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### Leslie meets Prey and Predators: From Modeling to Research

#### Predator-Prey Modelling Group (SMALL 2024) Steven J Miller (Williams College, Fibonacci Association) Email: sjm1@williams.edu https://web.williams.edu/Mathematics/sjmiller/public\_html/

AMS Special Session on New Trends in Difference and Differential Equations: Modeling, Analysis, and Applications: Hartford, CT: April 6, 2025.

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Overview				

SMALL 2024 SUMMER REU: Strong students, varying backgrounds.

Pre-reqs: Calculus, linear algebra.

Springboard to research: combine / extend simple models.

Fibonacci Quarterly: Math Bio / Science Section.

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#### **Classical Predator-Prey Interactions**



(Illustration from Premium Vector)

• Lotka-Volterra model: Evolution of predator / prey system.

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#### The Lotka-Volterra Equations

#### Definition

Prey population x(t) and a predator y(t), evolve by

$$\begin{cases} \frac{dx}{dt} = \alpha x - \beta xy\\ \frac{dy}{dt} = \delta xy - \gamma y. \end{cases}$$

Reasonable: look at signs, products.



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#### Typical Dynamics of Lotka-Volterra



(Courtesy of Prof. Mats Vermeeren)

- Solutions often exhibit perpetual oscillations in both populations.
- Interplay inspired extensions and variations, including blending with Leslie matrices.

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#### Leslie Matrices

Idea: split population into sub-populations by age. Assume die when turn d;  $a_n^{(1)}$  number newborns at time n,  $a_n^{(2)}$  number of one-year-olds, ....

Population vector at time n:  $\vec{p_n} := \left(a_n^{(1)}, a_n^{(2)}, \dots, a_n^{(d-1)}\right)^T$ . Simple model: evolve by

$$\vec{p}_{n+1} := \mathbf{L}\vec{p}_n = \underbrace{\begin{bmatrix} f_1 & f_2 & \cdots & f_{d-1} \\ s_1 & 0 & \cdots & 0 \\ 0 & s_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & s_{d-2} \end{bmatrix}}_{\substack{\text{Leslie matrix:} \\ f_i \text{- fertility rates} \\ s_i \text{- survival rates}}} \vec{p}_n,$$

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#### Example (3 Age Groups)



#### Leslie Matrix for this Scenario.

$$\mathbf{L} = \begin{bmatrix} 0 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{bmatrix}$$



#### Research problem: Combine Predator-Prey and Leslie.



Gather data and conjecture, build simple models, ....

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#### Representative Student Background at the Start of SMALL



(a) **Saad**: Senior, math and physics major



(b) Daniel: Junior, math and physics

# Relevant Background Courses. • Linear Algebra • Programming in MATLAB and Python • Quantum Mechanics SMALL 2024 Predator-Prey Modeling 9/34

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#### Whales and Plankton

#### Question

System of Whales and Plankton; Whales consume Plankton for food. Which parameters affect the population evolution? Is there a closed form solution?



A blue whale in the eastern North Pacific Ocean ingests an average of 16 tonnes of krill in a single day of feeding.

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#### Factors

#### Factors of Population Evolution.

- 1 f > 0, fertility rate of Whales,
- 2 F > 0, fertility rate of Plankton,
- **3** k > 0, predation rate,
- (a) m > 0, growth multiplier of the whale induced by the Plankton.

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#### Overconsumption



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#### Underconsumption



Figure: Both population grows exponentially.

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#### **Unrealistic Cases**



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#### **Competitive Model**

#### Definition (Leslie Competitive Predator-Prey Model)

Let  $\vec{\alpha}_n$ ,  $\vec{\beta}_n$  be the population vectors of the predator and prey species at time *n*. Define the competitive model as

$$\vec{\alpha}_{n+1} = \max(L\vec{\alpha}_n - km\vec{\beta}_n, \vec{0}) \vec{\beta}_{n+1} = \max(L\vec{\beta}_n - k\vec{\alpha}_n, \vec{0}),$$

where  $k, m \in (0, 1)$  are interaction and competitive advantage ratios, both between 0 and 1. First Stages 00000 Data Fitting

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#### The Perron-Frobenius Theorem in Action

#### Definition (The Perron-Frobenius Theorem (Simplified))

For a nonnegative (and irreducible) square matrix M, there is a *dominant eigenvalue* (the Perron root) with a corresponding positive eigenvector. This eigenvalue governs the long-term behavior in Leslie recurrence models.

- Why it Helps:
  - **Population Growth Rate:** The largest eigenvalue of the Leslie (or migration) matrix determines if over or under-consumption happens.
  - **Stable Age Distribution:** The corresponding eigenvector tells us the proportion of individuals across age classes in the long run.

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#### **Foundational Reference**



Hal Caswell - Senior Scientist in the Biology Department of the Woods Hole Oceanographic Institution



Matrix Population Models: Construction, Analysis, and Interpretation (Caswell 2001)

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#### Applying the Competitive Model



Population evolution of Parnaceum Aurelia and Parnaceum Caudatum (Gause, 1930s).

#### Challenge.

Conventional methods fail due to the recursive structure of the model.

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#### Supervised Machine Learning to the Rescue

#### Definition (Error of the fit)

Let  $\overline{\alpha}_t, \overline{\beta}_t$  be the total population of respective species predicted by the competitive model, while p(t), q(t) represent the real time populations. Then, we define the residual as

$$\chi(f,k,\beta_0,m) := \left(\sum_{t \leq T} \left(\frac{\overline{\alpha}_t - p(t)}{p(t)}\right)^2 + \sum_{t \leq T} \left(\frac{\overline{\beta}_t - q(t)}{q(t)}\right)^2\right).$$

#### Machine Learning Scheme

- Evaluate  $\chi$  for random choice of the four parameters. Among the random tuples, choose the tuple that minimizes the value of  $\chi$ .
- 2 Perform a general gradient descent involving all four parameters, starting from the point chosen in step 1. Find the admissible value of k, m first then use these to optimize for the remaining.

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#### Admissible Fit



**Competitive Coexistence** 

#### Migratory Populations: The Big Picture

- Real populations often occupy multiple regions.
- Individuals move between areas due to resources, climate, or human influence.
- Understanding spatial structure is crucial: migration can alter stability, growth, and distribution.



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#### **Incorporating Migration into Leslie Models**

- Classic Leslie matrices model age-structured populations without spatial movement.
- We extend these models to include migration between regions.
- Two main scenarios:
  - 1 Constant (unidirectional) migration
  - **2** Constant proportion (fraction-based) migration.



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#### **Constant Unidirectional Migration: Setup**

- Assume a fixed vector  $m_1$  moves out of population a each step.
- Assume a fixed vector  $m_2$  moves into population b each step.
- System of two populations a(t), b(t):

 $a(t) = \mathbf{L}_1 a(t-1) - m_1, \quad b(t) = \mathbf{L}_2 b(t-1) + m_2.$ 



#### **Closed Form Solutions.**

$$a(t) = \mathbf{L_1}^t a(0) - (\mathbf{I} - \mathbf{L_1})^{-1} (\mathbf{I} - \mathbf{L_1}^t) m_1.$$

$$b(t) = \mathbf{L_2}^t b(0) + (\mathbf{I} - \mathbf{L_2})^{-1} (\mathbf{I} - \mathbf{L_2}^t) m_2,$$

#### where **I** is the $n \times n$ identity matrix.



#### **Constant Proportion Migration: Motivation**

- Constant numbers might not be realistic: migration often depends on current population size.
- Constant proportion migration: a fixed fraction of each population moves each step.
- Reflects density-dependent dispersal: more individuals  $\rightarrow$  more migrants.



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#### Constant Proportion Migration: Setup

#### Definition

With  $k_1, k_2$  as fractions migrating, for two populations a(t), b(t):

$$a(t) = \mathbf{L}a(t-1) - k_1 \cdot a(t-1) + k_2 \cdot b(t-1)$$

$$b(t) = \mathbf{L}b(t-1) - k_2 \cdot b(t-1) + k_1 \cdot a(t-1).$$

- Migration is now proportional to a(t-1) and b(t-1).
- System complexity increases (which is why we assume the same Leslie matrix **L** for both populations), but more realistic.

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#### **Constant Proportion Migration: Closed-Form Expressions**

#### Definition (Closed-Form for Two-Population System)

Let  $\Sigma(t) := a(t) + b(t)$  and  $\Delta(t) := a(t) - b(t)$ , with migration rates  $k_1, k_2$  and  $\kappa = k_1 + k_2, \Delta_k = k_2 - k_1$ . Then:

$$\Sigma(t) = \mathbf{L}^{t} \Sigma(0),$$
  

$$\Delta(t) = \mathbf{L}^{t} \left( \frac{\Delta_{k}}{\kappa} \Sigma(0) \right) + (\mathbf{L} - \kappa \mathbf{I})^{t} \left( \Delta(0) + \frac{\Delta_{k}}{\kappa} \Sigma(0) \right).$$

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$$\Delta(t) = \mathbf{L}^{t} \left(\frac{\Delta_{k}}{\kappa} \Sigma(0)\right) + (\mathbf{L} - \kappa \mathbf{I})^{t} \left(\Delta(0) + \frac{\Delta_{k}}{\kappa} \Sigma(0)\right).$$

Sketch of Proof (Generating Functions):

- **1** Define  $X(z) = \sum_{t\geq 0} \Sigma(t) z^t$  and  $Y(z) = \sum_{t\geq 0} \Delta(t) z^t$ .
- **2** From the proportion-migration recurrences, derive functional equations for X(z) and Y(z).
- **3** Solve  $X(z) = (\mathbf{I} \mathbf{L}z)^{-1}\Sigma(0)$  and invert the generating function (via series expansion) to obtain closed form.

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#### The Inspiration Behind Our Proof

#### Challenges.

- Analytical solutions not feasible in arbitrary case → Simplified problem by fixing 2 populations and solving for arbitrary ages.
- Solution for the 1 age only is trivial solve coupled recurrence using generating functions → Inspiration for our proof.



Sensitivity Analysis (Caswell, 2019)

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- If  $\lambda_{\max}(\mathbf{L} \kappa \mathbf{I}) < 1$ , populations tend to die out or stabilize at a consistent level.
- This scenario can be interpreted as sub-critical growth rates dominated by mortality.



Illustration of convergent behavior (in the case when  $k_1 = k_2 = k \implies \kappa = 2k$ ).

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#### Divergent / Exponential Behavior

- If  $\lambda_{\max}(\mathbf{L} \kappa \mathbf{I}) > 1$ , each population can grow exponentially in isolation.
- Populations may explode unless factors like limited resources or predator pressure are included.



Illustration of divergent behavior (in the case when  $k_1 = k_2 = k$ ).

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- Complex eigenvalues  $(\lambda_{\max}(\mathbf{L} \kappa \mathbf{I}) \approx 1)$  can induce sustained oscillations or cycles.
- This manifests in a repeating boom-bust population cycle (similar to predator-prey) in each region.



Illustration of harmonic behavior (in the case when  $k_1 = k_2 = k$ ).

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#### Conclusions

#### Key Takeaways.

#### • Population Modeling with Predator Prey/Migration:

- Extensions of classic Leslie models capture spatial flow.
- Analytical solutions help clarify how migration affects stability.

#### • Applications and Practical Use:

- Empirical data + Machine Learning = parameter estimation.
- Results inform conservation strategies and resource management.

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#### **Potential Applications**



(a) Modeling marine ecosystems



(b) Conservation efforts for migratory birds



(c) Epidemic control

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#### **Future Directions**

#### **Open Challenges.**

- Multi-region and non-linear effects demand numerical approaches.
- Quantum-inspired methods offer potential new perspectives.



Energy level transitions in <sup>208</sup>Pb and its analogy to predator-prey and aging.

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#### Acknowledgements

## Thank you – Questions?

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