

AMS CLASSIFICATION

Primary: 92D25, 15A18; Secondary: 37N25, 81Q10

KEYWORDS

Predator-Prey Model; Leslie Matrix; Migration Model; Quantum Operators; Machine Learning

Leslie Population Models in Predator-prey and Competitive populations: theory and applications by machine learning

Pico Gilman^a, Steven J. Miller^a, Daeyoung Son^a, Saad Waheed^a, and Janine Wang^a

^aDepartment of Mathematics and Statistics, Williams College, Williamstown, MA 01267 USA

ARTICLE HISTORY

Compiled May 25, 2026

Article type: research

ABSTRACT

We introduce a new predator-prey model by replacing the growth and predation constants by a square matrix, and the population density as a population vector. The classical Lotka-Volterra model describes a population that either modulates or converges. Stability analysis of such models have been extensively studied by the works of Merdan [9, 10]. The new model adds complexity by introducing an age group structure where the population of each age group evolves as prescribed by the Leslie matrix.

The added complexity changes the behavior of the model such that the population either displays roughly an exponential growth or decay. We first provide an exact equation that describes the time evolution, and use analytic techniques to obtain an approximate growth factor. We also discuss the variants of the Leslie model, i.e., the complex-value predator-prey model and the competitive model. We then prove the Last Species Standing theorem that determines the dominant population in the large time limit.

The recursive structure of the model denies the application of simple regression. We discuss a machine learning scheme that allows an admissible fit for the population evolution of *Paramecium aurelia* and *Paramecium caudatum*. Another potential avenue to simplify the computation is to use the machinery of quantum operators. We demonstrate the potential of this approach by computing the Hamiltonian of a simple Leslie system.

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1. Introduction

Leslie matrices describe the time evolution of a homogeneous population with multiple age groups. Consider a discrete-time evolution of a whale population that is comprised of three age groups. We let $a_n^{(i)} : \mathbb{Z}_{\text{pos}} \rightarrow \mathbb{R}$ for $1 \leq i \leq 3$ be the time-dependent populations of each age group; for example, $a_n^{(1)}$ is the population of newborns at time n . We define the population vector as

$$\vec{a}_n := (a_n^{(1)}, a_n^{(2)}, a_n^{(3)})^T. \quad (1.1)$$

The total population is the sum of the populations of all age groups, or the sum of all entries in the population vector: $a_n^{(1)} + a_n^{(2)} + a_n^{(3)}$.

If we set the fertility rate of the whales to be $f > 0$, constant across all age groups, and assume that the whales have a survival rate of 1, that is, they do not die from reasons other than old age, then we

Email addresses: picogilman@gmail.com (Pico Gilman), sjm1@williams.edu (Steven J. Miller), ds15@williams.edu (Daeyoung Son), sw21@williams.edu (Saad Waheed), jjw3@williams.edu (Janine Wang)

obtain a set of equations that describes the time evolution of the population:

$$\begin{aligned} a_{n+1}^{(1)} &= f \cdot (a_n^{(1)} + a_n^{(2)} + a_n^{(3)}) \\ a_{n+1}^{(2)} &= a_n^{(1)} \\ a_{n+1}^{(3)} &= a_n^{(2)}. \end{aligned} \tag{1.2}$$

This equation can be rewritten in matrix form. For this, we define the Leslie matrix

$$L := \begin{bmatrix} f & f & f \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix},$$

and we get that

$$\vec{a}_{n+1} = L\vec{a}_n = \begin{bmatrix} f & f & f \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix} \vec{a}_n, \tag{1.3}$$

which models our whale population. The advantage of using Leslie matrices is that the population vector at any given time can be expressed as a matrix power. If the population vector at time zero is \vec{a}_0 , then the population vector at time n is

$$\vec{a}_n = L^n \vec{a}_0. \tag{1.4}$$

The expression can be further simplified for faster computation. If the population vector \vec{a}_0 is an eigenvector of the Leslie matrix L with an eigenvalue of $\lambda \in \mathbb{R}$, then we obtain

$$\vec{a}_n = \lambda^n \vec{a}_0, \tag{1.5}$$

and the growth rate of the population is characterized by the eigenvalue λ .

The same technique used to describe homogeneous populations can be applied to heterogeneous populations, as is the case in a predator-prey model. For this model, let us now assume that whales consume plankton, which only has one age group. We denote the plankton population by $b_n : \mathbb{Z}_{\text{pos}} \rightarrow \mathbb{R}^1$ and introduce a predation rate $k > 0$, a plankton population multiplier $m > 0$, as well as a plankton fertility rate $F > 0$. Writing the new population vector as

$$\vec{p}_n := (a_n^{(1)}, a_n^{(2)}, a_n^{(3)}, b_n)^T, \tag{1.6}$$

we arrive at a new model

$$\vec{p}_{n+1} := \tilde{L}\vec{p}_n = \begin{bmatrix} f & f & f & m \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -k & -k & -k & 1 + F \end{bmatrix} \vec{p}_n. \tag{1.7}$$

Depending on the parameters (f, F, m, k) , the model can either describe a situation where the predator population exhausts the prey population with too high a predation rate (itself eventually also becoming extinct due to starvation), or one where, with an appropriate predation rate, both populations grow.

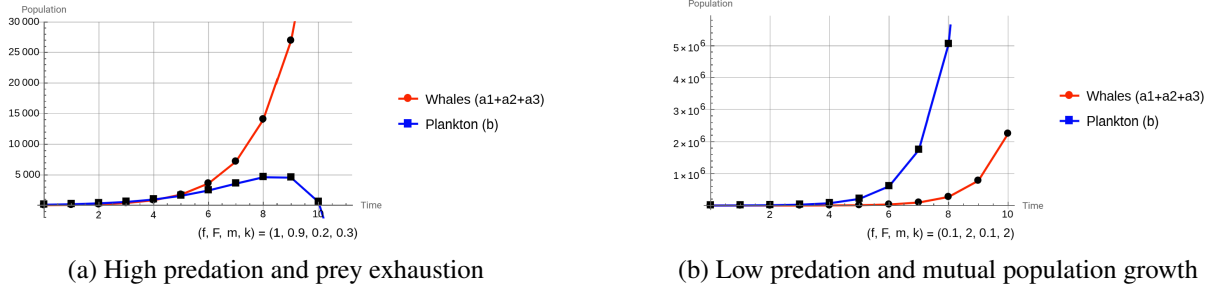


Figure 1: Plot of model 1.7 for varying parameters.

These two cases are illustrated in Figure 3.

Not all parameters predict a realistic population evolution. For example, for certain values of (f, F, m, k) , (1.7) displays an oscillatory behavior where the population is described as a negative number.

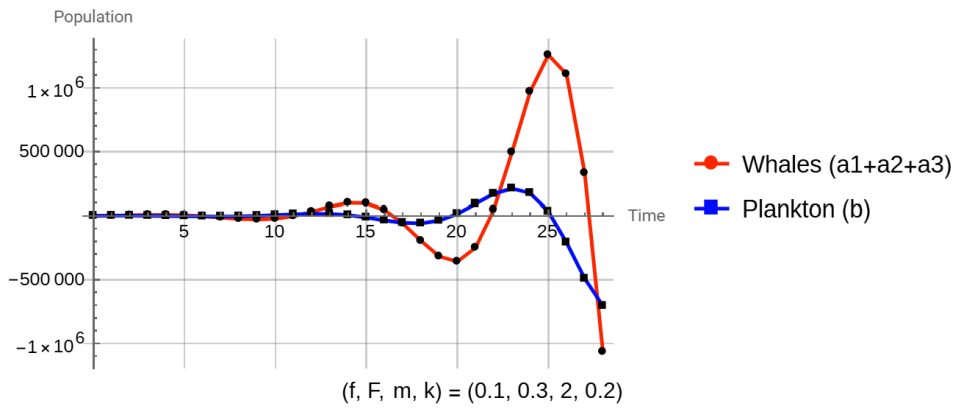


Figure 2: Figure of oscillatory population with high predation.

In the following sections, we begin by defining and studying the eigenvalues of a simple Leslie matrix. Furthermore, we show that a population model with nonsimple Leslie matrices can be approximated by a simplified version with simple Leslie matrices (Section 2). We then introduce the Leslie predator-prey model for real and complex values. The solution for the complex model follows nicely from these results. We also introduce the competitive population model where each population consumes the other to promote growth of their own species. We present a closed-form formula for the population of the predator-prey model with real value using a generating function approach (Section 3.2). The complexity of the closed-form formula motivates us to study the model for a small number of age groups, i.e., one age group for each predator and prey (Section 3.3). Next, using the observations made in Section 2, we provide an asymptotic growth rate for the complex model and prove the Last Species standing theorem for the competitive model (Section 4.1).

To test the presented theory of Leslie population models, we used the competitive model to explain the population evolution *Paramecium aurelia* and *Paramecium caudatum*. The recursive structure prevents application of standard regression techniques. A Machine Learning Scheme developed to generate an admissible fit is presented, along with a fit data with statistic significance (Section 5.2).

Finally, the complex predator-prey model motivates our study to consider the use of quantum mechanics to describe the population. We investigate a specific case of population evolution and compute the Hamiltonian² of the system under the assumption that the population obeys the time-dependent

¹In reality, the population is nonnegative. Nonetheless, for a simple presentation, we choose the domain of b_n to be over the reals. In practice, when the population reaches a negative value, the population is considered to be extinct.

²For more information on the standard theory, refer to [2].

Schrodinger equation.

2. Single Species Population

2.1. Definition of Simple Leslie Matrices and the Lotka-Euler Equation

As described in Section 1, Leslie matrices characterize changes in a species' population with different age groups given its survival and fertility rates. We focus on a specific class of Leslie matrices with a fixed fertility rate f and a survival rate 1.

Definition 2.1 (Leslie Matrices). *Suppose $N \in \mathbb{Z}^+$ is the number of age groups and $f_1, \dots, f_N \in \mathbb{R}$ are fertility rates of each age group. A simple Leslie matrix that characterizes the population evolution is defined as follows:*

$$(L_{f_1, \dots, f_N})_{ij} = \begin{cases} f_i & (i = 1) \\ 1 & (i \neq 1 \text{ and } j = i + 1) \\ 0 & \text{otherwise} \end{cases}$$

or, writing the matrix out,

$$(L_{f_1, \dots, f_N}) = \begin{bmatrix} f_1 & f_2 & \cdots & f_{N-1} & f_N \\ 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{bmatrix}.$$

If the fertility rates f_1, f_2, \dots, f_N are all equal to some fixed fertility rate f , then we say that the Leslie matrix is **simple**. Also, for a nonsimple Leslie matrix with variable fertility rates, we define the simplified Leslie matrix L_f by

$$L_f := \begin{bmatrix} f & f & \cdots & f & f \\ 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{bmatrix}$$

where f is the average fertility rate:

$$f := \frac{\sum_{i=0}^N f_i}{N}.$$

The population at time n can be modeled by a tuple of real numbers, which we write out as a vector.

Definition 2.2 (Time evolution of a single population). *Denote the population vector as $\vec{p}_n \in \mathbb{R}^N$. Given an initial population vector $\vec{p}_0 := \vec{v}$, the population at time n is given by*

$$\vec{p}_n = (L_{f_1, \dots, f_N})^n \vec{v}. \quad (2.1)$$

We present the following theorem, which allows us to focus our analysis on simple Leslie matrices.

Theorem 2.3 (Approximating general Leslie with simplified Leslie). *Assume that the fertility rate f_N , i.e., the fertility rate of the oldest age group, is less than the average fertility rate. For time n sufficiently large, the population vector for a model involving the general Leslie matrix with varying fertility rate can be approximated by the simplified Leslie matrix using the following formula:*³

$$(L_{f_1, \dots, f_N})^n \vec{v} \approx (L_f)^n \left[n \left(\sum_{k=1}^N v_k (f_k/f - 1) \right) \vec{e}_N + \vec{v} \right] := (L_f)^n (n \xi_{v,f} \vec{e}_N + \vec{v}). \quad (2.2)$$

Proof. It is straightforward to verify the following matrix identity:

$$L_f^{-1} L_{f_1, \dots, f_N} = I + C. \quad (2.3)$$

The matrix C is a square matrix of order N with $N - 1$ zero columns with one nonzero column.

$$(C)_{ij} = \begin{cases} f_i/f - 1 & (i = N) \\ 0 & (i < N). \end{cases} \quad (2.4)$$

Also, since C has $N - 1$ zero rows, for any integer $k > 1$, we observe that $C^k = (f_N/f - 1)^k E_N$ where

$$(E_N)_{ij} = \begin{cases} 1 & (i = N, j = N) \\ 0 & \text{otherwise.} \end{cases} \quad (2.5)$$

Raising both sides of (2.3) to the n th power and invoking the Binomial Theorem yield

$$(L_f^{-1} L_{f_1, \dots, f_N})^n = (I + C)^n = \sum_{k=0}^n \binom{n}{k} C^k = I + nC + \sum_{k=2}^n \binom{n}{k} C^k. \quad (2.6)$$

Using our observation on the powers of C , we find

$$\begin{aligned} (L_f^{-1} L_{f_1, \dots, f_N})^n &= I - E_N + nC - (f_N/f - 1)nE_N + E_N \sum_{k=0}^n \binom{n}{k} (f_N/f - 1)^k \\ &= I - E_N + nC - (f_N/f - 1)nE_N + E_N (f_N/f)^n \\ &\approx I - E_N + nC - (f_N/f - 1)nE_N, \end{aligned} \quad (2.7)$$

where the second equality follows from the binomial theorem and the approximation from the assumption that $f_N < f$, and so $(f_N/f)^n \rightarrow 0$ exponentially quickly. Multiply both sides by the initial population vector \vec{v} :

$$(L_f^{-1} L_{f_1, \dots, f_N})^n \vec{v} \approx \vec{v} + n \vec{e}_N \left(\sum_{k=1}^N v_k (f_k/f - 1) \right), \quad (2.8)$$

where vector e_N is the elementary basis vector

$$(\vec{e}_N)_i = \begin{cases} 1 & (i = N) \\ 0 & \text{otherwise.} \end{cases} \quad (2.9)$$

³We write $\xi_{v,f}$ to highlight that the quantity is dependent on the initial population vector \vec{v} and the fertility rates f_1, \dots, f_N .

Finally, multiplying both sides by $(L_f)^{-n}$ on the left yields the desired result. \square

The implication of (2.2) is that for sufficiently large time n , the major contribution comes from the term $\xi_{v,f}\vec{e}_N$, allowing an even cruder approximation

$$(L_{f_1, \dots, f_N})^n \vec{v} \approx (L_f)^n (n \xi_{v,f} \vec{e}_N). \quad (2.10)$$

The absolute error of this approximation will be large. However, when considering the relative growth rate between two different populations, which we will be mainly concerned about, the approximation suffices. The relative error tends to zero exponentially fast.

To demonstrate this, suppose we wish to compute the proportion of the total populations of two different populations. Suppose the first population has an initial population vector of \vec{v} and N age groups with fertility rates f_1, \dots, f_N . Let the second population have an initial population vector of \vec{w} and N age groups with fertility rates g_1, \dots, g_N . The total population of each population is the L^1 norm of the following two vectors, which are

$$(L_{f_1, \dots, f_N})^n \vec{v} \quad \text{and} \quad (L_{g_1, \dots, g_N})^n \vec{w}. \quad (2.11)$$

Thus the proportion of the two populations is

$$\frac{|(L_{f_1, \dots, f_N})^n \vec{v}|_1}{|(L_{g_1, \dots, g_N})^n \vec{w}|_1} = \frac{|(L_f)^n n \xi_{v,f} \vec{e}_N + (L_f)^n \vec{v}|_1}{|(L_g)^n n \xi_{w,g} \vec{e}_N + (L_g)^n \vec{w}|_1} = \frac{|(L_f)^n \xi_{v,f} \vec{e}_N|_1}{|(L_g)^n \xi_{w,g} \vec{e}_N|_1} + O\left(\frac{1}{n}\right). \quad (2.12)$$

Later, we verify that the eigenvalue with the largest modulus is a positive real value. We call this eigenvalue the **dominant eigenvalue**. The dominant eigenvalue of this matrix describes the asymptotic behavior of the population. To begin our discourse, we compute the matrix's characteristic equation and find its roots.

Theorem 2.4 (Lotka-Euler Equation). *The characteristic equation of a simple Leslie matrix L_f of order $N \geq 1$ is*

$$\text{ch}_N(x) = x^N - f(x^{N-1} + \dots + x + 1)$$

which, using the geometric series formula equals

$$x^N - f \frac{x^N - 1}{x - 1}.$$

Proof. We induct on N . It is trivial to see that the equation holds for $N = 1$. For the inductive step, consider $N > 1$. We write out the characteristic polynomial as a determinant expansion:

$$\text{ch}_{N+1}(x) := \det(xI - L_f) = \begin{vmatrix} x - f & -f & \cdots & -f & -f \\ -1 & x & \cdots & 0 & 0 \\ 0 & -1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & -1 & x \end{vmatrix}.$$

Expanding this with respect to the last column yields

$$\text{ch}_{N+1}(x) = (-f)(-1)^N(-1)^N + x \text{ch}_N(x).$$

By the inductive hypothesis, we have

$$\text{ch}_{N+1}(x) = -f + x(x^N - f(x^{N-1} + \dots + x + 1)) = x^{N+1} - f(x^N + \dots + x + 1),$$

which concludes the proof. \square

We focus on the case where the simple Leslie matrix describes a growing population. We comment that the roots of $\text{ch}_N(z)$ are exactly the eigenvalues of L_f . As a corollary of the theorems in Appendix A, we present the following result.

Corollary 2.5. *The eigenvalues of a simple Leslie matrix L_f all have moduli strictly less than 1, assuming $f < 1/N$. Otherwise, if $f \geq 1/N$, then there exists a unique positive real eigenvalue, greater than or equal to 1, that describes the asymptotic growth of the population. In other words, there exists $\lambda_{\max} \in [1, \infty)$ such that for any $\vec{v} \in \mathbb{R}^n$, there exists some $\vec{w} \in \mathbb{R}^n$ such that*

$$(L_f)^n \vec{v} \approx (\lambda_{\max})^n \vec{w} \quad (2.13)$$

for large enough $n \in \mathbb{Z}^+$. We call such eigenvalue of L_f the dominant eigenvalue.

We focus on populations that grow in the long term. Hence, we assume $f \geq 1/N$ for most cases.

3. The Leslie Predator-Prey Model

3.1. A continuous Lotka-Volterra type Predator-Prey Model

Let $x(t)$ and $y(t)$ be continuous functions that describe the respective densities of prey and predator populations. That is, both x and y have ranges within the interval $[0, 1]$. In [9], predator and prey populations are described by a system of differential equations

$$\begin{aligned} \frac{dx}{dt} &= rx(1-x) - axy \\ \frac{dy}{dt} &= ay(x-y), \end{aligned} \quad (3.1)$$

where $r, a > 0$ are the reproduction and predation ratios respectively. Studies of the classic model focus on finding the conditions for which the system reaches stability. In [10], Merdan explores a similar system that accounts for the Allee effect, where the population growth is diminished when the population size is small. The model is described by the equations below:

$$\begin{aligned} \frac{dx}{dt} &= r\alpha(x)x(1-x) - axy \\ \frac{dy}{dt} &= ay(x-y). \end{aligned} \quad (3.2)$$

The term $\alpha(x) := x/(\beta + x)$ captures the Allee effect. Merdan shows that under the condition

$$r - \alpha\beta > 0, \quad (3.3)$$

the population converges to a positive stable state:

$$(x_*, y_*) = ((r - \alpha\beta)/(a + r), (r - \alpha\beta)/(a + r)). \quad (3.4)$$

3.2. The Predator-Prey Model with Leslie Matrices

We wish to account for different age groups in the predator and prey populations. Hence, we replace population density, which was previously a scalar function, by a vector. We also replace the previous reproductive and predation ratios by Leslie matrices.

Definition 3.1 (Leslie Predator-Prey Model). *Let $\vec{\alpha}_n, \vec{\beta}_n \in \mathbb{R}_{\text{pos}}^N$ be the population vectors for the predator and prey species at time n . Let both populations have N different age groups, resulting in the following population vectors:*

$$\begin{aligned}\vec{\alpha}_n &= (\alpha_n^{(1)}, \dots, \alpha_n^{(N)})^T \\ \vec{\beta}_n &= (\beta_n^{(1)}, \dots, \beta_n^{(N)})^T.\end{aligned}\tag{3.5}$$

The population vectors are defined by the following system of matrix difference equations:

$$\begin{aligned}\vec{\alpha}_{n+1} &= L_a \vec{\alpha}_n + km \vec{\beta}_n \\ \vec{\beta}_{n+1} &= L_b \vec{\beta}_n - k \vec{\alpha}_n.\end{aligned}\tag{3.6}$$

The constants k and m are respectively the predation and nurturing ratios, both greater than zero.⁴ We set the predator and prey populations to be the sum of their vector entries. Symbolically, we let $P_{a,n}, P_{b,n}$ denote the predator and prey populations, given by the following sums:

$$P_{a,n} = \sum_{k=1}^N \alpha_n^{(k)} \quad \text{and} \quad P_{b,n} = \sum_{k=1}^N \beta_n^{(k)}.\tag{3.7}$$

We assume that L_α does not have a dominant eigenvalue and L_β has a dominant eigenvalue. In other words, the predator population decays in absence of prey and the prey population explodes in absence of predators.

Furthermore, the populations are fixed to be nonnegative. If a particular age group of a population reaches a nonpositive quantity at some time $n \in \mathbb{Z}^+$, we say the species has gone extinct. Notice that if the predation rate is too high, the prey population will be exhausted and subsequently the predator population will also become extinct. On the other hand, if the predation rate is too low, the predator population will be unable to sustain itself and will equally become extinct. Hence, it is natural to ask the following question.

Problem 3.2 (Optimal Predation Strategy). *What range of the real values k guarantees exponential growth of the predator population? Moreover, what value of k ensures maximum growth?*

Adding a factor of $i = \sqrt{-1}$ in the recursion allows time-delayed effects of predation on the prey population. The reasoning is that the newborns added to the predator population have less predatory capacity and the true predation rate relies on the predation rate of the penultimate predator population, i.e., prey population at timestep t_n is affected by the predator population at t_{n-2} not t_{n-1} .⁵

For the purpose of demonstration, consider a toy model consisting of whale population (predator) represented by a complex valued sequence $(\alpha_n)_{n=1}^\infty$ and plankton population (prey) also represented by a complex valued sequence $(\beta_n)_{n=1}$. The number of whales in the Pacific ocean⁶ is on the order of

⁴The predation ratio describes the amount of prey consumed by each predator. The nurturing ratio describes the population boost that comes from predation.

⁵The motivation for this formulations comes from phasor diagram in physics. Interactions between polarized laser beams are described by a complex phase, and their interaction by a 2x2 complex matrix. We test a model with complex phase in the hopes that the interaction between populations behave similarly to ray polarization. Our demonstration shows that this indeed is the case for whale-plankton population.

⁶In most biological systems, the population of resources is greater than that of the predators. Even without this assumption, the modeling can be achieved by re-normalizing the predator population by multiplying a constant $c \ll 1$.

$10^4 - 10^5$, and the number of plankton in a single liter of water is on the order of $10^5 - 10^6$. Thus, the total number of plankton in the entirety of the Pacific ocean is significantly greater compared to that of whales. Therefore, we assume

$$|\alpha_n| \ll |\beta_n| \quad (3.8)$$

for all positive integer n . As mentioned above, the argument/phase of the population vector describes the future evolution of the population. Therefore, we assume

$$\arg(\alpha_n) = \arg(\beta_n). \quad (3.9)$$

Let g_a, g_b, m be positive reals in the order of 1. Also, set the predation rate $k \ll 1$ which is reasonable for a model with a large prey population. Define the population evolution by a single age group model

$$\alpha_{n+1} = ig_a\alpha_n + km\beta_n \quad (3.10)$$

$$\beta_{n+1} = ig_b\beta_n - k\alpha_n \quad (3.11)$$

and the predator and prey population at time t_n to be $|\alpha_n|, |\beta_n|$ respectively. The prey population at time t_{n+2} can be approximated up to a leading order of k :

$$\beta_{n+2} = i(g_b\beta_{n+1} - kg_a\alpha_n) - k^2m\beta_n = i(g_b\beta_{n+1} - kg_a\alpha_n) + O(k^2). \quad (3.12)$$

Taylor expanding the population $|\beta_{n+1}|$ up to a second order of α_n/β_n gives the approximation

$$|\beta_{n+1}| = g_b\beta_n \left(1 - \frac{k^2\alpha_n^2}{g_b^2\beta_n^2} + O(\alpha_n^4/\beta_n^4) \right). \quad (3.13)$$

Thus, up to a leading order approximation, the prey population is

$$|\beta_{n+1}| = g_b\beta_n + O(\alpha_n^2/\beta_n^2) \quad (3.14)$$

$$|\beta_{n+2}| = (g_b\beta_{n+1} - kg_a\alpha_n) + O(k^2). \quad (3.15)$$

The effect of predation is ignored in the following step, but is taken into account in the step t_{n+2} by the term $-kg_a\alpha_n$. The utility of adding a complex term motivates us to study a complex-valued model.

Definition 3.3 (Complex Leslie Predator-Prey Model). *Let $\alpha_n, \beta_n \in \mathbb{R}_{\text{pos}}^N$ for $n = 0$ and $\alpha_n, \beta_n \in \mathbb{C}^N$ for $n > 0$ be the population vectors of the predator and prey species at time n :*

$$\begin{aligned} \vec{\alpha}_n &= (\alpha_n^{(1)}, \dots, \alpha_n^{(N)})^T \\ \vec{\beta}_n &= (\beta_n^{(1)}, \dots, \beta_n^{(N)})^T. \end{aligned} \quad (3.16)$$

The population vectors are defined by the following system of matrix difference equations:

$$\begin{aligned} \vec{\alpha}_{n+1} &= iL_a\vec{\alpha}_n + km\vec{\beta}_n \\ \vec{\beta}_{n+1} &= iL_b\vec{\beta}_n - k\vec{\alpha}_n, \end{aligned} \quad (3.17)$$

where k and m are respectively the predation and nurturing ratios, both greater than zero. We again set the predator and prey populations, $P_{a,n}$ and $P_{b,n}$, to be the sum of their vector entries. In symbols, we

have

$$P_{a,n} = \left\| \sum_{k=1}^N \alpha_n^{(k)} \right\| \quad \text{and} \quad P_{b,n} = \left\| \sum_{k=1}^N \beta_n^{(k)} \right\|. \quad (3.18)$$

Numerical results show that the populations of the complex model grow almost surely unless the predation rate k is zero. The natural question to ask for this model is therefore the following.

Problem 3.4 (Modeling Predator Growth). *What is the growth rate of the predator population as $n \rightarrow \infty$?*

By elementary substitutions, we obtain the following proposition.

Proposition 3.5 (Coupled 1st Order to 2nd Order). *Assuming both prey and predator populations are non-extinct within a given period of time, the populations satisfy the following second-order difference equations:*

$$\begin{aligned} \vec{\alpha}_n &= (L_a + L_b)\vec{\alpha}_{n-1} - L_b L_a \vec{\alpha}_{n-2} - m k^2 \vec{\alpha}_{n-2} \\ \vec{\beta}_n &= (L_b + L_a)\vec{\beta}_{n-1} - L_a L_b \vec{\beta}_{n-2} - m k^2 \vec{\beta}_{n-2}. \end{aligned} \quad (3.19)$$

For the complex model, we have equivalently

$$\begin{aligned} \vec{\alpha}_n &= i(L_a + L_b)\vec{\alpha}_{n-1} - L_b L_a \vec{\alpha}_{n-2} - m k^2 \vec{\alpha}_{n-2} \\ \vec{\beta}_n &= i(L_b + L_a)\vec{\beta}_{n-1} - L_a L_b \vec{\beta}_{n-2} - m k^2 \vec{\beta}_{n-2}. \end{aligned} \quad (3.20)$$

The coupled second-order difference equation can be solved using generating functions under the assumption that the Leslie matrices of the two populations are constant multiples of each other.

Theorem 3.6 (Generating Function of the Predator Population in the Real Case). *Let $\vec{\alpha}_n$ be the predator population vector in the real Leslie predator-prey model where $L_a = \rho L$ and $L_b = L$. The generating function of $\vec{\alpha}_n$ is*

$$G(x) = [(\rho L + m k^2 I - (\rho + 1)L)x \vec{\alpha}_0 + (\rho L + m k^2 I)x \vec{\alpha}_1] [x^2 I - x(\rho + 1)L + \rho L^2 + m k^2 I]^{-1}. \quad (3.21)$$

Proof. From the recurrence relation provided in Proposition 3.5, we have the following identity:

$$[x^2 - x(\rho + 1)L + (\rho L^2 + m k^2)] G(x) = -(\rho + 1)L \vec{\alpha}_0 x + (\rho L^2 + m k^2) \vec{\alpha}_0 + (\rho L^2 + m k^2) \vec{\alpha}_1 x. \quad (3.22)$$

This identity can be verified by substituting $G(x)$ and imposing the appropriate conditions on α_n . The expansion on the left-hand side has residues for terms that have an x power less than or equal to 2. Solving for $G(x)$ yields the desired result. \square

Using partial fraction decomposition, it is possible to obtain a closed form expression for $\vec{\alpha}_n$.

Theorem 3.7 (Formula for $\vec{\alpha}_n$). *When $n > 0$,*

$$\vec{\alpha}_n = \frac{(L^2 \rho + k^2 m)^{n-2}}{\sqrt{D}} \left[((k^2 m + L^2 \rho) \vec{\alpha}_1 - L(1 + \rho)(k^2 m + L^2 \rho) \vec{\alpha}_0) \delta_{n-1} + (k^2 m + L^2 \rho)^2 \vec{\alpha}_0 \delta_n \right], \quad (3.23)$$

where D is defined by

$$D := L^2(1 + \rho)^2 - 4(m k^2 + \rho L^2), \quad (3.24)$$

and the sequence δ_n is defined by

$$\delta_n = \left(\frac{1}{2}\right)^n (L^2\rho + k^2m)^{-n} \left[\sum_{\substack{l=1 \\ l \text{ odd}}}^{n+1} \binom{n+1}{l} [L(1+\rho)]^{t+1-l} (\sqrt{D})^l \right]. \quad (3.25)$$

Proof. The derivation follows by applying partial fraction decomposition to the previous generating function in Equation (3.21). \square

Though the theorem provides a closed-form expression for the predator population, the complexity of the formula poses difficulties in determining the optimal predation rate for maximal growth.

3.3. Real-Valued Predator-Prey Model with Scalar L

The following three propositions model the predator and prey populations when the dimension of the Leslie matrix is 1; that is, the population growth is characterized by an exponential of a scalar without interaction. To emphasize their scalarity, we write $l_a < 1$ and $l_b > 1$ instead of L_a and L_b .

Theorem 3.8 (Eigenvalues of the Companion Matrix). *Using Proposition 3.5, we write the companion matrix that describes the two populations:*

$$\begin{bmatrix} l_a + l_b & -l_a l_b - k^2 m \\ 1 & 0 \end{bmatrix}. \quad (3.26)$$

The eigenvalues of this matrix are real if and only if

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \quad (3.27)$$

Otherwise, the eigenvalues are complex conjugates of each other.

Proof. The characteristic equation of the companion matrix is

$$\lambda^2 - (l_a + l_b)\lambda + k^2 m + l_a l_b. \quad (3.28)$$

For both eigenvalues to be purely real, the discriminant D of this polynomial must be nonnegative:

$$\frac{D}{4} := \frac{(l_a + l_b)^2}{4} - k^2 m + l_a l_b \geq 0. \quad (3.29)$$

Using elementary algebra, we obtain

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \quad (3.30)$$

Otherwise, if $D/4 < 0$, the eigenvalues have an imaginary part, and the two eigenvalues are complex conjugates of each other. \square

Theorem 3.9 (Exponential Growth of Population for Small Predation Rate). *The following condition guarantees that neither predator nor prey populations vanish as $n \rightarrow \infty$:*

$$k \leq \sqrt{\frac{(1 - l_b)(l_a - 1)}{m}}. \quad (3.31)$$

Proof. We assume that the discriminant of the companion matrix (Equation (3.26)) is a nonnegative real value. Then the dominant eigenvalue must be

$$\frac{l_a + l_b}{2} + \frac{\sqrt{D}}{2}, \quad (3.32)$$

which must be greater than or equal to 1 for both populations to not vanish. \square

Theorem 3.10 (Extinction in the Case of Complex Eigenvalues). *If*

$$k > \frac{l_a - l_b}{2\sqrt{m}}, \quad (3.33)$$

then the population is guaranteed to go extinct.

Proof. It follows trivially that condition (3.33) implies the dominant eigenvalue is complex. Furthermore, the real part of the root is $(l_a + l_b)/2$, which is guaranteed to be positive. Let the two eigenvalues of the companion matrix be γ and $\bar{\gamma}$, with

$$\gamma = re^{i\theta} \quad \text{and} \quad \bar{\gamma} = re^{-i\theta}, \quad (3.34)$$

where $r > 0$ and $\theta \in (0, \pi/2)$. By Proposition 3.5, we note that the predator population at time n can be written as

$$\alpha_n = \nu_1 \gamma^n + \nu_2 (\bar{\gamma})^n. \quad (3.35)$$

We also observe that the populations α_0 and α_1 can be assumed to take positive real values. If $\alpha_1 \leq 0$, then the population has gone extinct at time 1. Equation (3.35) for $n = 0, 1$ is

$$\begin{aligned} \alpha_0 &= \nu_1 + \nu_2 \\ \alpha_1 &= \nu_1 \gamma + \nu_2 \bar{\gamma}. \end{aligned} \quad (3.36)$$

Since $\alpha_0, \alpha_1 > 0$, we deduce that $\nu_1 = \nu_2 := \nu/2 > 0$. Finally, we rewrite the population at time n :

$$\alpha_n = \Re(\nu \gamma^n) = \nu r^n \cos(n\theta). \quad (3.37)$$

We know that $\theta \in (0, \pi/2)$ and thus, there exists an integer n such that $\cos(n\theta) < 0$, which finishes showing that the predator population must go extinct. \square

3.4. The Complex-Valued Leslie Predator-Prey Model with $L_a = \rho L_b$

To solve the second-order matrix recurrence related to the predator-prey model, we solve a characteristic equation whose coefficients are matrices. Since the only matrices involved in this equation are I and L_β which commute, we can use the quadratic equation.

Theorem 3.11 (Dominant Eigenvalue in the General Case). *The population vector of the predator species in (2.1) can be characterized by*

$$\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2 \quad (3.38)$$

for vectors \vec{v}_1 and \vec{v}_2 , the eigenvectors of the system. The growth of the predator population is dominated by the dominant eigenvalue of Λ_1 . We denote the dominant eigenvalue of L_b by λ_{\max} and that of Λ_1 by Λ_{\max} . Then Λ_{\max} has the following modulus:

$$\|\Lambda_{\max}\| = \frac{(\rho + 1)\lambda_{\max} + \sqrt{(\rho + 1)^2\lambda_{\max}^2 + 4mk^2}}{2}. \quad (3.39)$$

Proof. It is possible to solve for Λ_1, Λ_2 directly. We wish to find a matrix Λ such that

$$\Lambda^2 - i(\rho + 1)L_b\Lambda + \rho L_b^2 + mk^2I = 0. \quad (3.40)$$

Applying the quadratic formula yields

$$\begin{aligned} \Lambda_1 &= \frac{(1 + \rho)L_b^2 + \sqrt{(1 - \rho)^2L_b^2 + 4mk^2}}{2}i \\ \Lambda_2 &= \frac{(1 + \rho)L_b^2 - \sqrt{(1 - \rho)^2L_b^2 + 4mk^2}}{2}i. \end{aligned} \quad (3.41)$$

Note that the magnitude of Λ_1 is greater than that of Λ_2 . We approximate the population of the predator species at the limit as $n \rightarrow \infty$:

$$P_{\alpha,n} = \|\vec{a}_n\| = \|\Lambda_1\|^n\|\vec{v}_1\| + \|\Lambda_2\|^n\|\vec{v}_2\| \approx \|\Lambda_1\|^n\|\vec{v}_1\|. \quad (3.42)$$

It remains to show that the vector \vec{v}_1 is nonzero. Let us assume for contradiction that $\vec{v}_1 = (0, \dots, 0)^T$. Then we can write the predator populations at times 0, 1 as

$$\vec{\alpha}_0 = \vec{v}_2 \quad \text{and} \quad \vec{\alpha}_1 = \Lambda_2\vec{v}_2, \quad (3.43)$$

which indicates that

$$\vec{\alpha}_1 = \Lambda_2\vec{\alpha}_0. \quad (3.44)$$

Since Λ_2 is purely imaginary, α_1 is therefore also purely imaginary. However, the initial condition of the model in Definition 3.3 dictates that each entry of $\vec{\alpha}_0$ and $\vec{\beta}$ is positive and real and that

$$\vec{\alpha}_1 = iL_\alpha\vec{\alpha}_n + km\vec{\beta}_n. \quad (3.45)$$

Therefore, α_1 cannot be purely imaginary and we arrive at a contradiction. \square

4. The Competitive Model

We can slightly modify one of the signs in the previous Leslie predator-prey model and study the following system. Suppose there exist two populations with the same growth matrix L . We assume the two populations are nonvanishing without interaction; that is, $f \geq 1/N$ and $L = L_f$ has a dominant eigenvalue.

Definition 4.1 (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 . The competitive model is defined by the following system of matrix*

difference equations:

$$\begin{aligned}\vec{\alpha}_{n+1} &= \max(L\vec{\alpha}_n - km\vec{\beta}_n, \vec{0}) \\ \vec{\beta}_{n+1} &= \max(L\vec{\beta}_n - k\vec{\alpha}_n, \vec{0}),\end{aligned}\tag{4.1}$$

where k and m are respectively the interaction and competitive advantage ratios, both between 0 and 1. The interaction ratio describes how much interaction, i.e., how much casualties are incurred by competition. The competitive advantage ratio describes the competitive ratio of species β over α .

4.1. Last Species Standing

A well-known fact in Biology is the competitive exclusion principle, which states that two species competing over a same type of species cannot mutually coexist. In such competitive scenarios, the subdominant specie is forced to find alternate resources or face extinction [6]. A similar analysis used for the predator-prey model can be applied to yield a mathematical quantification of this biological fact.

Theorem 4.2 (Last Species Standing). *Suppose $\vec{\alpha}_0 = (\alpha_0, \dots, \alpha_0)$ and $\vec{\beta}_0 = (\beta_0, \dots, \beta_0)$. In a Leslie competitive model, one of the two species is likely to vanish as $n \rightarrow \infty$. The fate of the two species is determined by the sign of the term*

$$D := \alpha_0 - \sqrt{m}\beta_0.\tag{4.2}$$

In particular, if $D > 0$, then the population α vanishes and population β grows exponentially. If $D < 0$, then the population β vanishes and the population α grows exponentially. If $D = 0$, either both species vanish or both grow exponentially.

Proof. Proposition 3.5 can be generalized by the substitution $m \mapsto -m$. From the recursive relation

$$\alpha_n = (2L)\alpha_{n-1} - L^2\alpha_{n-2} + mk^2\alpha_{n-2}\tag{4.3}$$

we obtain the characteristic equation

$$\Lambda^2 - 2L\Lambda + L^2 - mk^2I = O,\tag{4.4}$$

where I, O are the identity matrix and the zero matrix of dimension N -by- N , respectively. By the quadratic formula, we derive the following roots:

$$\begin{aligned}\Lambda_1 &= L + k\sqrt{m}I \\ \Lambda_2 &= L - k\sqrt{m}I.\end{aligned}\tag{4.5}$$

Notice that k and m are both nonnegative real values, and that L is assumed to guarantee positive population growth. Hence, Λ_1 has a positive eigenvalue.

From (3.11), we characterize the population as

$$\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2.\tag{4.6}$$

In the limit as $n \rightarrow \infty$,

$$\vec{\alpha}_n \approx \Lambda_1^n \vec{v}_1.\tag{4.7}$$

Thus, the population is nonvanishing if and only if \vec{v}_1 is positive. We compute \vec{v}_1 directly. From (4.6), we obtain two conditions:

$$\begin{aligned}\vec{\alpha}_0 &= \vec{v}_1 + \vec{v}_2 \\ \vec{\alpha}_1 &= \Lambda_1 \vec{v}_1 + \Lambda_2 \vec{v}_2.\end{aligned}\tag{4.8}$$

Solving for \vec{v}_1 yields

$$\begin{aligned}\vec{v}_1 &= \frac{\Lambda_2 \vec{\alpha}_0 - \vec{\alpha}_1}{\Lambda_2 - \Lambda_1} = \frac{L\vec{\alpha}_0 - k\sqrt{m}\vec{\alpha}_0 - L\vec{\alpha}_0 + km\beta_0}{2mk} = \frac{\sqrt{m}\vec{\beta}_0 - \vec{\alpha}_0}{2\sqrt{m}} \\ &= \frac{\sqrt{m}\beta_0 - \alpha_0}{2\sqrt{m}}(1, \dots, 1) = -\frac{D}{2\sqrt{m}}(1, \dots, 1).\end{aligned}\tag{4.9}$$

Similarly, we obtain

$$\beta_n \approx \Lambda_1 \vec{w}_1,\tag{4.10}$$

where

$$\vec{w}_1 = \frac{D}{2\sqrt{m}}(1, \dots, 1).\tag{4.11}$$

If $D \neq 0$, substituting the appropriate value of D yields the desired result. Now suppose $D = 0$ or $\alpha_0 = \sqrt{m}\beta_0$, then the conditions of (4.1) imply

$$\begin{aligned}\vec{\alpha}_1 &= L\vec{\alpha}_0 - k\sqrt{m}\vec{\alpha}_0 \\ \vec{\beta}_1 &= L\vec{\beta}_0 - k\sqrt{m}\vec{\beta}_0.\end{aligned}\tag{4.12}$$

By induction, it is possible to prove that

$$\vec{\alpha}_n = \sqrt{m}\vec{\beta}_n\tag{4.13}$$

for all nonnegative integers n . In turn, we obtain

$$\begin{aligned}\vec{\alpha}_{n+1} &= (L - k\sqrt{m})^n \vec{\alpha}_0 \\ \vec{\beta}_{n+1} &= (L - k\sqrt{m})^n \vec{\beta}_0,\end{aligned}\tag{4.14}$$

and the two populations grow or vanish simultaneously. \square

We provide two numerical simulations in Figure 3 to demonstrate the validity of the result.

5. Applications of the Competitive Model: Limitation of Resources and Machine Learning

In classical ecology, the competitive exclusion principle predicts that two populations that compete over the same resources are unlikely to coexist. The Last Species Standing theorem supports this principle. We apply the model to existing data on the population dynamics of species, and quantify the competitive advantage of one species over the other.

Though unlikely, competitive coexistence is possible in the case of $D = 0$. We study the dynamics at the equilibrium point of competitive coexistence, and demonstrate its coherence with P. H. Leslie's original observations.

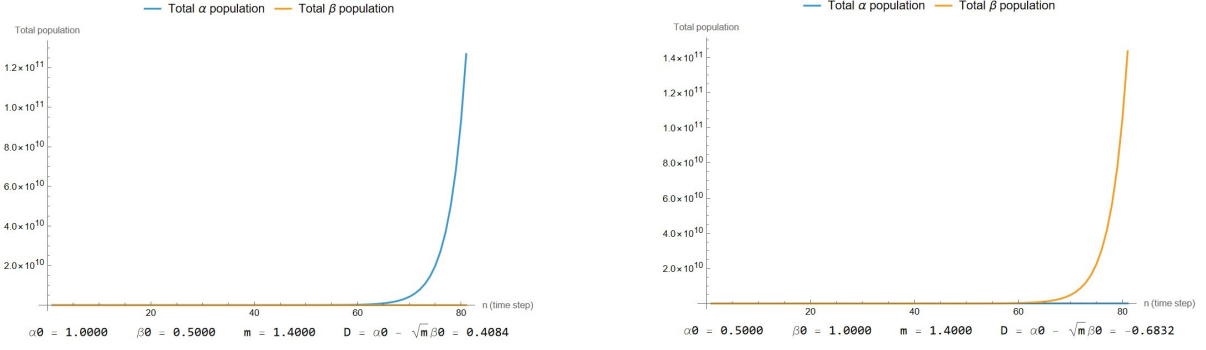


Figure 3: Numerical Verification of Theorem 4.2.

5.1. Adjusting for Limited Resources

Resources are limited in a realistic biological system, and it is impossible that both species display indefinite exponential growth. We assume that both populations of the model rely on the same resource with a logistical growth rate.

Let $r_n(t) : \mathbb{R}_{\geq 0} \rightarrow [0, 1]$ be a continuous function such that $r_n(t)$ describes the population density of the resource at the time interval $[(n-1)\tau, n\tau)$. $r_n(t) = 1$ implies maximum resource and $r_n(t) = 0$ implies absence of resource. Though $r_n(t)$ models the continuous population evolution in between the discrete timestep of the competitive model, our major concern is the value of $r_n(0)$ and $r_n(\tau)$ where τ is the unit time for one instance of (4.1).

Let T be the total population capacity of the system. If the combined population of the competitive species equals the total capacity, the resources are totally consumed. The consumption happens when the time is an integer multiple of τ . We deduce the initial condition and the logistic growth that allows the resource population to asymptote to 1. If the total population exceeds the capacity, the resources go extinct, and $r(t) = 0$. By the observation, the equation for $r_{n+1}(t)$ is given as

$$r_{n+1}(0) = \max\left(1 - \frac{\alpha_n + \beta_n}{T}, 0\right) \quad (5.1)$$

$$r_{n+1}(t) = \frac{\max(T - \alpha_n - \beta_n, 0)e^{mt}}{\max(T - \alpha_n - \beta_n, 0)e^{mt} + \alpha_n + \beta_n}. \quad (5.2)$$

The quantity m determines the replenishing rate of the resources. For high values of τ , we can estimate the $r_n(t)$ as the following indicator function,

$$r_{n+1}(\tau) = \mathbb{1}_{T > \alpha_n + \beta_n}. \quad (5.3)$$

To justify the claim, we plot the value of $r(\tau)$ for varying values of $\alpha_n + \beta_n$ in Figure 4.

Since the resources are exhausted when the population goes over the population capacity T , we deduce that growth and competition stops when $\alpha_n + \beta_n > T$. The natural death of the old age groups allow the resources to replenish [2]. As a consequence, a small perturbation is introduced around the equilibrium. To simplify our calculations, we ignore the perturbation at equilibrium and claim that the population stagnates once the population reaches its full capacity.

5.2. Competitive Coexistence and Machine Learning

A classical example of competitive coexistence is from the experiment of Gause in the 1930's. The population of *Paramecium aurelia* and *Paramecium caudatum*⁷ was observed under a controlled envi-

⁷P. aurelia and P. caudatum in short.

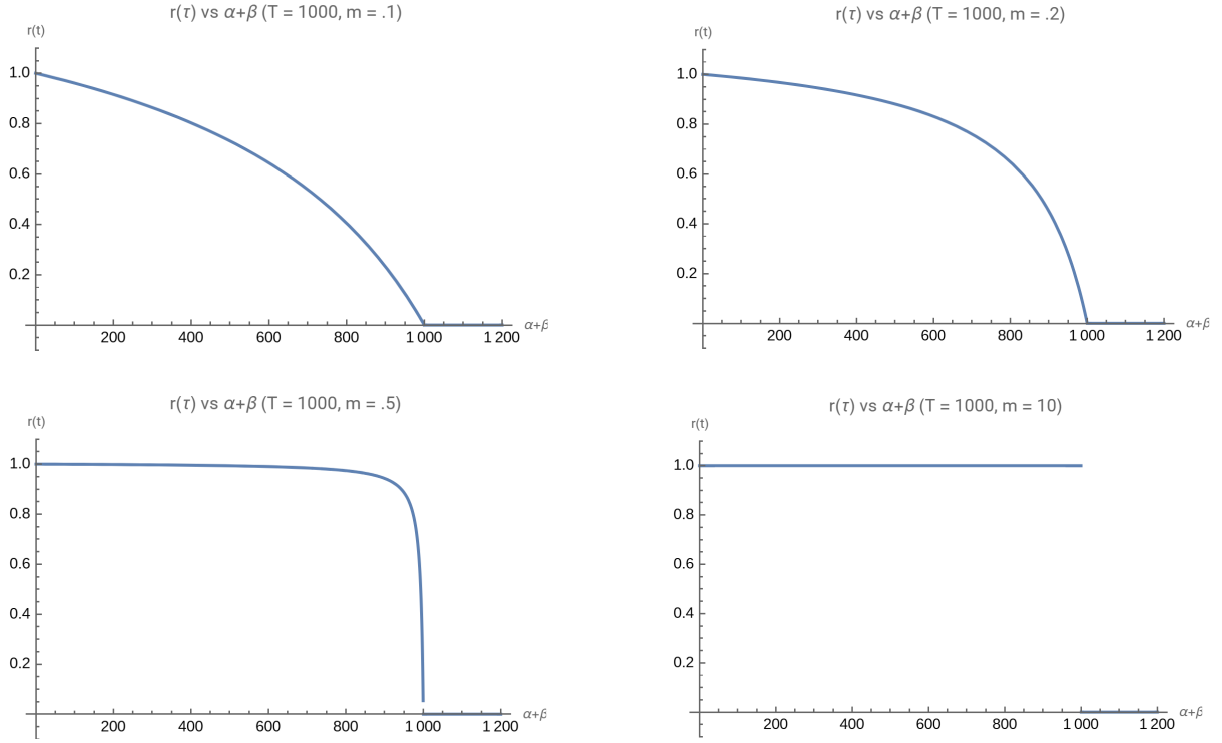


Figure 4: Plot of $r(\tau)$ versus $\alpha_n + \beta_n$.

ronment. Both species shared a resource of *Bacillus pyocyaneus*. The combined population of the two species display exponential growth until the equilibrium population is reached. At equilibrium, the two species coexist. *P. aurelia* possesses competitive advantage, and therefore has a faster growth rate along with a higher equilibrium population.

P. H. Leslie studied the population dynamics using the Lotka-Euler equations. We carry out a similar analysis using the Leslie model. In order to account for limited resources, we focus on the data before equilibrium is attained. In the experimental setup of Gause, the liquid medium containing nutrients were replaced everyday after the observation. Therefore, if the resources consumed per day by the combined population does not reach the threshold, the effect of the limitation can be ignored.

For a quantitative analysis, we consider the specifics of the Competitive model. Fix the number of population groups to be $N = 3$. The population dynamics depend on five quantities

$$(f, k, \alpha_0, \beta_0, m) \quad (5.4)$$

where each parameter describes fertility, predation, initial population of the dominant population, initial population of the subdominant population, and the multiplier. To ensure that $\vec{\alpha}$ is the dominant population, we set $m > 1$. The recursive equation for the competitive model is given from (4.1).

Since we assume competitive coexistence, $D = 0$ by Theorem 4.2. Therefore, we fix the initial population of the dominant species as

$$\alpha_0 = \sqrt{m}\beta_0. \quad (5.5)$$

Standard regression techniques fail to provide a fit of the theoretical model. The challenge is that the resulting curve of the population does not have an exact analytic expression, but rather is defined by a recursive relation determined by the parameter. In order to overcome the increasing complexity for larger values of T , we draw on techniques from machine learning.

Let $p, q : [T] \rightarrow \mathbb{R}$ be two functions that each describe the observed population of the dominant and subdominant species⁸. Also, define

$$\bar{\alpha}_t = \sum_{i \in [N]} \vec{\alpha}_t \cdot e_i \quad \text{and} \quad \bar{\beta}_t = \sum_{i \in [N]} \vec{\beta}_t \cdot e_i. \quad (5.6)$$

In this definition, $\vec{\alpha}_t, \vec{\beta}_t$ is the population vector at time t of a competitive model with parameters (f, k, β_0, m) . The vectors $e_i := (0, \dots, 0, 1, 0, \dots, 0)$ are the i th canonical bases.

In order to fit the model, we define a function $\chi : \mathbb{R}^4 \rightarrow \mathbb{R}$ that describes the fit:

$$\chi(f, k, \beta_0, m) := \left(\sum_{t \leq T} \left(\frac{\bar{\alpha}_t - p(t)}{p(t)} \right)^2 + \sum_{t \leq T} \left(\frac{\bar{\beta}_t - q(t)}{q(t)} \right)^2 \right). \quad (5.7)$$

Also fix the value of the number of populations to be $N = 3$.

By the nature of the model, the ratio between the equilibrium population depends on m , and the growth of both populations are determined by f . The system displays extreme sensitivity to the two values k, β_0 . The two values k, β_0 are fixed after they enter an admissible range.

We performed the following machine learning scheme to train the model to extract the parameters that minimizes χ .

MACHINE LEARNING SCHEME

- (1) 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 .
- (3) Define a subroutine, Opt_g , that performs a gradient descent solely on parameter g with all other parameters fixed.
- (4) Finally perform an optimized gradient descent on parameter m . In the beginning of each loop, invoke the subroutine Opt_g to adjust the parameter g .

Gause's original data includes population evolution over 16 days where equilibrium population is attained in day 10. We set $T = 10$ and tested for 20 parameters. The threshold value of admissible χ for a 5% significance and 20 degrees of freedom is 10.851 [11].

After training the model according to the scheme described above, we obtained a fit with $\chi = 3.11$. This means that we fail to reject the hypothesis of the model. Moreover, the obtained χ value is significantly lower than the threshold, suggesting statistical significance of the fit.

6. Future Works: Quantum Operators

6.1. Motivation

From Equation (3.11), we have already seen that a complex model approach allows us to extract a lot more information compared to a real model approach, where we have to work with more rigid closed-form solutions. Using this as a motivation, we now propose a quantum mechanical approach for modeling the time evolution of populations with discrete age demographics, by using bosonic ladder operators.

⁸ $[T] := \{1, 2, \dots, T\}$ describes the discrete timestep. For Gause's experiment, $t \in [T]$ describes the days elapsed from the beginning of the experiment.

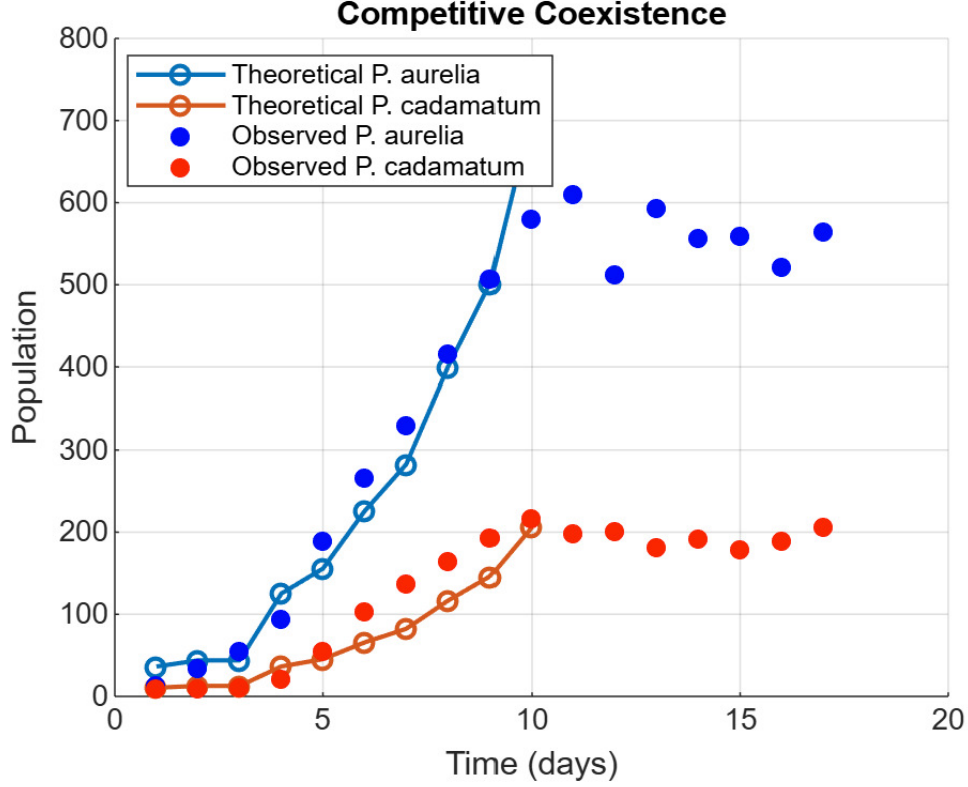


Figure 5: Fit of the competitive model to experimental data. Fit parameters are $(f, \beta_0, k, m) = (1.79, 0.56, 3.53, 9.42)$, and the associated error is $\chi(f, \beta_0, k, m) = 3.11$.

The application of ladder operators, or more colloquially creation and annihilation operators, from quantum mechanics to model complex real-world interactions between N systems is well studied [2]. Previously, a fermionic ladder operator approach was favored as it allowed for discrete evolutionary states, but in recent times, a truncated bosonic approach has been developed with great success, to study population evolution [1].

Recent developments have adopted not only the ladder operators but the general state evolution model using Hamiltonians and quantum operators. Salvo and Oliveri presented a bacterial growth model comprised of discrete time intervals governed by different Hamiltonians [4]. The state evolution within each interval is time-independent, and fluctuations of the system were applied by a discrete change to the Hamiltonian instead of a time-dependent evolution. Numerical results indicate equivalence between this discrete Hamiltonian model and the classical model. Robinson et al. adopted the approach of using number operators to model interactions between cells [12]. They comment that the dynamics of subsystem interaction within a many-body quantum system is analogous to cell interactions.

We use previous work on this subject as a motivation to develop a bosonic ladder operator approach to study populations with discrete age-structures and to relate it to the Leslie matrix approach from our previously developed model.

6.2. Hermitian of the Leslie Matrix

In a quantum system, the time evolution of a state $|\varphi\rangle$ can be described by the Schrodinger Equation:

$$\frac{\partial}{\partial t} i\hbar |\varphi(t)\rangle = iH |\varphi(t)\rangle. \quad (6.1)$$

The solution to this equation can be described by the exponential map:

$$|\varphi(t)\rangle = e^{iHt} |\varphi(0)\rangle. \quad (6.2)$$

A population model can also be described using quantum operators. In this case, the population vector becomes the state. We omit the normalization constant \hbar for better notation.

Proposition 6.1 (Hamiltonian for a Single-Population Leslie Matrix). *Consider a single non-interacting population that follows the time-evolution dictated by the Leslie matrix L . If*

$$\|L - I\| \leq 1, \quad (6.3)$$

where I denotes the identity operator, then our Hamiltonian has a closed form solution:

$$H = \frac{(-1)^k}{ik} (L - I)^k. \quad (6.4)$$

Proposition 6.2 (Algorithm to Compute the Hamiltonian). *The matrix logarithm of L is*

$$\log(L) = P \log(D) P^{-1}, \quad (6.5)$$

where

$$D = \text{diag}(d_1, \dots, d_N) \quad (6.6)$$

and

$$\log(D) = \text{diag}(\log(d_1), \dots, \log(d_N)). \quad (6.7)$$

Proof. We directly take the exponential and show that it matches L :

$$\begin{aligned} e^{\log(L)} &= \sum_{k=0}^{\infty} \frac{(\log(L))^k}{k!} = \sum_{k=0}^{\infty} \frac{(P \log(D) P^{-1})^k}{k!} = \sum_{k=0}^{\infty} \frac{P \log(D)^k P^{-1}}{k!} \\ &= P \left(\sum_{k=0}^{\infty} \frac{\log(D)^k}{k!} \right) P^{-1} = P D P^{-1} = L. \end{aligned} \quad (6.8)$$

We also provide an example use of the algorithm. We consider the population model described in the introduction (Equation 1.7) and set the parameters to be $(f, m, k, F) = (.2, .5, .5, 2)$. Numerically, the model simplifies to

$$\vec{p}_{n+1} := \tilde{L} \vec{p}_n = \begin{bmatrix} .2 & .2 & .2 & .5 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -.5 & -.5 & -.5 & 3 \end{bmatrix} \vec{p}_n. \quad (6.9)$$

We obtain

$$\log(\tilde{L}) \approx \begin{bmatrix} -0.3926 & -0.3606 & 0.5079 & 0.2940 \\ 1.9656 & -0.9006 & -0.8685 & -0.2296 \\ -3.2005 & 2.8342 & -0.0320 & 0.4569 \\ -0.5212 & -0.0644 & -0.2940 & 1.1627 \end{bmatrix}, \quad (6.10)$$

and by direct computation via MATLAB, we verify that

$$e^{\log(L)} \approx \begin{bmatrix} .2 & .2 & .2 & .5 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -.5 & -.5 & -.5 & 3 \end{bmatrix} = L. \quad (6.11)$$

□

Appendix A. Roots of $\text{ch}_N(z)$

In this section, we provide our observations on the roots of $\text{ch}_N(z)$ using Complex Analysis.

Theorem A.1. *If $f \geq 1/N$, then $\text{ch}(z)$ has a unique positive, real root that has a magnitude strictly greater than any of the other complex roots.*

Proof. Consider the polynomial

$$h(z) := (z - 1)\text{ch}_N(z) = z^{N+1} - (f + 1)z^N + f, \quad (A1)$$

which has a simpler algebraic expression. We split the polynomial $h(x)$ into two summands, and invoke Rouché's Theorem ([13] p. 91). Let $C_{1+\epsilon}$ be a circular contour centered at the origin with radius $1 + \epsilon$ for arbitrarily small ϵ . Write

$$h(z) = (z^{N+1} + f) + (1 + f)z^N \quad (A2)$$

and Taylor expand the two summands at $z = 1$:

$$(z^{N+1} + f) = 1 + f + (N + 1)\epsilon \quad (A3)$$

$$z^N(1 + f) = (1 + N\epsilon)(1 + f) = 1 + f + N(1 + f)\epsilon. \quad (A4)$$

By assumption, $f \geq 1/N$, which implies $(N + 1) \leq N(1 + f)$. The modulus of the two terms along the contour can be compared as follows:

$$|z^{N+1} + f| \leq |(1 + f)z^N|. \quad (A5)$$

By Rouché's theorem, $h(z)$ has the same number of roots as the term that has a larger modulus in the contour $C_{1+\epsilon}$, which is the summand $(1 + f)z^N$. It is trivial to see that this summand has N roots inside the contour, and by the Fundamental Theorem of Algebra, $h(z)$ has $N + 1$ roots.

We know that $\text{ch}_N(z)$ is positive somewhere in the interval $[1, \infty)$. We consider the following:

$$\text{ch}_N(1) = 1 - fN \leq 0. \quad (A6)$$

By the Intermediate Value Theorem, we conclude that the one root outside the unit circle is a positive real value. \square

Theorem A.2. *If $f < 1/N$, then all the roots of $\text{ch}_N(z)$ have a modulus strictly less than 1.*

Proof. It suffices to show that

$$\tilde{h}(z) = h(1/z)z^{N+1} = fz^{N+1} - (f+1)z + 1 \quad (\text{A7})$$

has exactly one root within the unit circle which comes from multiplying $(z-1)$. Again, consider the contour $C_{1+\epsilon}$ and split $\tilde{h}(z)$ into two summands:

$$\tilde{h}(z) = (fz^{N+1} + 1) - (f+1)z. \quad (\text{A8})$$

Taylor expand the two summands at $z = 1$, and notice that under the condition $f < 1/N$, the second summand has a larger modulus along the contour $C_{1+\epsilon}$:

$$fz^{N+1} + 1 = f(1 + (N+1)\epsilon) + 1 \quad (\text{A9})$$

$$(f+1)z = (f+1)(1+\epsilon). \quad (\text{A10})$$

Clearly, the second summand has one root inside the contour $C_{1+\epsilon}$, which originates from $(z-1)$. By Rouché's theorem, $\tilde{h}(z)$ has exactly one root inside the unit circle, i.e., $z = 1$, and all other roots have a modulus greater than 1. Consequently, $\text{ch}_N(z) = h(z)/(z+1)$ has all of its roots strictly inside the unit circle. \square

Theorem A.3 (Bounds for the largest root). *Given that $f \geq 1/N$, the largest root λ_{\max} of $\text{ch}_N(z)$ is given by*

$$1 + f - \frac{1}{N} \leq \lambda_{\max} < 1 + f. \quad (\text{A11})$$

Proof. The upper bound is trivial:

$$\text{ch}_N(1+f) = f > 0. \quad (\text{A12})$$

We have $\text{ch}_N(0) = -f < 0$, and thus by the Intermediate Value Theorem the maximum root is bounded.

To obtain the lower bound, we write $f = 1/N + \epsilon$ for some $\epsilon \geq 0$. With some algebra listed below, we compute $\text{ch}_N(z)$ at the claimed lower bound. If we show that this value is less than zero, the dominating root must be greater than the purported lower bound. We find

$$\text{ch}_N\left(1 + f - \frac{1}{N}\right) = -\left(1 + f - \frac{1}{N}\right)^N \left[\frac{1}{fN-1}\right] + \frac{fN}{fN-1}. \quad (\text{A13})$$

We wish to bound this value by zero. It suffices to show

$$fN - \left(1 + f - \frac{1}{N}\right)^N \leq 0, \quad (\text{A14})$$

which, using the ϵ substitution, converts to

$$1 + N\epsilon - (1+\epsilon)^N \geq 0. \quad (\text{A15})$$

Expanding the power term by the binomial theorem, we see that inequality indeed holds. □

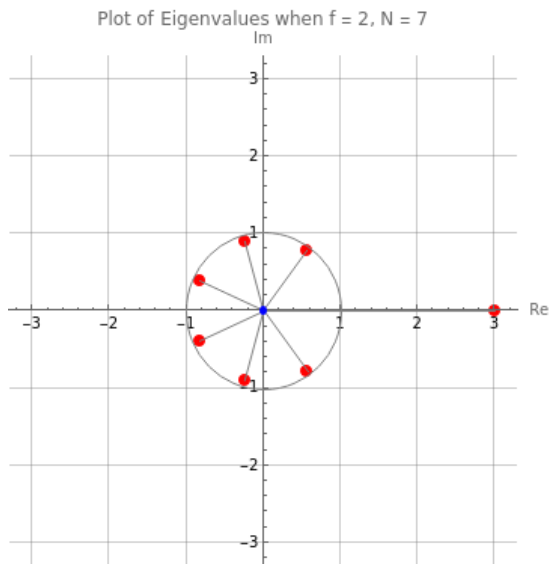
Figure A1 demonstrates the theorems in this section.

Acknowledgements

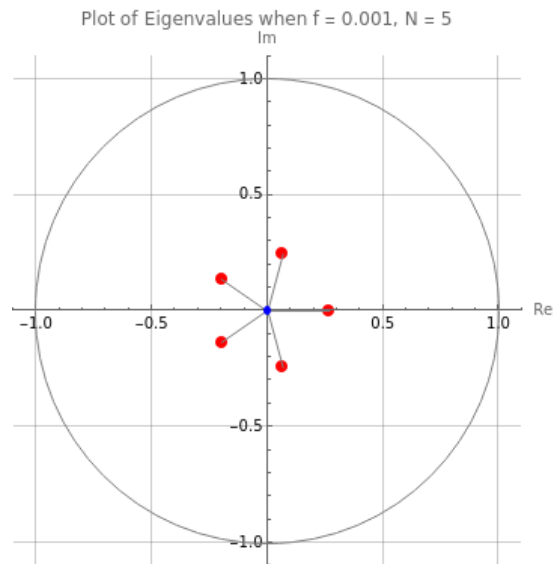
This work was partially supported by NSF Grant DMS2241623, Williams College, and The Finnerty Fund. We are grateful to Professor Allison L. Gill from the Williams Biology Department for her advice on gathering data for Section 5.

Disclosure statement

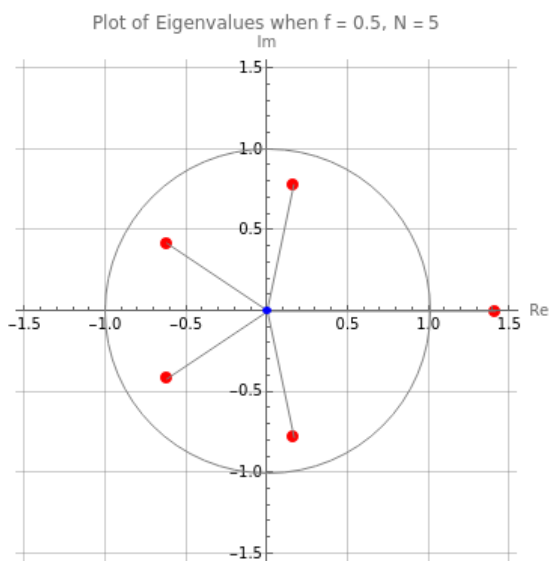
No conflict of interest has been reported by the authors.



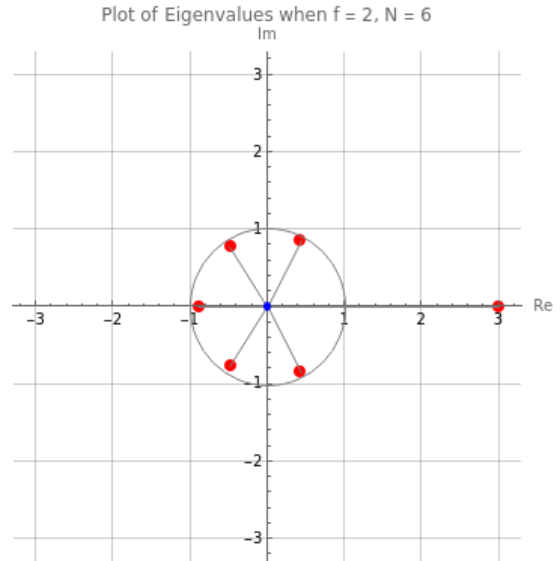
(a) $f > 1, N$ odd.



(b) $f \approx 0, N$ odd.



(c) $f < 1, N$ odd.



(d) $f > 1, N$ even.

Figure A1: Roots of $ch_N(z)$ for varying f, N in the complex plane.

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MSC2020: 92D25, 15A18, 37N25, 81Q10