What is the "equilibrium" or "long-term" state of an age-structured population model (and how do we find it)?

The matrix difference equation :

$$\mathbf{x}_{n+1} = \mathbf{L}\mathbf{x}_n$$

looks very similar to the (scalar) difference equation:

$$x_{n+1} = a x_n$$

and so in the long term, we can approximate:

$$\mathbf{x}_{n+1} = \mathbf{L}\mathbf{x}_n \qquad \text{as} \qquad \mathbf{x}_{n+1} = \lambda \mathbf{x}_n$$

where λ is a scalar (number) instead of a matrix.

Since the left-hand side of both of these equations is $\mathbf{x}_{n+1}$, we will set the right-hand sides of the equations equal to each other to get:

$$\mathbf{L}\mathbf{x} = \lambda \mathbf{x}$$

(We leave off the n subscript because we are talking about the "equilibrium" or "long-term" state of the model and not the state for a particular generation.)

This equation means that there is some special vector that, when we multiply it by the Leslie matrix, we get the same result as if we had instead multiplied it by some special scalar (number) (but we don't know what that vector or that number is yet).
This vector is called an "**eigenvector**," and the corresponding scalar (number) is called an "**eigenvalue**."
("Eigen" is the German word for "own" or "self," so we can think of the eigenvector as "the matrix's own vector" or the special vector that "belongs" to the matrix.)

Eigenvalues and eigenvectors can be found for any matrix, but for an age-structured model, we will interpret the eigenvalue of the Leslie matrix as the "equilibrium" or "long-term" growth rate of the population, and we will interpret the eigenvector as the "equilibrium" or "long-term" age distribution of the population.

Solving for the eigenvalue(s) of a matrix

As an example, we will use the coyote population with juveniles and adults and find the eigenvalues and (corresponding) eigenvectors for two different Leslie matrices. As we will find out, a matrix can have as many eigenvalues (and eigenvectors) as the number of rows (or columns) in the matrix. So a 2-by-2 matrix can have up to two eigenvalues (and eigenvectors.

To find λ and $\mathbf{x}$, we need to solve the matrix equation: $\mathbf{L}\mathbf{x} = \lambda \mathbf{x}$

$$\mathbf{L}\mathbf{x} = \lambda \mathbf{x}$$

$$\mathbf{L}\mathbf{x} - \lambda \mathbf{x} = \mathbf{0}$$

$$\mathbf{L}\mathbf{x} - \lambda (\mathbf{I}\mathbf{x}) = \mathbf{0}$$

$$\mathbf{L}\mathbf{x} - (\lambda \mathbf{I})\mathbf{x} = \mathbf{0}$$

$$(\mathbf{L} - \lambda \mathbf{I})\mathbf{x} = \mathbf{0}$$

From our earlier work on using matrices to solve systems of equations, we know that if:

$$(\mathbf{L}-\lambda\mathbf{I})\mathbf{x}=\mathbf{0}$$

this means that either $\mathbf{x}=\mathbf{0}$ or $\det(\mathbf{L}-\lambda\mathbf{I})=0$.

$\mathbf{x}=\mathbf{0}$ is a valid solution, but it isn't very interesting. So we are interested in what values of λ result in $\det(\mathbf{L}-\lambda\mathbf{I})=0$.

We will now find the values of λ that give us this result for the following Leslie matrices:

$$\begin{bmatrix} 0 & 0.2 \\ 0.75 & 0.55 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0 & 1.5 \\ 0.1 & 0.55 \end{bmatrix}$$

$$\begin{aligned}
&\det(\mathbf{L}-\lambda\mathbf{I})= \\
&=\det\left(\begin{bmatrix} 0 & 0.2 \\ 0.75 & 0.55 \end{bmatrix}-\begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}\right) \\
&=\det\left(\begin{bmatrix} -\lambda & 0.2 \\ 0.75 & 0.55-\lambda \end{bmatrix}\right) \\
&=(-\lambda)(0.55-\lambda)-(0.2)(0.75) \\
&=\lambda^2-0.55\lambda-0.15
\end{aligned}$$

$$\begin{aligned}
&\det(\mathbf{L}-\lambda\mathbf{I})= \\
&=\det\left(\begin{bmatrix} 0 & 1.5 \\ 0.1 & 0.55 \end{bmatrix}-\begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}\right) \\
&=\det\left(\begin{bmatrix} -\lambda & 1.5 \\ 0.1 & 0.55-\lambda \end{bmatrix}\right) \\
&=(-\lambda)(0.55-\lambda)-(1.5)(0.1) \\
&=\lambda^2-0.55\lambda-0.15
\end{aligned}$$

But we want to solve for the case when $\det(\mathbf{L}-\lambda\mathbf{I})=\lambda^2-0.55\lambda-0.15=0$.

We can use the quadratic formula to solve for λ:

$$\lambda=\frac{0.55\pm\sqrt{(-0.55)^2-4(1)(-0.15)}}{2}=\frac{0.55\pm\sqrt{0.3025+0.60}}{2}=\frac{0.55\pm\sqrt{0.9025}}{2}$$

$$\lambda=\frac{0.55\pm0.95}{2}=0.75,-0.2$$

So we end up with two eigenvalues, and we will find an eigenvector for each.

But first, which eigenvector gives us the "long-term" growth rate? The "long-term" growth rate is given by the **dominant eigenvalue**, which is the eigenvalue with the largest absolute value:

$$|0.75|>|-0.2|$$

So the dominant eigenvalue (and hence the "long-term" growth rate) is 0.75, which means that in the long-term, the population is decreasing by 25% each year.
(For a Leslie matrix, the dominant eigenvalue will <u>always</u> be <u>positive</u>.)

In general: If $0<\lambda<1$, this means that the population is declining.
If $\lambda>1$, this means that the population is growing.
If $\lambda=1$, this means that the overall population size is remaining constant.

SOLVING FOR THE EIGENVECTOR(S) OF A MATRIX

To find the corresponding eigenvectors for each eigenvalue, we will plug each eigenvalue back into the matrix equation:

$$\mathbf{Lx} = \lambda \mathbf{x}$$

and then solve for $\mathbf{x}$. Recalling our earlier work, we will find that $\mathbf{x}$ doesn't just have a single solution, but actually has a whole <u>class</u> of solutions.

$$\mathbf{Lx} = \lambda \mathbf{x}$$
$$\begin{bmatrix} 0 & 0.2 \\ 0.75 & 0.55 \end{bmatrix}\begin{bmatrix} j \\ a \end{bmatrix} = 0.75\begin{bmatrix} j \\ a \end{bmatrix}$$
$$\begin{bmatrix} 0.2a \\ 0.75j + 0.55a \end{bmatrix} = \begin{bmatrix} 0.75j \\ 0.75a \end{bmatrix}$$
$$\Rightarrow \begin{matrix} 0.2a = 0.75j \\ 0.75j + 0.55a = 0.75a \end{matrix}$$
$$\Rightarrow \begin{matrix} a = 3.75j \\ 0.75j = 0.2a \end{matrix}$$

$$\mathbf{Lx} = \lambda \mathbf{x}$$
$$\begin{bmatrix} 0 & 0.2 \\ 0.75 & 0.55 \end{bmatrix}\begin{bmatrix} j \\ a \end{bmatrix} = -0.2\begin{bmatrix} j \\ a \end{bmatrix}$$
$$\begin{bmatrix} 0.2a \\ 0.75j + 0.55a \end{bmatrix} = \begin{bmatrix} -0.2j \\ -0.2a \end{bmatrix}$$
$$\Rightarrow \begin{matrix} 0.2a = -0.2j \\ 0.75j + 0.55a = -0.2a \end{matrix}$$
$$\Rightarrow \begin{matrix} a = -j \\ 0.75j = -0.75a \end{matrix}$$

Notice that for each eigenvalue, we get two equations that are equivalent to each other, and we don't get specific values for a and j. This is because there are many eigenvectors corresponding to each eigenvalue, but their elements, a and j, must satisfy the equations above. For simplicity, we will pick a simple value for j (for example, $j = 1$), and then find the resulting value for a.

So for the eigenvalue, $\lambda = 0.75$, we get a corresponding eigenvector, $\mathbf{x} = \begin{bmatrix} 1 \\ 3.75 \end{bmatrix}$.

And for the eigenvalue, $\lambda = -0.2$, we get a corresponding eigenvector, $\mathbf{x} = \begin{bmatrix} 1 \\ -1 \end{bmatrix}$.

To find the "long-term" age distribution of the population, we want the **normalized eigenvector** that corresponds to the dominant eigenvalue. To "normalize" an eigenvector, we simply divide the eigenvector by the sum of its elements ($j + a = 1 + 3.75 = 4.75$) to get:

$$\begin{bmatrix} 1 \\ 3.75 \end{bmatrix} \div 4.75 = \begin{bmatrix} 1/4.75 \\ 3.75/4.75 \end{bmatrix} = \begin{bmatrix} \frac{4}{19} \\ \frac{15}{19} \end{bmatrix}$$

So, in the long-term, about $\frac{4}{19}$ of the population will be juveniles and $\frac{15}{19}$ will be adults.

By the way, we can't normalize the eigenvector $\begin{bmatrix} 1 \\ -1 \end{bmatrix}$ because $1 + (-1) = 0$ and division by 0 isn't allowed.

SOLVING FOR THE EIGENVALUE(S) OF A GENERIC 2-BY-2 MATRIX

To find the eigenvalues of the generic 2-by-2 matrix:

$$\mathbf{A} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

we will solve $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$ for λ.

$$\det(\mathbf{A} - \lambda\mathbf{I}) = \det\left(\begin{bmatrix} a & b \\ c & d \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}\right) = \det\left(\begin{bmatrix} a-\lambda & b \\ c & d-\lambda \end{bmatrix}\right) = (a-\lambda)(d-\lambda) - bc$$

$$\det(\mathbf{A} - \lambda\mathbf{I}) = ad - a\lambda - d\lambda + \lambda^2 - bc = \lambda^2 - (a+d)\lambda + ad - bc$$

Since we want $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$, we can find the eigenvalues by solving:

$$\lambda^2 - (a+d)\lambda + ad - bc = 0$$

for λ.

Recall that the trace of $\mathbf{A}$ is $tr(\mathbf{A}) = a + d$ and $\det\mathbf{A} = ad - bc$, which allows us to write the above equation as:

$$\boxed{\lambda^2 - tr(\mathbf{A})\cdot\lambda + \det\mathbf{A} = 0}$$

It is also possible to find the eigenvalues (and eigenvectors) for a 3-by-3, 4-by-4, or any size square matrix, but doing this by hand is very difficult. So instead we will use a computer program like Matlab (or a calculator) that can do matrix algebra to find the eigenvalues (and eigenvectors) of larger matrices.