\lambda_2^{k+1}\mathbf{v}_2$$

We can consider what happens depending on the size of the eigenvalues.

To illustrate with one case: when $|\lambda_1| > 1$ and $|\lambda_2| < 1$

Write

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

\vdots

$$\mathbf{x}_k = c_1\lambda_1^k\mathbf{v}_1 + c_2\lambda_2^k\mathbf{v}_2$$

If $c_1 = 0$: Then $\mathbf{x}_k = c_2\lambda_2^k\mathbf{v}_2$ and $\mathbf{x}_k \rightarrow \mathbf{0}$

If $c_1 \neq 0$: Since $c_2\lambda_2^k\mathbf{v}_2 \rightarrow \mathbf{0}$ as $k \rightarrow \infty$, we get that, for large k ,

$$\mathbf{x}_k \approx c_1\lambda_1^k\mathbf{v}_1$$

$$\mathbf{x}_{k+1} \approx c_1\lambda_1^{k+1}\mathbf{v}_1 = \lambda_1\mathbf{x}_k$$

So, for large k , \mathbf{x}_k will grow approximately by a factor of λ_1 each time so λ_1 controls the long term growth rate of the system.

Example: Predator and prey: owl and wood rat population in a forest (*see Example 1, p. 302 in the textbook*)

O_k = number of owls, R_k = number of rats (measured in
"rat-units" = 1000's)

Model:

$$\begin{aligned} O_{k+1} &= .5 O_k + .4 R_k \\ R_{k+1} &= -p O_k + 1.1 R_k \end{aligned}$$

$$\mathbf{x}_{k+1} = \begin{bmatrix} O_{k+1} \\ R_{k+1} \end{bmatrix} = \begin{bmatrix} .5 & .4 \\ -p & 1.1 \end{bmatrix} \begin{bmatrix} O_k \\ R_k \end{bmatrix} = \begin{bmatrix} .5 & .4 \\ -p & 1.1 \end{bmatrix} \mathbf{x}_k$$

1) For $p = 0.205$, the eigenvalues are approximately .7106 and .8894. What happens?

2) For $p = 0.08$, the eigenvalues are approximately $\lambda_1 = 1.0408$ and $\lambda_2 = .5592$, with

corresponding eigenvectors $\mathbf{v}_1 = \begin{bmatrix} .5946 \\ .8040 \end{bmatrix}$ and $\mathbf{v}_2 = \begin{bmatrix} .9892 \\ .1463 \end{bmatrix}$.

So, for large k $\mathbf{x}_k = c_1 \lambda_1^k \mathbf{v}_1 + c_2 \lambda_2^k \mathbf{v}_2 \approx c_1 \lambda_1^k \mathbf{v}_1$ (since $\lambda_2^k \rightarrow 0$)

$$\mathbf{x}_k = \begin{bmatrix} O_k \\ R_k \end{bmatrix} \approx c_1 (1.0408)^k \begin{bmatrix} .5946 \\ .8040 \end{bmatrix}$$

(The value of the constant c_1 , of course, is determined by the initial population \mathbf{x}_0 .)

This says that for large k , the ratio of owls to rats $= \frac{O_k}{R_k} \approx \frac{c_1 (1.0408)^k (.5946)}{c_1 (1.0408)^k (.8040)}$

$$= \frac{.5946}{.8040} \approx .74 \approx \frac{3}{4} \quad (3 \text{ owls} / 4000 \text{ rats})$$

Also, $\begin{bmatrix} O_{k+1} \\ R_{k+1} \end{bmatrix} \approx (1.0408) \begin{bmatrix} O_k \\ R_k \end{bmatrix}$ so for large k (and as long as the model

holds up) both populations grow at a rate of about 4.08%/month.

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Rats

Slope 4/3 rather than 3/4 here, only
because I used the horizontal axis
✓ for the "owl-axis."

