Population Modeling Using Matrix Systems in `MATLAB`

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1 Introduction to Leslie and Lefkovitch Systems

One of the most common models in population ecology (the subfield of ecology that studies large groups of the same species, how they interact with the environment as a group, and how the size of the population changes) is the Leslie model, named after British ecologist Patrick H. Leslie. Leslie is credited with the idea of dividing species into age classes, and treating each age class as a separate population in order to model growth and survivorship of a population.

The Lefkovitch model is similar to the Leslie matrix model, but rather than using age classes, the Lefkovitch model uses "stage-structured" growth, rather than "age-structured" growth. That is, the different classes within a species are not necessarily based on age in a Lefkovitch system, but could be based on size, development, or some other factor which determines the reproduction and survivorship of an organism within a population. In order to model the population as a matrix equation, we need two main sets of data: the **survivorship** of each class, and the **fecundity** of each class. We make the following definitions.

- n_x is the count of individuals of age class x.
- ℓ_x is the probability that an individual will survive to age x.
- $s_x = \ell_{x+1}/\ell_x$, the survivorship of class x, is the proportion of individuals who survive from age x to age $x+1$.
- f_x, the fecundity of class x, is the average number of surviving offspring produced by each member of age class x.
- ω is the maximum age or final class attainable in the population.
- For a Leslie model, note that we only consider the number of reproductive individuals...that is, for many animals we will only consider the number of females in the population.
- For a Lefkovitch model just ignore the word "age".

Now recall our work on Markov chain models. The general form of Leslie and Lefkovitch systems are extremely similar. A Leslie matrix model will take the following form:

$$\begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_{t+1} = \begin{bmatrix} f_0 & f_1 & f_2 & \dots & f_{\omega-2} & f_{\omega-1} \\ s_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & s_{\omega-2} & 0 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_t \tag{1}$$

In matrix-vector notation, we have

$$\vec{n}_{t+1} = \mathbf{L}\vec{n}_t.$$

We learned that we can write this system as

$$\vec{n}_t = \mathbf{L}^t\vec{n}_0. \tag{2}$$

(This is the form you should use to make any calculations.)

The sum of all elements in $\vec{n}$ will be the current total population size, and furthermore if we let λ be the dominant eigenvalue of $\mathbf{L}$ is the stable growth rate of the population.

2 Modeling Population Systems and Using MATLAB

Suppose we have a population of arctic terns whose age distribution is given in the following table.

x	s_x	f_x
0	0.34	0
1	0.40	1.5
2	0.44	1.8
3	0	1.3

Table 1: Life table for a population of arctic terns. Note that small birds have a type II survivorship curve–meaning their survivorship is roughly the same at any given age.

Suppose we start with 25 birds at age 0, 54 birds at age 1, 23 birds at age 2, and 65 birds at age 3 (assume $\omega = 4$). We want to answer the following questions:

1. What is the total population of birds after the next ten years, assuming nothing changes?
2. Will the arctic tern population increase or decrease over the next ten years, if none of the parameters change?

First, we need to set up the Leslie matrix as shown in 1 above. Then, we can use the equation in 2 to calculate the distribution of birds after 10 years. We will get the following equation.

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}_t = \begin{bmatrix} 0 & 1.5 & 1.8 & 1.3 \\ 0.34 & 0 & 0 & 0 \\ 0 & 0.40 & 0 & 0 \\ 0 & 0 & 0.44 & 0 \end{bmatrix}^t \begin{bmatrix} 25 \\ 54 \\ 23 \\ 65 \end{bmatrix}_0$$

In order to get the age distribution every year for the next 10 years, you can do a simple calculation the same way we did Markov chains.

```
tern_leslie = [0, 1.5, 1.8, 1.3; 0.34, 0 0 0; 0, 0.40, 0, 0; 0, 0, 0.44, 0];
tern_initial = [25; 54; 23; 65];
tern_ten_year = tern_leslie^t * tern_initial;
```

You should get the following result:

$$\begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \end{bmatrix}_{10} = \begin{bmatrix} 61.38 \\ 22.82 \\ 9.56 \\ 4.74 \end{bmatrix}$$

and the total population will be about 98.5 terns.

In order to find whether the total population is increasing or decreasing we can either compare the total population value after 10 years (98.5 terns) to the initial population (167 terns), which will give us an answer at this specific time point, or we can use the **dominant eigenvalue** to determine the rate at which we can expect the population size to change.

```
max(abs(eigs(tern_leslie)))
```

Using this MATLAB code we get that the dominant eigenvalue is $\lambda = 0.9293$. So, we can expect the tern population to decrease by about 7.1% every year.

3 Problems

On the next page, there are five example problems for you to work on. For each problem, you should include your Leslie or Lefkovitch system modeling the problem, your final conclusions or answers for the problem, and any plots and MATLAB codes (in a listing environment) which are relevant to your answer.

3.1 Sickly Tapirs[1]

Suppose the following data table describes a population of Baird's tapir, *Tapirus bairdii.* Poaching and habitat destruction are responsible for declining tapir populations, and Baird's tapir is considered an endangered species by the IUCN. You are concerned that your local population of Baird's tapir will become extinct within the next 25 years (you can assume none of your data will change within the next 25 years).

x	n	s_x	f_x
0	120	0.411	0
1	131	0.893	0
2	87	0.970	0
3	23	0.992	0
4	76	0.989	0
5	84	0.980	0
6	139	0.991	1.54
7	87	0.962	2.34
8	90	0.718	1.02
9	67	0.439	0.54
10	43	0.211	0
11	32	0	0

Table 2: The data you have collected for the population of Baird's tapir you are monitoring. Assume $\omega = 12$ in your population.

1. Based on your data, if none of these parameters change, can you expect the tapir population to go extinct? If so, when? Provide any results or charts you think would be helpful to illustrate your result.
2. You are particularly worried about the susceptibility of your tapir population to two detrimental diseases. One of these diseases, a bacteria, kills the tapirs directly, and the second is a virus which is nonlethal to the host, but directly affects reproductive success. Both diseases are extremely contagious and you can assume that once a single tapir gets the disease, the whole population will have the disease before the end of the current year.
3. The bacterial disease effectively halves the survivorship of all tapirs ages $0-6$ and $9-11$ (both inclusive). How does this affect the extinction of your tapir population?
4. Now suppose the viral disease halves the fecundity of all of your tapirs. Describe what happens to the tapir population in the long-term after this.
5. What is more detrimental to the tapirs: a loss in survivorship, or a loss in fecundity? Which disease should you be more worried about?
6. Suppose instead that the bacterial disease has another strain which halves the survivorship of tapirs aged $6-9$, inclusive, and has no effect on young or old tapirs. How does this affect the extinction of your tapir population? Would this be worse, or better, for your tapir population than the original strain of the bacterial disease?
7. Finally, consider two more strains of the viral disease: strain A halves the fecundity of tapirs aged 6 and 7, and halves the survivorship of tapirs aged 8 and 9, while strain B halves the survivorship of tapirs aged 6 and 7 and halves the fecundity of tapirs aged 8 and 9. Which disease has a stronger impact on the tapir population?

[1] This problem was modified from a handout I got from Dr. Pechmann; I do not know the original source but he likely does.

3.2 Butterfly Effect[2]

We can model butterflies using a Lefkovitch matrix with a structure described in the graphic below.

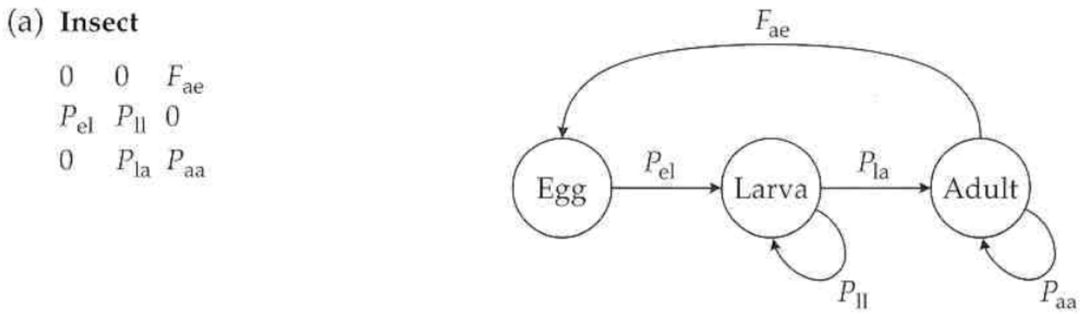

Figure 1: This diagram and the associated matrix show you how the Lefkovitch system for this model should be set up. Lefkovitch matrices tend to be slightly more difficult to set up than Leslie systems, but this graphic should have all the information you need.

A certain exotic butterfly, Hoops' Longwing (*Heliconius hoopsus*), has the following growth parameters: the probability that an egg hatches into a larva is 0.1, the probability that a larva remains a larva is 0.05, the probability that a larva metamorphoses into an adult is 0.5, the probability that an adult remains alive for another month is 0.67, and each adult can be expected to have 10 surviving larva children per month. Assume all parameters are in terms of months, and thus t should be in months also.

You are an avid butterfly collector and you order 25 Hoops' Longwing adults in the mail. You are, for your own nefarious purposes, interested in nurturing these butterflies and their progeny for the next two years.

1. Use the parameters above and the Lefkovitch model structure given to you in Figure 1 to determine the amount of adult butterflies you will have after two years if all 25 butterflies survive the shipping process.

2. Unfortunately, insect shipping is not an optimal process, so it is unlikely that all 25 butterflies will survive their journey. Calculate how many adult butterflies you will have after two years depending on the number of butterflies which survive. Use every initial condition from $1 - 25$, inclusive. Plot the number of adult butterflies after two years as a function of the number of initial butterflies. (Hint: I would probably use a `for` loop for this.)

3. Now, let's go back to our idealized world where all of your butterflies survive the trip. Butterfly reproductive success can be heavily dependent on the environment in which they live, and you have no good way to estimate how successful the butterflies will be in whatever place you are keeping them. Now, vary F_{ae} from $1 - 25$ as well (this value in the Lefkovitch system corresponds to how many surviving eggs each adult butterfly lays per month if you have set your system up correctly). Plot the number of adult butterflies after two years as a function of F_{ae}.

4. Now, what if we want to vary both parameters at the same time? We can actually visualize a three-dimensional graph pretty easily with `MATLAB` by using the `surf` function. But, it has a lot of quirks (in my opinion, moreso than Mathematica). You will probably need to use a nested `for` loop and/or the `meshgrid` function to make this work; you should really look at the documentation for `surf`. Your plot might not look excellent, but that's not a big deal–if you want it to look smooth, you'll need to use the `interp2` function, which I think is often more trouble than it's worth.

[2]This model, and the next two, are taken from A Primer in Ecology, Godelli, 2008; I made up numbers.

3.3 Trees and Harvesting

Suppose that you want to replicate Carol's acorn and beet cookies, which you saw in *The Walking Dead*. Your friend is a beet farmer, and will continue to be a beet farmer for the foreseeable future, so you will have no problem getting as many beets as you need.

However, you only have two oak trees in the forest near your house due to a recent disturbance and ensuing primary succession pattern. You need one kilo of acorn flour to make the amount of cookies that you want. Assume 2.5 kilos of raw acorns are needed for you to make one kilo of acorn flour and an acorn weighs 10 grams on average. First, compute the number of acorns you will need to make enough acorn flour.

Then, suppose you have the given Lefkovitch matrix system modeling the population structure of the oak trees. Assume t is in months.

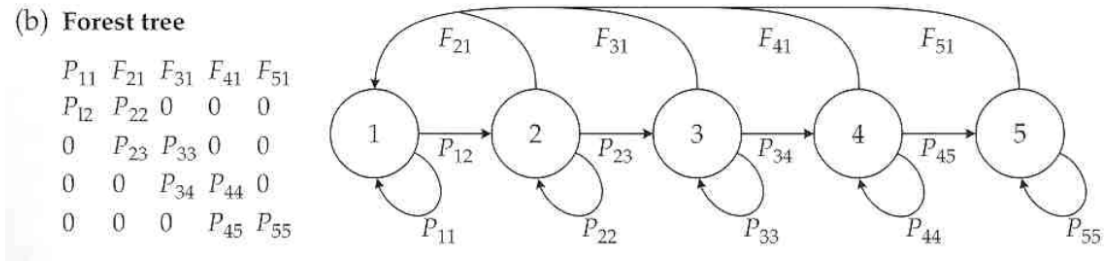

Figure 2: The diagram and matrix showing how the Lefkovitch model for forest trees could be structured.

$$\vec{n}_t = \begin{bmatrix} 0.2 & 0 & 10 & 100 & 500 \\ 0.1 & 0.5 & 0 & 0 & 0 \\ 0 & 0.3 & 0.7 & 0 & 0 \\ 0 & 0 & 0.15 & 0.8 & 0 \\ 0 & 0 & 0 & 0.01 & 0.98 \end{bmatrix}^t \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 2 \end{bmatrix} \tag{3}$$

1. First of all, how many acorns will there be after one month? (Hint: you can see this in the matrix without doing any `MATLAB` calculations if you look in the right place.)

2. At the end of this first month, you collect the number of acorns you need to make your one kilo of acorn flour. Calculate the stage distribution of the population for the second month, both with and without harvesting. How does the distribution change when you harvest the acorns?

3. Suppose your organic cookie business is booming and you harvest part of the acorns from the forest each year. We can include this in the model by accommodating for harvesting with a **harvest matrix**, as shown below.

$$\vec{n}_t = (\mathbf{L} - \mathbf{HL})^t \vec{n}_0 = ((\mathbf{I} - \mathbf{H})\mathbf{L})^t \vec{n}_0 \tag{4}$$

In 4, **I** is the identity matrix with the same dimensions as **L**, and **H** is a matrix with the following structure, where h_1 is the proportion of individuals harvested (or removed) from age class i.

$$\begin{bmatrix} h_1 & 0 & 0 & \dots & 0 \\ 0 & h_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & h_n \end{bmatrix} \tag{5}$$

Compare the results of your model after 25 years with a few different harvesting rates. Assume your initial condition is the result of your previous calculation. What happens to the age structure as you harvest different amounts of acorns?

3.4 Turtles All the Way Down[3]

Suppose that you are a politician who cares a lot about the environment (they are rare but they exist). You have just liasoned with your state's Wildlife Service, and they have presented you three predictions about a population of mud turtles in your state. These mud turtles are *critical* to the health of the ecosystem in which they reside, and without these turtles the ecosystem will almost surely collapse.

Global climate change, agricultural runoff, and industrial pollution are potential sources of concern which could endanger the mud turtle population. The three projections made by the wildlife population indicate the worst-case, best-case, and average-case population projections for the turtle species. Now, you may not have studied conservation biology, but you did study math as an undergrad, so you know the following result from linear algebra.

Theorem 1 (Perron-Frobenius Theorem)**.** *Any matrix where all entries are strictly positive will have a unique, maximal positive real eigenvalue and a corresponding eigenvector with strictly positive entries.*

And, you know that this result applies heavily in demography and population dynamics: the unique maximal eigenvalue will be the **dominant eigenvalue** of the Leslie matrix system, corresponding to the asymptotic rate of growth for the mud turtle population, and the corresponding eigenvector will give you information about the **steady-state distribution** of the population.

	Best Case		Average Case		Worst Case	
x	s_x	f_x	s_x	f_x	s_x	f_x
1	0.340	0	0.261	0	0.175	0
2	0.876	0	0.521	0	0.164	0
3	0.876	0	0.721	0	0.568	0
4	0.774	0	0.801	0	0.730	0
5	0.762	1.07	0.877	0.96	0.874	0.86
6	0.877	1.07	0.875	0.96	0.865	0.86
7	0.585	1.07	0.876	0.96	0.240	0.86
8	0.432	1.07	0.267	0.96	0	0.86
9	0.431	1.07	0.142	0.96		
10	0.342	1.07	0	0.96		
11	0.253	1.07				
12	0	1.07				

Table 3: Data on keystone mud turtle populations in three different cases provided to you by the state Wildlife Service.

1. For each of the three cases described to you, produce the corresponding Leslie matrix.
2. Compute the asymptotic growth rate for each of the cases, and interpret the value (i.e. explain what it means for the value to be less than one vs. greater than one).
3. Provide the associated steady state age distribution for each population.
4. Compute each of the population distributions after ten years, and determine if the population will be at the steady state.
5. If nothing is done to protect turtle populations, about how long will it take (rounded to the nearest 5 years) for the turtle population to go extinct in each case, if at all?
6. Use the evidence you have created to argue in which cases you would need to push legislation to protect the turtle population.

[3]Data adapted from Frazer et al., Life History an Demography of the Common Mud Turtle *Kinosternon subrubrum* in South Carolina, USA in Ecology: 72(6).