Stage Based Population Projection Matrices and Their Biological Applications

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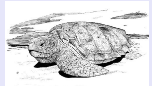
Abstract

A useful tool in investigating population demographics is the Leslie matrix population projection technique. Lefkovitch refined this technique for populations where ages of individuals were unclear. This paper helps to explain both techniques and shows an example of the use of the Lefkovitch technique.

1. Introduction

The Leslie matrix population projection technique was developed by P.H. Leslie in 1945. The heart of his technique is based on the Leslie matrix, which uses mortality and fecundity rates to give a projection of an organisms population distribution based on initial population distribution of age groups. The Leslie model will also provide simulations of changes in population growth rates.

A more specific form of this matrix, the Lefkovitch matrix, was originally deduced to study populations of cigarette beetles, but has now spread to many biological and botanical studies. It is similar to the Leslie Matrix, but divides populations into stage classes instead of age groups, since many species cannot be identified as to age due to lack of knowledge of their population demographics.



Here we will use a study of Loggerhead Sea Turtles to demonstrate the effectiveness of the Lefkovitch model. We will do this by constructing a Lefkovitch matrix which uses the seven life stages of the Loggerhead. Then we will test the sensitivity of different stage classes to changes in mortality rates. We will then demonstrate how this will give a good indication as to which stages should be the focus of conservation efforts.

2. The Leslie Matrix

The Leslie matrix is, in effect, a special variation of the matrix A such that

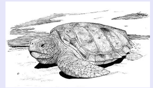
$$An_t = n_{t+1}$$

where A is the population projection matrix, whose elements incorporate fecundity, mortality, and growth rates, with the population divided into equal age classes.

$$A = \begin{pmatrix} a_{11} & a_{12} & \dots & a_{1s} \\ a_{21} & a_{22} & \dots & a_{2s} \\ \vdots & \vdots & \ddots & \vdots \\ a_{s1} & a_{s2} & \dots & a_{ss} \end{pmatrix}$$

n_t gives the abundance of individuals in each life stage at time t.

$$n_t = \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}_t$$



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n_{t+1} gives the abundance of individuals in each life stage at time $t+1$.

$$n_{t+1} = \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}_{t+1}$$

The complete matrix equation incorporates A, n_t, and n_{t+1} such that

$$\begin{pmatrix} a_{11} & a_{12} & \dots & a_{1s} \\ a_{21} & a_{22} & \dots & a_{2s} \\ \vdots & \vdots & \ddots & \vdots \\ a_{s1} & a_{s2} & \dots & a_{ss} \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}_t = \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_s \end{pmatrix}_{t+1} .$$

3. The Lefkovitch Matrix

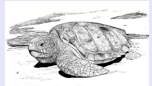
The Lefkovitch matrix population projection technique uses the same matrix equation, however the elements in Lefkovitch's matrix A are divided into stage classes, with age having little relation to stage, which is merely a measure of growth and breeding maturity. It is, however, assumed that all individuals in each stage class are subject to the same mortality, fecundity, and growth rates. The dominant eigenvalue λ_m of this matrix is equal to e^r, with r being the population's intrinsic growth rate as seen in the following equation.

$$N_t = N_0 e^{rt}$$

So, in order for the population to remain stable, the growth rate r must equal zero, making e^r, and in turn λ_m, equal to 1.

$$\lambda_m = e^r = 1 \Rightarrow r = 0$$

According to Lotka, when the environment is constant, the age distribution of individuals in different stage classes will be relatively stable. The result is that population matrix A has a right eigenvector w_m which represents this stable stage distribution, as in this equation.



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$$Aw_m = \lambda_m w_m$$

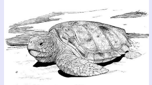
For the matrices we will be considering, initial population stage structures will be projected forward and approach stable stage distribution w_m, so each stage class will increase in size λ_m times each period. Reproductive values, which estimate the possible reproductive contribution of each stage class to population growth, are given by the elements of the left eigenvector v, which corresponds to the left eigenvalue λ_m.

$$v'A = \lambda_m v'$$

As we can see, the primary difference between this Lefkovitch stage class matrix and the Leslie age class matrix are that here, individuals may remain in a stage from one time t to the next, and also that the durations of the stage classes may be different. It is necessary, that for our example, we use this stage class model developed by Lefkovitch, because knowledge of age-specific rates and characteristics in Loggerhead sea turtles is lacking and thus prevents the use of other age-based models such as the Leslie matrix population projection technique. The frequent use of the Lefkovitch stage class matrix technique by both botanists and by Lefkovitch himself during his study of Cigarette Beetles, attests to its effectiveness and also to its adaptability to many populations.

4. Loggerhead Study Background

Data used in Table 1 comes from a study done by Richardson and Frazer on Little Cumberland Island, Georgia. Using this data, Frazer created a preliminary life table for wild loggerhead turtles. It assumes a closed population, 1:1 sex ratio, first reproduction at 22 years, average life span of 54 years, and population declining at a rate of 3 percent per year. Since no method has been devised to find the actual age of sea turtles, the data from this study is based mostly on size classes. Some of the life stages are very distinct looking, while some are only different in size or other small characteristics. Frazer's data was divided into seven different life stages as follows: eggs and hatchlings, small juveniles, large juveniles, sub-adults, novice breeders, 1st year remigrants, and mature breeders.



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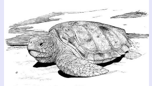

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Stage Num.	Class	Size (cm)	Approx. age	Annual Survivorship	Fecundity
1	eggs, hatchlings	<10.0	<1	0.6747	0
2	small juveniles	10.1-58.0	1-7	0.7857	0
3	large juveniles	58.1-80.0	8-15	0.6758	0
4	subadults	80.0-87.0	16-21	0.7425	0
5	novice breeders	>87.0	22	0.8091	127
6	1st-yr remigrants	>87.0	23	0.8091	4
7	mature breeders	>87.0	24-54	0.8091	80

Table 1: Stage based life table, assuming a 3 percent per year population decline.

5. Theoretical Population Projections

The model used divides the life cycle of the Loggerhead sea turtle into seven different life stages, using fecundity, growth rates, and survival rates previously estimated by Frazer. It is necessary, in developing a stage-based projection, to estimate reproductive output F_i, probability of surviving and growing into the next stage G_i, and probability of surviving but remaining in the same stage P_i for each separate stage. F_i, or fecundity, is given in Table 1. G_i and P_i can both be calculated using the stage-specific survival probabilities p_i and stage durations d_i, and it must be assumed, since little is known about growth rates and variations within each stage, that every turtle in a stage is subject to identical survival probability and stage durations.

Some individuals in a stage may have been there for 1 year, while some might have been there for 2, 3, ... ,or d_i years, and there are some who may have just entered the stage. Let us set the number of turtles alive in the fist group of stage class i to one and the probability of individuals in the group surviving to the next year to p_i. Then the probability of those individuals surviving d years is equal to pi^d. Now, if the age distribution inside of each stage is stable, then the relative abundance of these groups is equal to $1, p_i, p_i^2, \ldots, p_i^d$. During the time from t to $t+1$, the oldest individuals, should they survive, will move into the next stage. P_i, the proportion of the turtles surviving and remaining in the same stage is given by

$$P_i = \frac{1 + p_i + p_i^2 + \ldots + p_i^{d_i - 2}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i - 1}} p_i.$$

Since the geometric series $1+p+p^2+\ldots+p^{d-1}$ can be rewritten as

$$\frac{1-p^d}{1-p},$$

and P_i can be rewritten as well.

$$P_i = \frac{1-p_i^{d_i-1}}{1-p_i^{d_i}} p_i$$

This illustrates that the number of turtles in any group within a stage class decreases as a function of both the stage-specific annual survival probability and the number of years spent within that specific stage. Similarly, G_i, the proportion of turtles that survives and grows into the next stage class is estimated by using the proportion of individuals in the oldest group of the stage and multiplying by the annual survival rate for that stage.

$$G_i = \frac{p_i^{d_i-1}}{1+p_i+p_i^2+\ldots+p_i^{d_i-1}} p_i$$

By again rewriting the geometric series, G_i can also be simplified to

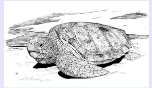
$$G_i = \frac{P_i^{d_i}(1-p_i)}{1-P_i^{d_i}}$$

.

6. The Loggerhead Population Matrix

The Lefkovitch stage class population matrix has the following form.

$$\begin{pmatrix} P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{pmatrix} \qquad (1)$$



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In the Lefkovitch matrix (1), F_i is the stage-specific fecundity, P_i is the probability of surviving and remaining in the same stage, and G_i is the probability of surviving and growing into the next stage class. When the data found previously is inserted, the stage class population matrix for Loggerhead sea turtles is represented by matrix (2).

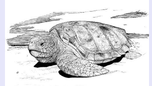
$$\begin{pmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747 & 0.7370 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6610 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & .8091 & 0.089 \end{pmatrix} \tag{2}$$

7. Population Projections

The power method was then used to take successively higher powers of matrix (2) and then postmultiplying by the projection vectors until the vectors which resulted differed by only a scalar factor.

This scalar factor was in fact equal to λ_m, which is the dominant eigenvalue of matrix (2). The resultant vector was proportional to the right eigenvector, w. This dominant eigenvector is equal to the stable stage distribution, meaning that it is the proportion of individuals in the specific age class at that time. By using the same process of taking successively higher powers and then postmultiplying the transpose of matrix (2), one can also find the left eigenvector v. This vector v is the reproductive value, given in Table 2.

By comparing λ_m, the dominant eigenvalue 0.9450, and r, our intrinsic rate of increase which equals -0.0565, to Frazer's estimates of $\lambda_m = 0.9719$ and $r = -0.0285$, we can confirm that the seven-stage matrix technique that we've used has successfully and accurately represented the population recorded by Frazer in Table 1. As shown in Table 1, reproductive values for the first three stages of life are low, then much higher for the fourth stage, and then dramatically higher for the fifth, sixth, and seventh stages.



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Stage Class	Stable stage Distribution	Reproductive values
eggs/hatchlings	20.65	1.00
small juveniles	66.975	1.40
large juveniles	11.46	6.00
subadults	0.66	115.845
novice breeders	0.04	568.78
1st year remigrants	0.03	507.37
mature breeders	0.18	597.67

Table 2: Stable stage distribution and reproductive values.

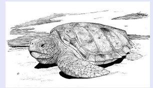
Stage Number	Altered Growth Rate
1	-0.04
2	0.033
3	0.11
4	0.04
5	-0.04
6	0.04
7	0.02

Table 3: Impact of various stages when their survival is set to 100 percent individually.

8. Sensitivity Analysis

Having constructed a population matrix, it is now possible to easily test the sensitivity of population growth rates to changes in fecundity, mortality, and survival rates by simulating changes in those parameters. One can simulate the same proportional change for each stage class and then compare the relative effect by calculating each λ_m, and then r of each new matrix. When survival is set to 100 percent for each stage individually, we find that stages three and four have the greatest effect on overall population growth. As illustrated in Table 3.

This means that increasing survival rates of stages three and four would be the most ap-



propriate focus of conservation. But not only does this data show where to focus conservation efforts for greatest effect, it also shows that even if 100 percent of all eggs and hatchlings where to survive, this alone would not stop the decline of the loggerhead sea turtle population. Previous efforts had been focused on this stage (nest protection), and as we can see, this is not necessarily the best use of time and money.

9. Conclusion

The Leslie and Lefkovitch matrix population projection techniques are useful in many studies of biology involving populations which can be divided into either age classes or stage classes, respectively. By finding eigenvalues and eigenvectors of special matrices, it is possible to test sensitivity of different life stages in a population to change in either mortality or survival rates.

By applying these same Linear Algebra techniques to the study of Loggerhead Sea Turtles, it was possible to find that change in the first stage (eggs) was not as effective as change in the second and third stages. The second and third stages caused a much larger decrease of λ_m and in turn a much larger decline in the population's growth rate. This can be interpreted also to mean that positive change in the most sensitive life stages, the second and third, will most effectively reverse the current decline in populations, meaning that although it is good to protect eggs, it's better to protect small and large juveniles, as adjustments in their numbers most greatly affect how many adult turtles will survive to breed in the future.

The specific example of the Loggerhead Sea Turtle shows how powerful the Lefkovitch stage based population modelling technique is. We have used this method to determine where to focus conservation efforts, a real world application of linear algebra. This method was actually used as is described in this paper by biologists to stabilize the population of Loggerheads in Florida. Lefkovitch's methods may have saved a species from extinction, shaping the world around us.

References

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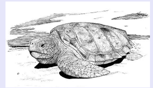

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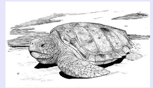

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