USING MATRIX ALGEBRA TO UNDERSTAND POPULATION GROWTH RATE

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ABSTRACT. This module introduces students to the use of matrix algebra in population ecology. In particular, it examines the construction of population projection matrices from life table graphs, how the population projection matrix can be used to determine population growth rates λ, and how manipulating the population projection matrix can be used to determine which aspects of the population projection matrix are most responsible for driving λ. This module will allow students to gain a better understanding of 1) the underlying matrix algebra of population projection matrices, 2) the linkages between vital rates (e.g., survivorship, fecundity) and λ, 3) relationships between stable age distributions and λ, and 4) the use of life table response experiments to determine the importance of each vital rate for determining λ.

1. OVERVIEW

This module is designed for two populations of students. One target group is students in an introductory finite mathematics course and the other population is students in an upper-level course in ecology [2]. Completion of the module requires no prior knowledge of matrix algebra, nor does it assume prior knowledge of population growth models or life tables. Thus, this module is appropriate for either a finite mathematics or ecology course.

To make the module as accessible as possible, the module includes a Microsoft Excel® spreadsheet that allows students to explore the computation of λ and stable age distributions, as well as to conduct life table response experiments: Age-BasedEx.xlsx, StableAgeDistribution.xlsx.

2. INTRODUCTION: LIFE TABLES

For population ecologists and conservation biologists one of the most important parameters to understanding population dynamics is the population growth rate. A population growth rate is determined by the birth or fecundity rate, the number of babies born in a given time, and death or mortality rate, the number of individuals dying in a given time.

While it might appear fairly easy to find the fecundity rate and mortality rate of a population, the population ecologists job of understanding the dynamics of a

population is made difficult by the fact that both the birth rate and the death rate for an individual can change over the course of its life, and this change can have implications for how fast a population grows.

For many species, ecologists can use life tables to estimate population growth rates (see Table ??). Life tables use basic arithmetic, addition and multiplication, to calculate an estimate of population growth rate (R_0). For example, to calculate R_0 we use the age-specific fecundity, m_x (the average number of female offspring the typical female has at age x), and survivorship to a particular age l_x (survivorship from birth to the start of age class x). R_0 is simply the sum of $l_x m_x$. That is, R_0 is the sum of the product of l_x and m_x. If R_0 is greater than 1 the population is growing. If R_0 is less than 1 the population is decreasing. $R_0 = 1$ means the population is stable. We see that the deer population represented in Table ?? is growing as $R_0 = 1.3.16 > 1$.

If we take a closer look at how we calculated R_0 we can see that this measure essentially gives us the average number of female offspring a female has over her expected lifetime. Thus, we can use it to determine if a female replaces herself or not (hence R_0 is sometimes referred to as the net replacement rate).

TABLE 1. Example life table of a red deer population (modified from Lowe [6]).

x	Nx	l_x	m_x	$l_x m_x$	$x l_x m_x$
1	1000	1.000	0	0	0
2	863	0.863	0	0	0
3	778	0.778	0.311	0.242	0.726
4	694	0.694	0.278	0.193	0.772
5	610	0.610	0.308	0.134	0.670
6	526	0.526	0.400	0.210	1.260
7	442	0.442	0.476	0.210	1.470
8	357	0.357	0.358	0.128	1.024
9	181	0.181	0.447	0.081	0.729
10	59	0.059	0.289	0.017	0.170
11	51	0.051	0.283	0.014	0.154
12	42	0.042	0.285	0.012	0.144
13	34	0.034	0.283	0.010	0.130
14	25	0.025	0.282	0.007	0.098
15	17	0.017	0.285	0.005	0.075
16	9	0.009	0.284	0.003	0.048

e.g.T:Lowe

3. Beyond Life Tables

While life tables make our work easy, the use of life table analyses is primarily restricted to species with relatively simple life histories. A life history is the schedule
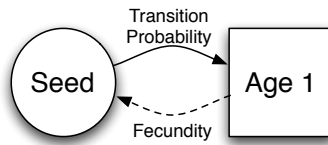
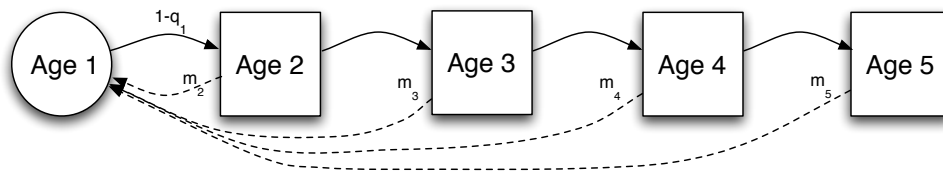FIGURE 1. A linear annual, semelparous life history.

FIGURE 2. A linear perennial, iteroparous life history.

of reproduction and mortality for an average individual in a population. For example, the following diagrams illustrate such simple life histories (see Figures 1,2).

Such a life history is easily put into a life table. However, not all life histories are so simple. Some species have developmental stages or do not move through their life histories or life cycles in a linear fashion. Consider the following figure where a plant species produces a seed that may or may not germinate in a given growing cycle (see Figure 3).
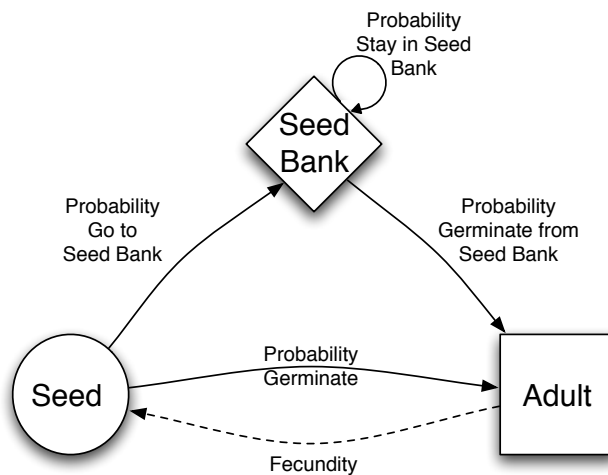

FIGURE 3. A seed bank example where seeds may lay dormant for a number of growing cycles.

Another interesting example is the stage-based life cycle where individuals are grouped according to the stage of their life cycle as opposed to age. For example, consider Figure 4 which represents the life cycle of frogs. An individual is placed in a stage and has a certain probability of remaining in that stage and a certain probability of moving to the next stage. It should be noted that an individual can only move one stage at a time and that sequence of developmental stages is not reversible.
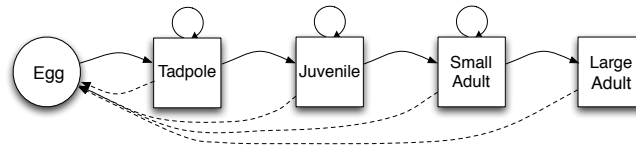

FIGURE 4. Frogs demonstrate a stage-based life cycle.

Similarly, there is a size-based life cycle, where an individual is in a particular size class and has a certain probability of moving to the next size class or remaining in the current size class. We assume no individual can move more than one size class per growing cycle. Certain species of fish are a natural example of this life cycle.

4. The Power of Linear Algebra

While certain life histories are conducive to using life tables to estimate population growth rates, as we have seen in Section 3, many are not. Fortunately, we can use matrix or linear algebra to examine population growth in such species. We can also use matrix algebra to figure out what aspects of the life history are most influential on the population growth rate, which is particularly useful for trying to conserve species and populations.

4.1. Example: The Matrix Model.

To see how matrix algebra can be used in population models, we consider the following example. Suppose we have a population that models a linear perennial, iteroparous life history (i.e., an individual lives more than one year and reproduces more than once) with four ages, Age 1-4. The probability of an individual moving from Age 1 to Age 2, Age 2 to Age 3, or Age 3 to Age 4 is each 0.5. We also have the following age-specific fecundity rates: $m_1 = 1$, $m_2 = 2$, and $m_3 = 3$. This life cycle is modeled in Figure 7.

This figure is more than a useful pictorial description of the life cycle. We can capture this information using matrix algebra. Let $\vec{n}(t)$ represent the vector that contains the number of individuals in each life stage, Age 1-4. For our example,
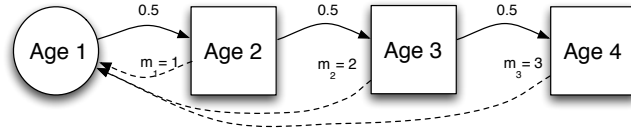
FIGURE 5. A linear perennial, iterparous life history.

suppose at time t that there are 600 individuals of Age 1, 100 of Age 2, 100 of Age 3, and 100 of Age 50. This can be summarized in the vector,

$$\vec{n}(t) = \begin{bmatrix} 600 \\ 100 \\ 100 \\ 100 \end{bmatrix}.$$

Given our transition probabilities and fecundity rates, how do we compute the number of individuals at each age at time $t + 1$? Notice that the number of individuals of Age 1 is solely determined by the fecundity rate of each of the Ages 2-4 and the number of individuals at those age levels. That is, the number of individuals of Age 1 at time $t + 1$ is determined by:

$$
\begin{aligned}
\text{Age 1} &= m_1 * \text{Age 2} + m_2 * \text{Age 3} + m_3 * \text{Age 3} \\
&= 1 * 100 + 2 * 100 + 3 * 100 \\
&= 600
\end{aligned}
$$

Similarly, Age 2-4 at time $t + 1$ is determined by the number of individuals who move from the previous age stage. This is determined solely by the transition rates. So we have

$$
\begin{aligned}
\text{Age 2} &= 0.5 * \text{Age 1} \\
&= 300 \\
\text{Age 3} &= 0.5 * \text{Age 2} \\
&= 50 \\
\text{Age 4} &= 0.5 * \text{Age 3} \\
&= 50
\end{aligned}
$$

However, all these calculations can be captured with matrix multiplication in the equation

$$\vec{n}(t + 1) = A\vec{n}(t)$$

where the vectors $\vec{n}(t)$ and $\vec{n}(t+1)$ represent the number of individuals in each age stage at times t and $t + 1$ respectively The matrix A is the population projection matrix that contains the transition rates and fecundity rates for each age stage. The row one represents the outcome for Age 1, row two for Age 2, etc. Column 1 represents how Age 1 affects the other Ages, column 2 represents how Age 2 affects

the other Ages, etc. For example, if we allow $t = 0$, we have the following.

$$
\begin{aligned}
\vec{n}(1) &= A\vec{n}(0) \\
&= \begin{bmatrix} 0 & 1 & 2 & 3 \\ 0.5 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} \begin{bmatrix} 600 \\ 100 \\ 100 \\ 100 \end{bmatrix} \\
&= \begin{bmatrix} 600 \\ 300 \\ 50 \\ 50 \end{bmatrix}
\end{aligned}
$$

Question 1. How would we use $\vec{n}(1)$ to compute $\vec{n}(2)$, that is the population of each stage at time 2?

As you can see, the calculations to project population sizes into the future are relatively simple, if tedious, using basic matrix algebra. Using a computer to do these multiple iterations will be much faster and much less tedious. Before we try this, let's first get some more practice with creating population projection matrices and life cycle graphs.

Question 2. For the following life table from Lawler (2011: Population Ecology 53: 229-240), create a *generalized* population projection matrix. That is, the matrix will not have specific values for the entries, but the general entries, F_i, P_i, or G_i in the appropriate locations in the matrix. You may want to look at the example in the next question for clarification.
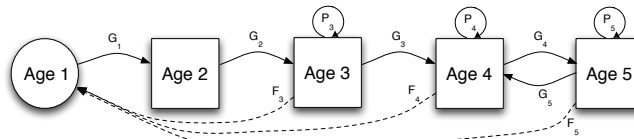

FIGURE 6. Life table from Lawler.

Question 3. For the following matrix from Crowder et al [4], create a life table graph.

The *generalized* matrix A below provides a "key" for the matrix in Table 2.

$$
A = \begin{bmatrix} P_1 & F_2 & F_3 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix}
$$

TABLE 2. Five-stage population matrix A for loggerhead sea turtles.

0	0	0	4.665	61.896
0.675	0.703	0	0	0
0	0.047	0.657	0	0
0	0	0.019	0.682	0
0	0	0	0.061	0.8091

In this case, P_i is the probability of surviving and remaining in the same stage, G_i is the probability of surviving and growing into the next stage, and F_i is the stage-specific reproductive output.

Question 4. For the life table below, create a population matrix and a life table graph. Note that q_x denotes the age-specific mortality (e.g., q_{egg} is the proportion of the eggs that dies before they become size 1).

TABLE 3. Five-stage life table for loggerhead sea turtles.

x	N_x	l_x	q_x	m_x
egg	625	1.00	0.12	0
Size 1	550	0.88	0.05	0
Size 2	525	0.84	0.19	1
Size 3	425	0.68	0.53	2
Size 4	200	0.32	1.00	0

4.2. **Exploration: Population Projection Matrix with Excel.**
Lets see how we can use a basic spreadsheet program to do these simple matrix calculations (see AgeBasedEx.xlsx). For this exploration, we will be using the following life cycle graph.
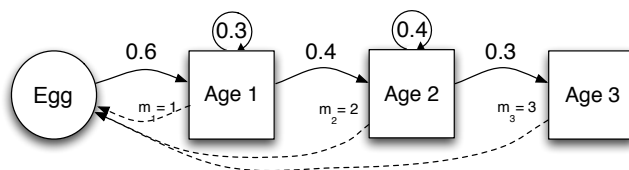

FIGURE 7. A life cycle graph.

Question 5. Use the information on the life cycle graph to set up a population projection matrix.

Question 6. Let's assume that you went out and censused the population represented in this life cycle graph and found 20 eggs, 15 age 1 individuals, 10 age 2 individuals, and 10 age 3 individuals. Use the population projection matrix and the census results to project the population size 2 times into the future.

Question 7. Using the Excel spreadsheet, *AgeBasedEx.xlsx*, complete the matrix entries in red and the initial population vector (also in red) and compare to your results from the above question.

Question 8. Is the population from Question 7 increasing or decreasing? Can you determine by how much for each time interval?

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5. Estimating Population Growth

While basic matrix algebra provides an iterative process to estimate how a population will grow over time, we would like to estimate basic growth for a population. For certain populations, the long term population growth trend stabilizes over time. That is, after a certain point, the age distributions (or stage distributions) stabilize so that the ratios of ages classes is constant from iteration to iteration. We saw this type of behavior in Question 8 above.

When the growth of a population stabilizes, we can compute the rate of growth of a population, λ, as

$$(1) \qquad \lambda = \frac{N_{t+1}}{N_t}$$

where N_t is the total population at time t. This rate is known as the geometric rate of increase and can be used to interpret the projected growth of a population over a short period of time. When $\lambda > 1$, the population is growing. When $\lambda < 1$, the population is declining. When $\lambda = 1$, the population is stable. In many ways λ is very similar to the R_0 we saw earlier and in some specific cases they are interchangeable.

5.1. Exploration: λ and the Stable Age Distribution with Excel.
Lets use our Excel worksheet, StableAgeDist.xlsx, to see what the link is between the stable age distribution and λ. To do this, we will manipulate various parameters in the population projection matrix and in doing so we will be changing λ. For the following manipulate the Adjustment Matrix on the right hand side of the worksheet and keep the Original Matrix on the left as a reference matrix.

   (1) To begin, we will increase the value of λ from the Adjustment Matrix by manipulating the fecundities (m_x) to increase λ. Double the values of the fecundities in the Adjustment Matrix. Record the stable age distribution and λ.

(2) Now repeat the manipulations in the Adjustment Matrix by tripling original fecundity rates. Record the stable age distribution and λ.
(3) What happens if we reduce the fecundity rates? Set the fecundity rates to half the original values. Record the stable age distribution and λ.
(4) Given your observations of changes in λ and the stable age distribution, what conclusions can you draw about the relationship between λ and stable age distributions?

5.2. **Exploration: The initial population, λ and the Stable Age Distribution with Excel.**
In our calculations of the stable age distributions in Exploration: λ and the Stable Age Distribution with Excel, we noticed that the stable age distribution varied with λ. Now lets see if the stable age distribution is also a function of the original population vector. Be sure to reset the Adjustment Matrix to the original values before starting.

(1) To start, invert the initial population in the Adjustment Initial Population Vector (i.e., take the number of individuals in age class 3 and put them in age class Seed, take the number of individuals in age class Seed and put them in age class 3, etc.). What happens to the stable age distribution? λ?
(2) Now make your own changes in the Adjustment Initial Population Vector. What happens to the stable age distribution? λ?
(3) Given your observations in the above two questions, what appears to be the determining factor for the stable age distribution? λ? Is it the matrix elements or the vector elements?

5.3. **Exploration: Intro to Sensitivity Analysis with Excel.**
In Exploration:λ and the Stable Age Distribution with Excel you manipulated the fecundities for this population. Now lets examine how changing each of the matrix parameters affects λ. To do this we will manipulate one matrix element of the Adjustment Matrix at a time and see how it changes λ. We won't manipulate each element, but enough to get a flavor of how ecologists conduct what is known as sensitivity analysis. That is, how sensitive is the population to a particular entry in the matrix. Be sure to reset the Adjustment Matrix back to the original values every time.

(1) Increase the fecundity of Age 3 individuals by 50% in the Adjustment Matrix (so change it from 3 to 4.5). Calculate the proportional change in λ that occurred as a result of this change.
(2) Increase the survivorship of Eggs by 50% in the Adjustment Matrix (so change it from 0.6 to 0.9). Calculate the proportional change in λ that occurred as a result of this change.
(3) Increase the proportion of Age 2 individuals that stay Age 2 individuals by 50% in the Adjustment Matrix (so change it from 0.4 to 0.6). Calculate the proportional change in λ that occurred as a result of this change.

(4) Which element had the greatest impact on λ? How did you come to that conclusion?

One issue with using Equation 1 to compute λ is that it can only be done once a stable age distribution has been reached. In other words, we would have to iteratively find the age distributions until the ratios of the age, or stage, classes is constant from iteration to iteration.

Surprisingly, matrix algebra once again comes to our aid. It turns out that the population projection matrix, A, holds enough information to determine the growth rate for the population it represents. This information is known as the eigenvalue of a matrix. Before we see how to apply eigenvalues to population rates, we first give a brief introduction of eigenvalues.

Eigenvalues are actually computed simultaneously with their corresponding eigenvector. The vector $\vec{n}$ is an eigenvector of the square matrix A with eigenvalue λ if the following equation holds:

$$A\vec{n} = \lambda\vec{n}.$$

Usually when a vector, like $\vec{n}$, is multiplied by a matrix, the resulting vector has changed in both magnitude (length) and direction. However, in the special case where $\vec{n}$ is an eigenvector of A, multiplication by A leaves the direction unchanged. Depending on the sign and magnitude of the eigenvalue λ corresponding to $\vec{n}$, the operation $A\vec{n} = \lambda\vec{n}$ compresses or stretches $\vec{n}$ by a factor of λ.

Example 1. The vector $\vec{n} = \begin{bmatrix} 1 \\ 2 \end{bmatrix}$ is an eigenvector of

$$A = \begin{bmatrix} 3 & 0 \\ 8 & -1 \end{bmatrix}$$

corresponding to the eigenvalue $\lambda = 3$, since

$$A\vec{n} = \begin{bmatrix} 3 & 0 \\ 8 & -1 \end{bmatrix} \begin{bmatrix} 1 \\ 2 \end{bmatrix} = \begin{bmatrix} 3 \\ 6 \end{bmatrix} = 3\vec{n}$$

While computing the eigenvectors of a square matrix takes methods beyond the scope of this work, we can compute eigenvalues for small matrices. For a more complete treatment of eigenvalues, we refer the reader to Anton [1] or Lay [5].

Example 2. Suppose we want to find the eigenvalues of $A = \begin{bmatrix} 2 & 3 \\ 3 & -6 \end{bmatrix}$. Notice that through a little matrix algebra, we have

$$\begin{aligned} A\vec{n} &= \lambda\vec{n} \text{ or} \\ A\vec{n} - \lambda\vec{n} &= \vec{0} \text{ or} \\ (A - \lambda I)\vec{n} &= \vec{0} \end{aligned}$$

Since the eigenvector $\vec{n}$ must be nonzero and $(A - \lambda I)\vec{n} = \vec{0}$, by the Invertible Matrix[1] Theorem, we need $(A - \lambda I)$ to be non-invertible. Otherwise, if $(A - \lambda I)$ was invertible, then we would have $\vec{n} = 0$. For our example, we now have

$$A - \lambda I = \begin{bmatrix} 2 & 3 \\ 3 & -6 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} 2 - \lambda & 3 \\ 3 & -6 - \lambda \end{bmatrix}.$$

We have seen that a matrix is not invertible if its determinant is zero. We want to find λ such that the determinant of $(A - \lambda I)$ is zero. So the eigenvalues of A are the solutions of the equation

$$\det(A - \lambda I) = \det \begin{bmatrix} 2 - \lambda & 3 \\ 3 & -6 - \lambda \end{bmatrix} = 0.$$

Recall that

$$\det \begin{bmatrix} a & b \\ c & d \end{bmatrix} = ad - bc.$$

So

$$\begin{aligned} \det(A - \lambda I) &= (2 - \lambda)(-6 - \lambda) - (3)(3) \\ &= -12 + 6\lambda - 2\lambda + \lambda^2 - 9 \\ &= \lambda^2 + 4\lambda - 21 \\ &= (\lambda - 3)(\lambda + 7). \end{aligned}$$

If $\det(A - \lambda I) = 0$, then $\lambda = 3$ or $\lambda = -7$. So the eigenvalues of A are 3 and -7.

While finding the eigenvalues for a 2×2 matrix reduces to solving a quadratic equation, as the size of the matrix increase, so does the degree of the accompanying polynomial (known as the characteristic polynomial). So to find the eigenvalues of a 4×4 matrix, we would have to solve a fourth degree polynomial, i.e., a polynomial with λ^4 terms. In general, this is a very difficult task. Luckily, we can turn to technology for help.

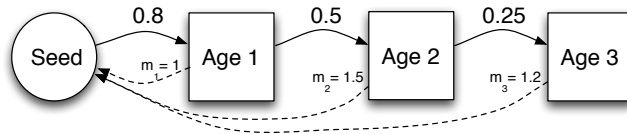Consider the following age-based population graph.

FIGURE 8. An age-based population graph.

It has the corresponding projection matrix

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[1]The Invertible Matrix Theorem is *the* central theorem for Linear Algebra. It has many equivalent statements, one of which is that a square matrix A is invertible if and only if the equation $A\vec{x} = \vec{0}$ has on the trivial solution $\vec{x} = 0$.

$$A = \begin{bmatrix} 0 & 1 & 1.5 & 1.2 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

To consider the long term behavior of this population, would could iterate $A^n \vec{n}(0)$ until the age distributions stabilize. Instead, we will compute the eigenvalues of this matrix. Since this is a 4×4 matrix, we can have up to four eigenvalues. To compute this we use the web-based program WolframAlpha® to find the eigenvalues are approximately 1.18, -0.31, -0.43+0.36i, and -0.43-0.36i, please see Figure 9. So which value determines the population growth? Also, notice that some of the values are imaginary? First, imaginary solutions come with the territory. Even simple quadratic equations such as $x^2 + 4 = 0$ have imaginary solutions. With regard to which of the four values we use, we choose the one with the largest magnitude, which in this case is $\lambda = 1.18$. The eigenvalue with the largest magnitude is known as the dominant eigenvalue. For those interested in why the dominant eigenvalue is the one that determines the rate of growth in the population, we refer to you to Caswell [3].
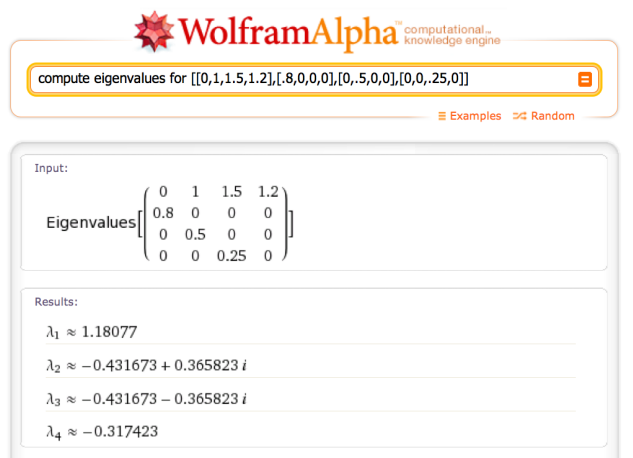

FIGURE 9. Using WolframAlpha to compute eigenvalues.

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