

# Math 636 - Mathematical Modeling

## Age-Structured Models

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# Outline

- 1 Leslie Models
  - U. S. Population Model
  - Loggerhead Turtles

**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

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

- Let  $L$  be the Leslie matrix with  $\mathbf{X}_n = [x_1, x_2, \dots, x_m]^T$ , 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  $i^{\text{th}}$  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

**Analysis of the Leslie Model:** Assume that the matrix  $L$  has a complete set of *eigenvalues*,  $\lambda_i$ ,  $i = 1, \dots, m$  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  $n^{\text{th}}$  population,  $\mathbf{X}_n$ , is given by:

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

## Analysis of the Leslie Model

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

If

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

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

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

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**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

**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:

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

- 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<sup>th</sup> 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

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**Loggerhead Turtles:** Crowder <sup>1</sup> 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.

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<sup>1</sup>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

**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

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

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

with

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

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:

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

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

## Example of Loggerhead Turtles

**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:

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

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