The Leslie Matrix and Population Change

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What is a Leslie Model?

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- A model for the growth of *female* portion of a population
- Age classes of *equal* duration
- Developed in 1941

What is a Leslie Model?

- **L** = Maximum age attained by any female,
  m = number of age classes:

Age Class	**Age Interval**
1	[0, L/m)
2	[L/m, 2L/m)
3	[2L/m, 3L/m)
...	...
m-1	[(m-2)L/m, (m-1)L/m)
m	[(m-1)L/m, L)

Table: Labeling of The Age Classes

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Population Growth Factors

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Remark

1. $n_{i+1,k} = s_i n_{i,k-1};\ i = 1, \ldots, m-1$
2. $n_{1,k} = b_1 n_{1,k-1} + b_2 n_{2,k-1} + \ldots + b_m n_{mk-1}$

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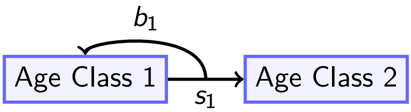
Life-cycle Graph

$$\boxed{\text{Age Class 1}} \xrightarrow[s_1]{} \boxed{\text{Age Class 2}}$$

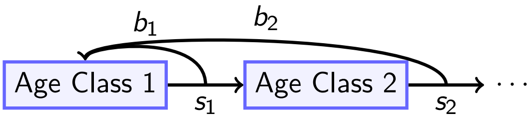
Life-cycle Graph



Life-cycle Graph

$$\boxed{\text{Age Class 1}} \xrightarrow[s_1]{} \boxed{\text{Age Class 2}} \xrightarrow[s_2]{} \cdots$$

Life-cycle Graph



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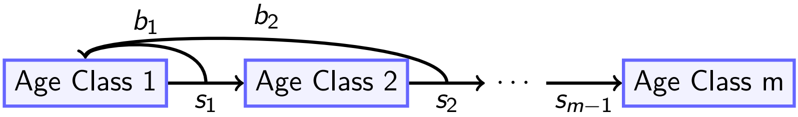

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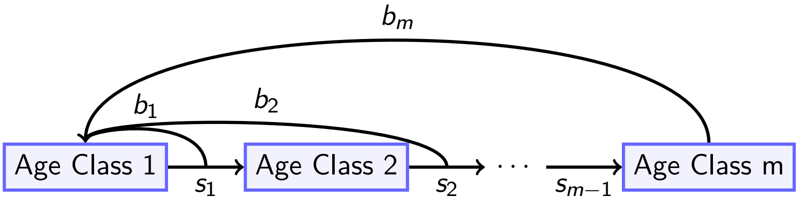

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Leslie Matrix

$$\mathbf{N_k} = \begin{bmatrix} n_{1,k} \\ n_{2,k} \\ n_{3,k} \\ \vdots \\ n_{m,k} \end{bmatrix} = \begin{bmatrix} b_1 & b_2 & b_3 & \cdots & b_{m-1} & b_m \\ s_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & s_{m-1} & 0 \end{bmatrix} \begin{bmatrix} n_{1,k-1} \\ n_{2,k-1} \\ n_{3,k-1} \\ \vdots \\ n_{m,k-1} \end{bmatrix} = \mathbb{L}\mathbf{N_{k-1}}$$

Leslie Matrix

Definition

$\mathbb{L}$ is the **Leslie Matrix** and summarizes the information necessary to describe the growth of the population.

$$\mathbb{L} = \begin{bmatrix} b_1 & b_2 & b_3 & \cdots & b_{m-1} & b_m \\ s_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & s_{m-1} & 0 \end{bmatrix}$$

Dependence on Initial Conditions

- $k = 1$:

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Leslie Equation

$$\mathbf{N_k} = \mathbb{L}\mathbf{N_{k-1}} = \mathbb{L}^k\mathbf{N_0}$$

Challenges of Computing $\mathbf{N_k}$

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- High computational cost of computing $\mathbb{L}^k$
- Exact description of the population at a given time instead of the general trend of the population

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Definition

Eigenvalues are the values λ for which $\mathbb{L}x = \lambda x$ for some vector $x \neq 0$.

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Eigenvalues of the Leslie Matrix:

$$\det(\mathbb{L} - \lambda \mathbb{I}) = \lambda^m - b_1\lambda^{m-1} - b_2 s_1 \lambda^{m-2} - b_3 s_1 s_2 \lambda^{m-3} - \cdots \\ - b_m s_1 \ldots s_{m-1} = 0$$

The Dominant Eigenvalue

With $\lambda \neq 0$:

$$\begin{aligned} q(\lambda) = & \frac{b_1}{\lambda} + \frac{b_2 s_1}{\lambda^2} + \cdots \\ & + \frac{b_m s_1 \ldots s_{m-1}}{\lambda^m} = 1 \end{aligned}$$

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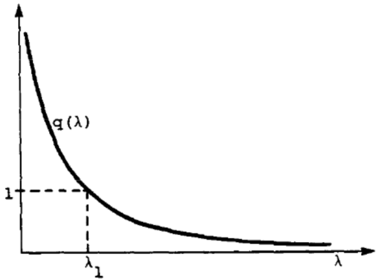

Figure: The only positive solution is $\boldsymbol{\lambda_1}$.

The Dominant Eigenvalue

Theorem

Perron Frobenius: *If all enteries of a $n \times n$ matrix A are positive, then it has a unique maximal eigenvalue. Its eigenvector has positive entries.*

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λ_1 is a simple root of $q(\lambda) = 1$.

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λ_1 is a simple root of $q(\lambda) = 1$.

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λ_1 is the dominant eigenvalue.

The Dominant Eigenvector

$$(\mathbb{L}-\lambda_1\mathbb{I})x_1=\begin{bmatrix} b_1-\lambda_1 & b_2 & b_3 & \cdots & b_{m-1} & b_m \\ s_1 & -\lambda_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & -\lambda_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & s_{m-1} & -\lambda_1 \end{bmatrix} x_1 = 0$$

The Dominant Eigenvector

Solution

$$x_1 = \begin{bmatrix} 1 \\ \frac{s_1}{\lambda_1} \\ \frac{s_1 s_2}{\lambda_1^2} \\ \vdots \\ \frac{s_1 s_2 \dots s_{m-1}}{\lambda_1^{m-1}} \end{bmatrix}$$

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Diagonalization of $\mathbb{L}$

For the matrix $\mathbb{L}$ with m distinct eigenvectors, we have:

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- A : an $m \times m$ diagonal matrix with the eigenvalues of L on the diagonal
- $\mathbb{S}$: the matrix with the eigenvectors of $\mathbb{L}$ as its columns

Computation of $\mathbb{L}^k$

An easy method for computing $\mathbb{L}^k$ with the help of diagonalization:

$$\mathbb{L}^2 = \mathbb{S}A\mathbb{S}^{-1}\mathbb{S}A\mathbb{S}^{-1} = \mathbb{S}A^2\mathbb{S}^{-1}$$

$$\mathbb{L}^k = \mathbb{S}A^k\mathbb{S}^{-1}$$

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$$\mathbb{L}^k = \mathbb{S}A^k\mathbb{S}^{-1}$$

Remark

Substituting $\mathbb{L}^k$ in $\mathbf{N_k} = \mathbb{L}^k\mathbf{N_0}$:

$$\mathbf{N_k} = \mathbb{S}A^k\mathbb{S}^{-1}\mathbf{N_0}$$

Dividing $\mathbf{N_k} = \mathbb{S}A^k\mathbb{S}^{-1}\mathbf{N_0}$ by λ_1^k:

$$\frac{1}{\lambda_1^k}(\mathbf{N_k}) = \mathbb{S}\begin{bmatrix} 1 & 0 & \cdots & 0 \\ 0 & \frac{\lambda_2^k}{\lambda_1^k} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \frac{\lambda_m^k}{\lambda_1^k} \end{bmatrix}\mathbb{S}^{-1}\mathbf{N_0}$$

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Limiting Behavior

By strict dominance of λ_1:

$$\lim_{k\to\infty} \frac{\lambda_i^k}{\lambda_1^k} = 0; i = 2, \ldots, m$$

Limiting Behavior

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- $\mathbb{S}^{-1}\mathbf{N_0}$: the only entry of importance is the first component which we call c.
- The product of the matrix $\mathbb{S}$ with the matrix next to it: the first column of $\mathbb{S}$, the eigenvector x_1.

An Approximation for $\mathbf{N_k}$

A good approximation of the population distribution for large values of k:

$$\lim_{k\to\infty} \mathbf{N_k} = \lim_{k\to\infty} \lambda_1^k c x_1$$

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- $\lambda_1 < 1$: The population is dying out.
- $\lambda_1 = 1$: The population is stable. (The popular term *Zero Population Growth*)

Net Production Rate

Definition

Net Production Rate:
The average number of daughters born to each female during her lifetime.

$$R := b_1 + b_2 s_1 + b_3 s_1 s_2 + \cdots + b_m s_1 \ldots s_{m-1}$$

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An Example

Example

1. Construct the Leslie matrix for a population of fish which live three age periods with $\frac{1}{2}$ surviving from the first to second period and $\frac{1}{3}$ from the second to the third. The 3 year-old females each produce 6 daughters.

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Solution

1. $$\mathbb{L} = \begin{bmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix}$$

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2. Find the eigenvalues and the dominant eigenvector of this matrix. What is the modulus of each eigenvalue?

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Solution

2.
$$\det(\mathbb{L} - \lambda\mathbb{I}) = -\lambda^3 + 1 = 0$$
$$\lambda_1 = 1, \lambda_2 = \frac{-1 + i\sqrt{3}}{2}, \lambda_3 = \frac{-1 - i\sqrt{3}}{2}$$
$$x_1 = \begin{bmatrix} 1 & \frac{1}{2} & \frac{1}{6} \end{bmatrix}^T, |\lambda_i| = 1, i = 1, 2, 3.$$

An Example

Example

3. Suppose the population has the initial distribution $\mathbf{N_0} = \begin{bmatrix} 100 & 100 & 100 \end{bmatrix}^T$. Find the population distributions $\mathbf{N_1}$ through $\mathbf{N_6}$. What do you notice? Can you draw any conclusions?

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Solution

3.
$$\mathbf{N_0} = \begin{bmatrix} 100 \\ 100 \\ 100 \end{bmatrix} = \mathbf{N_3} = \mathbf{N_6},$$

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Solution

3. $$\mathbf{N_1} = \begin{bmatrix} 600 \\ 50 \\ 33.3 \end{bmatrix} = \mathbf{N_4},$$

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Solution

3. $$\mathbf{N}_2 = \begin{bmatrix} 200 \\ 300 \\ 16.7 \end{bmatrix} = \mathbf{N}_5.$$

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Solution

3.
$$\mathbf{N_2} = \begin{bmatrix} 200 \\ 300 \\ 16.7 \end{bmatrix} = \mathbf{N_5}.$$

The population is oscillating every third time period.

References

[1] P. H. Leslie, *On the use of matrices in certain population mathematics*, Biometrika 35, 213-245, 1968.

[2] H. Anton, C. Rorres, *Elementary linear algebra with applications*, 11th ed., 673 (2014)

[3] Perron-Frobenius theorem