Calculating growth rate from a matrix of fecundities and survival probabilities (the Leslie or Lefkovitch matrix).

Leslie and Lefkovitch matrices are a way of representing contributions of each age (Leslie) or stage (Lefkovitch) to the population next year. For example, if we have just two stages of development, juvenile and adult, then a Lefkovitch matrix for the population would look like this matrix to the right:

		From: Juvenile	Adult
To:	Juvenile	f_J	f_A
	Adult	s_J	s_A

Juveniles all enter the population through births, so the first row representing contributions to the juvenile age class is made up of fecundities (which are births that survive one year, per individual in the population). Adults in the population next year either transition from being juveniles, or if they are already adults they survive another year. The transition from juvenile to adult is represented by the survival probability s_J, and survival of adults from one year to the next is represented by the survival probability s_A.

This matrix can be used to project a population over time by multiplying by a starting number of juveniles and adults held in a 2 row by 1 column matrix (or vector). After several years of projecting the population, we can take the ratio of the population size at t+1 to the population size at t to calculate the population growth rate. But, because we have all of the demographic rates that dictate the growth of the population in a matrix, we can use some matrix algebra to calculate the growth rate without having to project the population over time.

To do this calculation, we are going to make use of a theorem from matrix algebra that states:

$$|L-\lambda I|=0$$

This states that the determinant of the Lefkovitch matrix minus a scalar (λ) multiplied by the identity matrix (**I**) equals zero. the two vertical lines are matrix algebra symbols for the determinant, which is a scalar property of a square matrix (that is, a single value that is calculated from a matrix with an equal number of rows and columns). The values of λ that satisfy this equation are the "eigenvalues". Eigenvalues are a way of characterizing the information from a matrix in an alternative form, and it turns out that the largest positive eigenvalue for a Lefkovitch matrix is the growth rate for the population. For a simple life history like ours, with only two stages, it's fairly easy to calculate eigenvalues by hand, like so...

First, let's put in the matrices:

$$\left|\begin{bmatrix} f_J & f_A \\ s_J & s_A \end{bmatrix} - \lambda \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}\right| = 0$$

Multiplying λ (a scalar) by the identity matrix gives us:

$$\left|\begin{bmatrix} f_J & f_A \\ s_J & s_A \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}\right| = 0$$

Subtracting the matrices gives us:

$$\left|\begin{bmatrix} f_J-\lambda & f_A \\ s_J & s_A-\lambda \end{bmatrix}\right|=0$$

The determinant for a 2x2 matrix like this is simply the products of the two elements on the main diagonal (the one going from the upper left to the lower right) minus the products of the two elements on the off-diagonal (the one going from the upper right to the lower left). This gives us:

$$(f_J-\lambda)(s_A-\lambda)-f_A s_J=0$$

If we expand, we get:

$$f_J s_A-f_J\lambda-s_A\lambda+\lambda^2-f_A s_J=0$$

Collecting terms, simplifying, and putting the equation in standard form gives us:

$$\lambda^2-(f_J+s_A)\lambda+(f_J s_A-s_J f_A)=0$$

This is called the "characteristic equation" for the Lefkovitch matrix, and hopefully you can see it's simply a quadratic equation in λ. The quadratic formula that gives solutions for λ based on the coefficients is:

$$\frac{-b\pm\sqrt{b^2-4\mathrm{ac}}}{2\mathrm{a}}$$

where a, b, and c are the coefficients λ^2 (which is 1), λ (which is $-(f_J+s_A)$), and the constant (which is (fJsA - $s_J f_A$). Substituting in the terms from the characteristic equation we get:

$$\frac{f_J+s_A+\sqrt{(-(f_J+s_A))^2-4(1)(f_J s_A-s_J f_A)}}{2}$$

The Lefkovitch matrix from our array formula lab assignment looks like this:

$$L=\begin{bmatrix} 0 & 1.7 \\ 0.2 & 0.8 \end{bmatrix}$$

If we plug in these numbers to the quadratic formula we get:

$$\frac{0+0.8+\sqrt{(-0-0.8)^2-4(1)(0-(0.2)(1.7))}}{2}=1.107107$$

which matches the growth rate we calculated by projecting the population for ten years.