Abstract

In order to have an adequate program for the protection of various threatened species, there must be a thorough understanding of population dynamics. Many management groups are unaware of such an important need. Those that are uninformed have incorrect perceptions about conservation methods and how they affect the species they are dealing with. Our goal is to identify the most critical parameters for understanding the general population of the loggerhead sea turtles (*Caretta caretta*). Using a Lefkovitch stage class matrix model, we can refine our practices to more accurately project the sensitive areas in which populations are affected. Through the comprehension of these important findings, better management practices can be designed to further encourage turtle populations to flourish.
1. Introduction

The human population’s increasing numbers threaten many species each day. Our consumption of resources and daily practices affect the habitats and routines of all classes of animals. Many have dedicated their lives to the study and practice of conservation for these endangered groups. Various laws, programs, and agencies incur the practices of conservation to strengthen almost extinct populations. These institutions have a profound impact on the natural world and its ability to withstand the carelessness of everyday human life.

On the other hand, many of the aforementioned methods (which are well intended) yield insufficient protection practices. The reason for this is a lack of understanding regarding the implications of certain efforts. For example, many rely on certain programs’ ease of implementation such as accessibility to certain age groups or life stages of the species. Past programs for conserving turtle populations focused on the eggs and nests as the culmination of their efforts. The nests are easily monitored and protected. But it seems efforts that pertain solely to egg protection will not ultimately secure the entire species. Hence, the poor understanding of populations as a whole inhibits their goals.

The Leslie and Lefkovitch matrix models give us a way to quantitatively understand the population data given to us. Using these models, we will explore various stimuli which affect the growth and maturation of the loggerhead sea turtle population. We will then be able to utilize the various results yielded by these stimuli and develop possibilities for future management of the species in question.
2. Stage Class Models

2.1. Leslie Model

The matrices that we will utilize in determining population dynamics are the Leslie matrix and the Lefkovitch matrix. These matrices are modeled for each stage of life that corresponds to the species studied (which in this case is the loggerhead sea turtle). The first of these is the Leslie population model. Its classes are divided into reproductive cycles (which is usually one year), and it is actually the more general model in that it doesn’t take into account the variables associated with a species survival. The system has the form of

\[ An_t = n_{t+1} \]

where \( n_t \) gives the population of individuals in a particular life stage \( t \) and \( n_{t+1} \) is the population of the next stage.

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

The \( s \) in this system denotes the number of particular age classes. The Leslie model equally partitions the entire population according to age. The matrix \( A \) is what is known as the population projection matrix which incorporates the intrinsic survival rates of any given age for any time period. It contains three distinct types of rates: fecundity or birth rate (\( F_i \)), survival in a stage (\( P_i \)) and growth (\( G_i \)). This matrix then projects the rates of a given age onto the individuals, leading us to an understanding of our new population.
2.2. Lefkovitch Model

The Lefkovitch model does not correlate its classes to any particular age group. Instead, it was devised under the assumption that its classes have identical rates for fecundity, mortality and growth. This model can be used to project itself onto the population vector of any given species. Our model

\[ N_t = N_0 e^{rt} \]

contains the eigenvalue \( \lambda_m = e^r \) where \( r \) equals the natural rate of the increase in a population. \( N_t \) is equated to the original population \( N_0 \) multiplied by \( \lambda_m \). The population will remain at a stable size if \( \lambda_m = 1 \); thus when \( r = 0 \) or the rate of increase is zero, the population remains stable.

\[
N_t = N_0 \lambda^t \\
= N_0 (e^r)^t \\
= N_0 (e^0)^t \\
= N_0 (1) \\
= N_0
\]

If an environment remains constant, then the population of individuals in all stages will reach a stable point. There exists a right eigenvector \( w_m \) that multiplies the general matrix \( A \) (from the Leslie model) to create that unchanging distribution.

\[ A w_m = \lambda_m w_m. \]

The matrices considered would reach the equilibrium point \( w_m \) with each stage increasing by \( \lambda_m \). The reproductive rate of a given stage is stated in the left eigenvalue \( v' \) such that

\[ v' A = v' \lambda_m. \]

These projection yield the expected amount of reproduction in all stages (fecundity).
2.3. Comparison

The two models obviously have differences in the way they project a population. The Leslie model is based strictly on age; the Lefkovitch model has classes that differ in length (or the duration of each class) and the amount of individuals in each class. Hence, the Lefkovitch model seems like a more accurate choice for our goal. This model is less rigid which is valuable since it parallels the dynamics of populations.

3. Theoretical Projections

In order to have a working model for our projection, we need enough data to calculate the rates $F_i$, $P_i$, and $G_i$. Our data will come from the study of *caretta caretta* on Little Cumberland Island (LCI), Georgia. Over the course of a twenty year study, sufficient data was collected to let us prepare our model. The stages (delineated in Frazer’s life tables and the corresponding work done on LCI) relate to the given size (in centimeters) of an individual. These sizes are then grouped into age ranges (based on previously calculated growth curves); the divisions range from hatchlings to subadults to mature breeders (seven total stages).

3.1. Calculating the Rates

The three rates discussed include these: fecundity ($F_i$), the probability of survival and stage advancement ($G_i$), and the probability of survival while remaining in a particular stage ($P_i$). The first of these, the fecundity rate $F_i$ of each stage, is found in column 6 of table 1 (see below).

The rates $G_i$ and $P_i$ can be found from the probability of survival in each stage $p_i$ (column 5, table 1) and the stage length $d_i$ (column 4, table 1). We are working under the assumption that these probabilities are constant within each stage since little is
known about the survival and growth rates within a stage. When more accurate data is available we can easily insert it into our model.

\subsection{G \textsubscript{i} Survival and Stage Advancement}

First we will calculate the initial total growth rate $G_i$ by determining the probability of those that will advance to the next stage. In a given stage, individuals exist for a duration of $1, 2, \ldots, d_i$ years. We can state that the proportion of individuals in a stage $i$ within the first time period equal to 1. Also, the probability of survival to the next time period is $p_i$; it follows that the probability for surviving $d$ years is given as $p_i^{d_i}$.

Let our first group within a given stage $i$ contain all individuals that have survived from 1 to $d_{i-1}$ years. This represents the cohorts of a stage that exist, but those having lived to $d_{i-1}$ years can potentially advance. Thus we see that the total probability for the whole stage is equal to

$$1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}$$ (1)
With these key facts in mind, let us assume that stages themselves are stable (meaning that the population and age distribution remain constant). As the time interval increases, the oldest members of a stage move to the next stage; \( p_d \) is the final cohort within a life stage, so individuals can only advance from this point. Then the relative population in each cohort within a stage becomes \( 1, p_i, p_i^2, \ldots, p_i^{d_i-1} \). Therefore, the younger individuals remain in stage \( i \).

Let the oldest cohort that has the potential to advance in a given stage be \( p_i^{d_i-1} \). Then the proportion of all individuals in one stage that are eligible to advance is equal to the fraction

\[
\frac{p_i^{d_i-1}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}}
\]  

(2)

where the numerator represents the proportion of individuals that are eligible to advance and the denominator represents the entire group. When we hit this expression with the stage specific probability \( p_i \) it gives us the total proportion that actually advances (whereas before it was only those who were eligible). Therefore, the probability of surviving a stage and advancing to the next is equal to our initial expression (2) multiplied by \( p_i \).

\[
G_i = \left( \frac{p_i^{d_i-1}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}} \right) p_i
\]  

(3)

Rewriting this geometric series yields the final result

\[
G_i = \frac{p_i^{d_i}(1 - p_i)}{1 - p_i^{d_i}}
\]

which is the probability of both surviving and advancing through a stage.
3.3. $P_i$ Survival Rate

Next we will calculate our survival rate $P_i$ that keeps individuals in their respective stages. Individuals that have survived from 1 to $d_i-2$ years are not yet eligible to advance (since only those having lived to $d_i-1$ years have the potential to advance).

Working from our $G_i$, we know that the equation

$$G_i = \left( \frac{p_i^{d_i-1}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}} \right) p_i$$ \hspace{1cm} (4)

gives us the survival of those eligible to advance. If $p_i^{d_i-1}$ is those eligible to advance, then we can conclude that those ineligible to advance is the entire rest of the stage. So when we compare the number of those eligible to remain in the class

$$1 + p_i + p_i^2 + \ldots + p_i^{d_i-2}$$ \hspace{1cm} (5)

to our entire stage survival probability

$$1 + p_i + p_i^2 + \ldots + p_i^{d_i-2} + p_i^{d_i-1}$$ \hspace{1cm} (6)

and then hit this expression with its stage specific survival rate $p_i$ we get the actual percentage of those that survive and remain in a class. The resultant equation for $P_i$ is

$$P_i = \left( \frac{1 + p_i + p_i^2 + \ldots + p_i^{d_i-2}}{1 + p_i + p_i^2 + \ldots + p_i^{d_i-1}} \right) p_i$$ \hspace{1cm} (7)

where the numerator is the survival rates of those eligible to continue survival and the denominator represents the total survival within a class, and these are multiplied throughout with another survival rate. This gives us the actual percentage of those who continue to survive from those that were eligible. If we simplify by rewriting the geometric series $1+p + p^2 + \ldots + p^{d-1}$ as $(1 - p^d)/(1 - p)$, then $P_i$ becomes
As you can see, the amount of each class depends on the stage-specific survival rate and the years spent in a stage.

3.4. Loggerhead Population Matrix

We can now use the probabilities that were calculated to set up our system. The individuals in a given class are calculated by the rates $F_i$, $P_i$, and $G_i$. The population of eggs/hatchling (class $i = 1$) in a given time period $t + 1$ can be expressed as the sum of all births and the surviving members of their class. We can write this sum as

$$n_1^{(t+1)} = P_1n_1^{(t)} + F_2n_2^{(t)} + F_3n_3^{(t)} + \ldots + F_7n_7^{(t)}$$

which gives us the total amount of individuals in time period $t + 1$ from period $t$. Since no one can be born into any stage but the first, this is the only equation which involves the fecundity $F_i$.

The populations of our second through seventh classes can be found by adding all surviving members (in their respective classes). The number of survivors comes from our survival rates $P_i$ and $G_i$. In short, the total number of individuals in any class except class 1 ($i = 2, 3...7$) is given as

$$n_i^{(t+1)} = G_{i-1}n_i^{(t)} + P_in_i^{(t)}.$$ 

So for any $i$ value greater than 1, this equation gives the population of survivors in the class. We substitute values of $i$ into our equation and place them in a matrix, with the equations corresponding to stages they relate to. These equations are put into matrix
The combination of the columns with respect to the population will give us the expected population of the next time period. When we post-multiply this matrix by our population vector \( n_t \)

\[
\begin{pmatrix}
P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\
G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\
0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\
0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\
0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\
0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\
0 & 0 & 0 & 0 & 0 & G_6 & P_7 \\
\end{pmatrix}
\]

(8)

The combination of the columns with respect to the population will give us the expected population of the next time period. When we post-multiply this matrix by our population vector \( n_t \)

\[
\begin{pmatrix}
P_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\
G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\
0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\
0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\
0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\
0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\
0 & 0 & 0 & 0 & 0 & G_6 & P_7 \\
\end{pmatrix}
\begin{pmatrix}
n_1 \\
n_2 \\
n_3 \\
n_4 \\
n_5 \\
n_6 \\
n_7 \\
\end{pmatrix}
\]

\[=\]

\[
\begin{pmatrix}
n_1 \\
n_2 \\
n_3 \\
n_4 \\
n_5 \\
n_6 \\
n_7 \\
\end{pmatrix}_{t+1}
\]

\[
t+1
\]

to give the result \( n_{t+1} \), which is our new population of turtles after one iteration of our model (see Figure 1). Inserting the calculated stage specific survival rates into our general matrix model,
We now have a way to project our population model many years into the future, which will be valuable in understanding how the population can be effected by the tiniest details in the long run.

### 3.5. Stable Stage Distribution

As previously mentioned, our matrix model will, after a certain amount of iterations, will reach a stable stage distribution such that the resulting population vector is some scalar multiple on the initial population $w$:

$$Lw_m = \lambda_m w_m$$

where $L$ is our matrix (8) that includes the rates $F_i$, $P_i$ and $G_i$.

In order to find out what our population looks like after many iterations, we must take higher powers of the matrix $L$. For example, our population after 100 years would involve $L^{100}$. This can be quite tedious. We make this easier by factoring this matrix into $L = V\Lambda V^{-1}$, where matrix $V$ contains the eigenvectors of $L$ and $\Lambda$ contains the eigenvalues. With this in mind, our population to the $k$th iteration is equal to $L^k$.

$$\vec{x}^k = L^k \vec{x}_0$$
Since $L$ can be diagonalized, $\vec{x}^k$ can be written as

$$\vec{x}^k = (V \Lambda^k V^{-1}) \vec{x}_0.$$ 

If we label the multiplication $V^{-1} \vec{x}_0$ as $\vec{c}$, then our population vector takes the form

$$\vec{x}^k = c_1 \lambda_1^k \vec{v}_1 + \cdots + c_n \lambda_n^k \vec{v}_n$$

which is a linear combination of the columns of our diagonalized $L$. 

Figure 1: A Steady Decline.
Figure 2: The Stable Stage Distribution.
As we can see, only the eigenvalues are subject to the exponent $k$. This takes much less work to compute than calculating $L^k$. We can conclude that if any of the eigenvalues are less than one, then they will go to zero when taken to higher powers (or high values of $k$). Therefore, any eigenvalues greater than one will remain, making them our dominant eigenvalues. This causes our population vector to be just a scalar factor of the dominant eigenvalue and eigenvector pair.

$$\vec{x}^k \approx c\lambda^k \vec{v}$$ \hspace{2cm} (9)

4. Results

Now we can change the parameters of $F_i$, $P_i$ and $G_i$. This will allow us to see which rates from which classes have the greatest effect on the population. We can use our model to project any effects on the population from our altered parameters. This in turn gives us a stable stage distribution and we can easily weigh the effects of changing the survival of any given class $i$.

We can alter any of the three rates discussed. However, realistically it would be improbable to alter the birth rate of a given class. Also, growth is more important to the population as a whole versus stage survival (which affect one stage). So our goal is to see how growth affects our population. By setting $G_i$ to one or 100% (which is to say that everyone in class $i$ survives and advances) we can easily see the effects garnered by this change. In table 2, we see the effect of setting our $G_i$ values to one for each stage individually; we can see that stages 2, 3 and 4 have some eigenvalues greater than one. These are the dominant eigenvalues.

In equation (9) we stated that the population is proportional to its dominant eigenvalue. Since any eigenvalues less than one will go to zero when taken to significant powers, only the eigenvalues greater than one will give us an increasing population (or stability when our dominant eigenvalue is equal to one). As we can see, the only eigen-
values greater than one can be found in stages 2, 3 and 4; thus these are the stages that have the potential to see an increase in population.

After several projections, it became clear that stage 3 had the most profound impact on the population as a whole. After setting $G_3 = 1$ we obtained a population projection (see Figure 3) that grew exponentially faster than any of our other projections.

Setting the growth rate to 100% is just unfeasible as attempting to change the fecundity. As a result, we began making projections with different values of $G_3$ ranging from 2.5% to 100%. We found that 4% resulted in a stable population projection (Figure 4) which makes this the minimum target value for conservation efforts. Anything above that minimum target value will result in an increasing population (Figure 5).

5. Conclusion

The goal of our projection model was to understand the effects of any stage class on the population as a whole. If one class has a greater effect on the entire species survival, then conservation methods can be applied more rigorously to that specific class. After

<table>
<thead>
<tr>
<th>$G_i = 1$</th>
<th>$\lambda_1$</th>
<th>$\lambda_2$</th>
<th>$\lambda_3$</th>
<th>$\lambda_4$</th>
<th>$\lambda_5$</th>
<th>$\lambda_6$</th>
<th>$\lambda_7$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial</td>
<td>-0.095</td>
<td>-0.095</td>
<td>0.314</td>
<td>0.314</td>
<td>0.753</td>
<td>0.753</td>
<td>0.953</td>
</tr>
<tr>
<td>Stage 1</td>
<td>-0.100</td>
<td>-0.100</td>
<td>0.317</td>
<td>0.317</td>
<td>0.750</td>
<td>0.750</td>
<td>0.963</td>
</tr>
<tr>
<td>Stage 2</td>
<td>-0.230</td>
<td>-0.230</td>
<td>0.320</td>
<td>0.320</td>
<td>1.16</td>
<td>0.778</td>
<td>0.778</td>
</tr>
<tr>
<td>Stage 3</td>
<td>-0.320</td>
<td>-0.320</td>
<td>1.30</td>
<td>0.791</td>
<td>0.791</td>
<td>0.336</td>
<td>0.336</td>
</tr>
<tr>
<td>Stage 4</td>
<td>-0.225</td>
<td>-0.225</td>
<td>0.320</td>
<td>0.320</td>
<td>1.15</td>
<td>0.775</td>
<td>0.775</td>
</tr>
<tr>
<td>Stage 5</td>
<td>-0.090</td>
<td>-0.090</td>
<td>0.314</td>
<td>0.314</td>
<td>0.753</td>
<td>0.753</td>
<td>0.953</td>
</tr>
<tr>
<td>Stage 6</td>
<td>-0.095</td>
<td>-0.095</td>
<td>0.314</td>
<td>0.314</td>
<td>0.753</td>
<td>0.753</td>
<td>0.953</td>
</tr>
</tbody>
</table>
significant amounts of projection research, we have concluded that current conservation methods are indeed focused stages that do not significantly contribute to population growth. Small juveniles, large juveniles, and subadults (stages 2, 3, and 4) have a much greater effect on the Loggerhead Sea Turtle population than hatchlings; therefore, we suggest that conservation efforts focus on these three classes rather than waste time and resources on protecting classes that do not dramatically increase the population.
Figure 4: Population stable at $G_3 = 4\%$. 
Figure 5: Population shows substantial growth at $G_3 = 5\%$. 
References


   
   *http://en.wikipedia.org/wiki/Loggerhead_Sea_Turtle*
