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Leslie meets Prey and Predators: From Modeling to Research

Predator-Prey Modelling Group (SMALL 2024) Speakers: Steven J Miller, Saad Waheed (Williams College) Email: sjm1@williams.edu, sw21@williams.edu https://web.williams.edu/Mathematics/sjmiller/public_html/

AMS-SIMODE Special Session on Modeling Matters in Teaching and Learning Differential Equations Joint Math Meetings, Seattle January 8, 2025.

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Introduce students to higher mathematics and research.

SMALL 2024 SUMMER REU: Strong students, varying backgrounds.

Pre-reqs: Calculus, linear algebra.

Springboard to research: combine / extend simple models.

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Classical Predator-Prey Interactions



(Illustration from Premium Vector)

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

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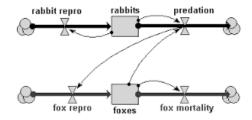
The Lotka-Volterra Equations

Definition

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

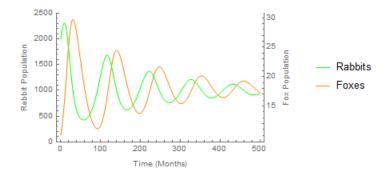
$$\begin{cases} \frac{dx}{dt} = \alpha x - \beta xy\\ \frac{dy}{dt} = \delta xy - \gamma y. \end{cases}$$

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

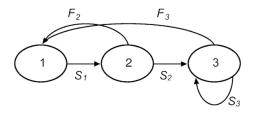
Idea: split population into sub-populations by age. Assume die when turn d; $a_n^{(1)}$ number newborns at time n, $a_n^{(2)}$ number of one-year-olds,

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)

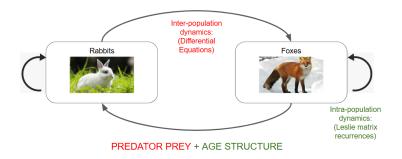


Leslie Matrix for this Scenario.

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



Research problem: Combine Predator-Prey and Leslie.



Gather data and conjecture, build simple models,

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Student Background at the Start of SMALL



Saad: Senior, math and physics major



Daniel: Junior, math and physics

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Student Background at the Start of SMALL



 ${\bf Saad:}$ Senior, math and physics major



Daniel: Junior, math and physics

Relevant Background Courses.

- Linear Algebra
- Programming in MATLAB and Python
- Quantum Mechanics

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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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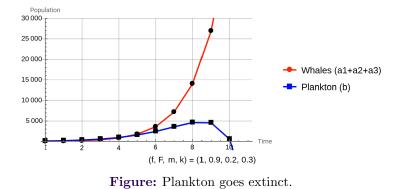
Factors

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

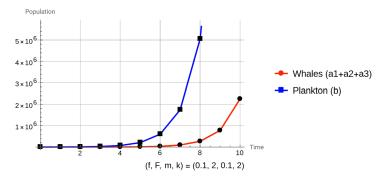
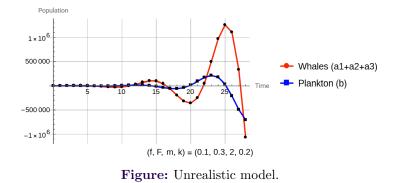


Figure: Both population grows exponentially.

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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



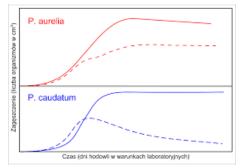
Hal Caswell - Senior Scientist in the Biology Department of the Woods Hole Oceanographic Institution



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 χ for random choice of the four parameters. Among the random tuples, choose the tuple that minimizes the value of χ .
- 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.

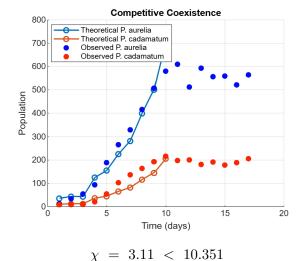
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Admissible Fit



Migratory Populations: The Big Picture

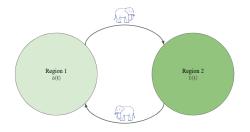
- Real populations often occupy multiple regions.
- Individuals move between areas due to resources, climate, or human influence.
- Understanding spatial structure is crucial: migration can alter stability, growth, and distribution.



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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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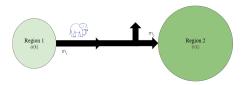
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Constant Unidirectional Migration: Setup

- 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 for 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.

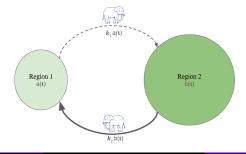
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Constant Proportion Migration: Motivation

- 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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Constant Proportion Migration: Closed-Form Expressions

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Sketch of Proof (Generating Functions):

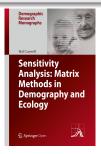
- **1** Define $X(z) = \sum_{t\geq 0} \Sigma(t) z^t$ and $Y(z) = \sum_{t\geq 0} \Delta(t) z^t$.
- **2** From the proportion-migration recurrences, derive functional equations for X(z) and Y(z).
- **3** Solve $X(z) = (\mathbf{I} \mathbf{L}z)^{-1}\Sigma(0)$ and invert the generating function (via series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

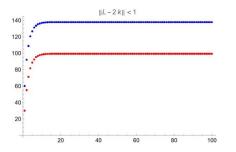


Illustration of convergent behavior (in the case when $k_1 = k_2 = k \implies \kappa = 2k$).

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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.

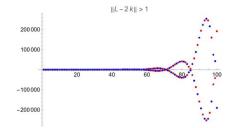


Illustration of divergent behavior (in the case when $k_1 = k_2 = k$).

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Oscillatory	Behavior			

- 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.

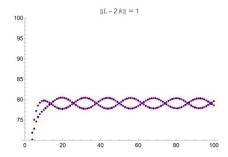


Illustration of harmonic behavior (in the case when $k_1 = k_2 = k$).

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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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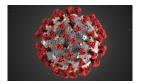
Potential Applications



Modeling marine ecosystems



Conservation efforts for migratory birds



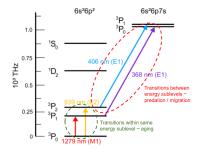
Epidemic control

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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 ²⁰⁸Pb and its analogy to predator-prey and aging.

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Acknowledgements

Thank you – Questions?

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