# Math 636 - Mathematical Modeling

## Age-Structured Models

Joseph M. Mahaffy,
⟨jmahaffy@mail.sdsu.edu⟩

Department of Mathematics and Statistics
Dynamical Systems Group
Computational Sciences Research Center
San Diego State University
San Diego, CA 92182-7720

http://jmahaffy.sdsu.edu

Fall 2018





## Outline







## Leslie Models 1

**Leslie Models**: Earlier examined discrete models combining all members of the population in a single group.

- Reproduction and survival depend highly upon age.
- Improved population models include some *age-structure* in the model.
- The simplest *age-structured model* is the ***Leslie model*** (Patrick H. Leslie (1900-1974)), developed in the 1940s.
- This ***discrete population model***, in which the population of one sex (usually females) is divided into *discrete age classes*.
- The population is closed to migration and only considers *births* and *deaths* amongst the ages classes or life stages.
- This model studies the growth of a population and determines the relative size of each of the age classes.





## Leslie Models 2

**Leslie Models**: The population, $\mathbf{X}_n$, is a vector, which varies discretely in time.

- Let $L$ be the Leslie matrix with $\mathbf{X}_n = [x_1, x_2, ..., x_m]_n^T$, the population vector at time $n$ divided into $m$ age classes, then the Leslie model is:

$$\mathbf{X}_{n+1} = L\mathbf{X}_n.$$

- Let $b_i$ be the *per capita birth rate* of the $i^{th}$ class into the first class, and $s_i$ be the *survival rate* of individuals of class $i$ at time $n$ into class $i+1$ at time $n+1$, then the ***Leslie matrix*** takes the form:

$$L = \begin{pmatrix} b_1 & b_2 & b_3 & \cdots & b_m \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & \ddots & & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & s_{m-1} & s_m \end{pmatrix}.$$

- $s_m = 0$ if the older classes not considered in the population or all the population dies after class $m$.
- The survival $s_m \neq 0$, if the oldest class includes all the oldest individuals past the age class of $m-1$.

## Analysis of the Leslie Model 1

**Analysis of the Leslie Model**: Assume that the matrix $L$ has a complete set of ***eigenvalues***, $\lambda_i$, $i = 1, ..., m$ with associated eigenvectors, $\xi_i$ spanning $\mathbb{R}^m$, then the ***initial population*** can be written:

$$\mathbf{X}_0 = \sum_{i=0}^{m} c_i \xi_i,$$

for some constants, $c_i$.

The ***Leslie model*** gives:

$$\mathbf{X}_1 = L\mathbf{X}_0 = \sum_{i=0}^{m} c_i \lambda_i \xi_i,$$

The ***Leslie model*** follows a ***Markov process***, so the $n^{th}$ population, $\mathbf{X}_n$, is given by:

$$\mathbf{X}_n = L^n \mathbf{X}_0 = \sum_{i=0}^{m} c_i \lambda_i^n \xi_i, \qquad n = 1, ...$$





## Analysis of the Leslie Model 2

**Analysis of the Leslie Model**: Assume that the ***Leslie matrix***, $L$, has a ***single dominant eigenvalue***, $\lambda_1$.

If

$$|\lambda_1| > \max_{i=2,..,m} |\lambda_i|,$$

then for $n$ sufficiently large $|\lambda_1|^n \gg |\lambda_i|^n$ for $i = 2, ..., m$.

Asymptotically, it follows that

$$\mathbf{X}_n \simeq c_1 \lambda_1^n \xi_1.$$

It follows that the ***population grows*** or ***decays*** much like a ***Malthusian growth model*** with the exponential growth, $\lambda_1$ and the age classes having a distribution of $\xi_1$.





## Example of U. S. Population Growth 1

**Example of U. S. Population Growth**: The female population is divided into **3** age groups of 20 years.

A detailed study of these age groups give the fertility of each group and the survival of each age group.

Let $x_1$ represent females age 0-20, $x_2$ represent females age 20-40, and $x_3$ represent females age 40-60, then a ***Leslie model*** for the dynamics of these age classes in the U. S. is given by:

$$\begin{pmatrix} x_1(n+1) \\ x_2(n+1) \\ x_3(n+1) \end{pmatrix} = \begin{pmatrix} 0.4271 & 0.8498 & 0.1273 \\ 0.9924 & 0 & 0 \\ 0 & 0.9826 & 0 \end{pmatrix} \begin{pmatrix} x_1(n) \\ x_2(n) \\ x_3(n) \end{pmatrix}.$$





## Example of U. S. Population Growth 2

**Example (cont)**: The ***Leslie matrix*** satisfies:

$$L = \begin{pmatrix} 0.4271 & 0.8498 & 0.1273 \\ 0.9924 & 0 & 0 \\ 0 & 0.9826 & 0 \end{pmatrix}.$$

The ***Leslie matrix*** implies:

- The typical female age 0-20 produces 0.4271 female offspring in a twenty year period.
- The typical 20-40 year old females produce the most female offspring (peak fertility) with a per capita rate of 0.8498
- Females age 40-60 have significantly fewer female offspring at only 0.1273 per woman in those older years.
- Survival rate to successive classes is very high with 0-20 year olds having a 99.24% chance of making it into the 20-40 age group
- The 20-40 year olds having a 98.26% chance of surviving into the 40-60 year old age class.
- This model ignores the contribution of any female over 60 (though it would not be hard to include them in a 40 and older class and not have the $L_{33} = 0$).

## Example of U. S. Population Growth: Analysis

**Analysis of Example**: An *eigenvalue analysis* of the *Leslie matrix*, $L$, gives:

$$\lambda_1 = 1.2093, \qquad \lambda_2 = -0.6155, \qquad \text{and} \qquad \lambda_3 = -0.1668.$$

- The *dominant eigenvalue* is $\lambda_1 = 1.2093$, which implies that the population growth is approximately 21% in a twenty year period.
- This is consistent with the *Malthusian growth rate* obtained earlier for the U. S. population from the census data in the latter part of the $20^{th}$ century.
- The *normalized eigenvector associated* with $\lambda_1$ is

$$\xi_1 = [0.4020, 0.3299, 0.2681]^T.$$

- This shows that the current distribution of females should be approximately 40.2% in the 0-20 age group, 33% in the 20-40 age group, and 26.8% in the 40-60 age group.
- From the U. S. Census Bureau, the data from 2010 gives the current distribution of females as 33.5% in the 0-20 age group, 34.5% in the 20-40 age group, and 32.0% in the 40-60 age group (with these classes composing 79.8% of all women in the country).
- What causes the discrepancies between the Leslie model and the actual data?





## Example of Loggerhead Turtles 1

**Loggerhead Turtles**: Crowder [1] used a modified version of the Leslie matrix model to predict the impact of turtle excluder devices (TEDs) on the populations of *loggerhead sea turtles*.

- Crowder *et al.* updated an earlier model to examine how enforcing the use of TEDs might impact the *loggerhead sea turtle* population.
- Studies have shown TEDs can be up to 97% effective in preventing mortality of large turtles.
- A high percentage of dead sea turtles on beaches can be shown to have died from shrimp fishing with nets.
- Crowder *et al.* used a ***stage-based population model***, which is closely related to ***Leslie models***.
- ***Model analysis*** showed different scenarios, which could result in population recoveries of this vanishing species.

[1] Larry B. Crowder, Deborah T. Crouse, Selina S. Heppell, and Thomas H. Martin, (1994) Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Populations, *Ecological Applications*, **4**, 437-445.





## Example of Loggerhead Turtles 2

**Loggerhead Turtles**: The earlier model of Crowder *et al.* was a detailed study of data on *loggerhead sea turtles*.

- The study carefully measured survivorship and fecundity of different age groups of *loggerhead turtles*.
- The original model had **7** age groups, which were reduced to **5** age groups.
- Adult turtles lay their eggs on sandy beaches.
- Only about 1% of turtles surviving the first year reach sexual maturity around age 20 and can reproduce.
- Much of their life cycle remains a mystery, complicating conservation efforts.





## Example of Loggerhead Turtles 3

**Loggerhead Turtle Example**: The model is based on a **5** *stage-classified model*:

$$\mathbf{X}_{n+1} = A\mathbf{X}_n,$$

with

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

where $P_i$ is the probability of surviving and remaining in the same stage, $G_i$ is the probability of surviving and growing to the next stage, $F_i$ is the stage-specific reproductive output, and $n$ is in years.

$\mathbf{X}_n$ gives **5** stages of turtle development:

| Stage | Description | Duration (yrs) |
|---|---|---|
| 1 | Eggs/hatchlings | 1 |
| 2 | Small Juveniles | 7 |
| 3 | Large Juveniles | 8 |
| 4 | Subadults | 6 |
| 5 | Adults | $> 22$ |

## Example of Loggerhead Turtles



**Loggerhead Turtle Example**: The **5** ***stage-classified model*** from the data gives:

$$\mathbf{X}_{n+1} = \begin{pmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{pmatrix} \mathbf{X}_n,$$

which shows the primary reproduction is from adult turtles, and the adult turtles have a fairly high survivorship.

As with the ***Leslie model***, the ***eigenvalues*** and ***eigenvectors*** are found with the ***dominant eigenvalue*** and its ***normalized eigenvector*** being:

$$\lambda_1 = 0.9516 \qquad \text{and} \qquad \xi_1 = \begin{pmatrix} 0.2385 \\ 0.6477 \\ 0.1033 \\ 0.007284 \\ 0.003118 \end{pmatrix}.$$

This model suggests a **5% decline** in population each year.



Leslie Models | U. S. Population Model | Loggerhead Turtles

## Example of Loggerhead Turtles

4

**Loggerhead Turtle Example**: If the TEDs could increase ***survivorship*** of larger turtles by 20%, then the **5** ***stage-classified model*** becomes:

$$\mathbf{X}_{n+1} = \begin{pmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.719 & 0 & 0 \\ 0 & 0 & 0.021 & 0.723 & 0 \\ 0 & 0 & 0 & 0.071 & 0.847 \end{pmatrix} \mathbf{X}_n.$$

This ***stage-classified model*** has a ***dominant eigenvalue***, $\lambda_1$, and its ***normalized eigenvector*** being:

$$\lambda_1 = 1.00854 \qquad \text{and} \qquad \xi_1 = \begin{pmatrix} 0.2714 \\ 0.5995 \\ 0.1168 \\ 0.008588 \\ 0.003774 \end{pmatrix}.$$

This model suggests a **slight increase** in population each year.