

# ANALYSIS OF LESLIE POPULATION MODELS IN PREDATOR-PREY, COMPETITIVE, AND MIGRATORY CONTEXTS

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**ABSTRACT.** We introduce a new predator-prey model based the Lotka-Volterra model. Extensive study has been conducted on stability on the simple model which considers an homogenous population. For example, Merdan [MeD09, Mer10] carries out a stability analysis by computing the Jacobian and drawing from methods of differential calculus and Zhou [ZhL05] studies different types of Allee effects and the corresponding stability.

We replace the population evolution constants with a Leslie matrix, taking account of multiple age groups. Replacing the constant coefficients to Leslie matrices motivates the study of dominant eigenvalues which can be conducted using techniques in Complex Analysis. Using the theory of dominating eigenvalues, we provide a bound for maximum predation rate for population survival in a long term. We also discuss the competitive model and prove the last species standing theorem, which describes the unlikelihood of stable equilibrium between two competitive species.

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## 1. INTRODUCTION

Leslie matrices describe the time evolution of a homogeneous population with multiple age groups. For example, say we wish to model in discrete time a whale population with 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 the entries of 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 obtain a set of equations that describe the time evolution of the population:

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

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

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

and we get that

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

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. Given that the population vector at time zero is  $\vec{a}_0$ , the population vector at time  $n$  is

$$\vec{a}_n = L^n \vec{a}_0. \quad (1.4)$$

If the population vector  $\vec{a}_0$  is an eigenvector of the Leslie matrix  $L$  with an eigenvalue of  $\lambda \in \mathbb{R}$ , we obtain

$$\vec{a}_n = \lambda^n \vec{a}_0, \quad (1.5)$$

and the growth rate of the population is characterized by the eigenvalue  $\lambda$ .

The same technique used to describe homogenous populations can be applied to heterogenous 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  $b_n : \mathbb{Z}_{\text{pos}} \rightarrow \mathbb{R}$  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

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

we arrive at a new model:

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

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 grows. These two cases are illustrated in Figure 1.

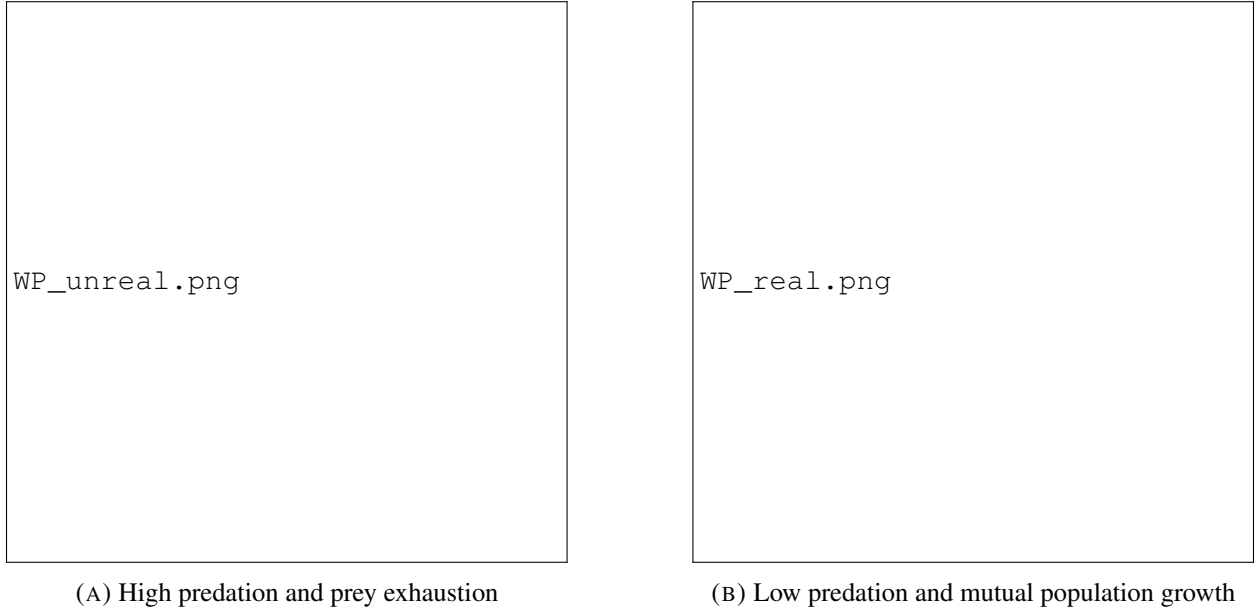


FIGURE 1. Plot of model 1.7 for varying parameters.

*(Please edit this part after completion of the Migration Model.)* We observe that the model described in 1.7 also displays oscillatory behavior. To study such oscillatory behavior in a coherent biological system, we define the migration model.

In the following sections, we begin by defining and studying the eigenvalues of a simple Leslie matrix using complex analysis (Section 2). We then introduce the Leslie predator-prey model for real values. The complex valued model is defined to account for time-delayed response. The solution for the complex model follows nicely from these results. We also introduce the competitive population model. We present a closed form formula for the population of the real valued predator-prey model 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). Finally, the complex predator-prey model motivates our study to consider the use of quantum ladder operators to describe the population. We investigate a specific case of population evolution and compute the Hamiltonian<sup>1</sup> of the system under the assumption that the population obeys the Schrodinger's equation.

<sup>1</sup>For more information on the standard theory, refer to [Bag19].



FIGURE 2. Figure of oscillatory population with high predation.

## 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's 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  $N \in \mathbb{Z}_{\text{pos}}$  is the number of age groups and  $f_1, \dots, f_N \in \mathbb{R}$  be fertility rates of each age group. A simple Leslie matrix that characterizes the population evolution is defined as follows:*

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

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 rate  $f_1, f_2, \dots, f_N$  are constantly equal to some fixed fertility rate  $f$ , then we say that the Leslie matrix is **simple**. Also, for a non-simple Leslie matrix with a variable fertility rate, we define the simplified Leslie matrix  $L_f$  as follows.

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

The quantity  $f$  is the average fertility rate, which is defined as

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

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 using simplified Leslie matrix using the following formula.

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

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*Proof.* It is straightforward 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

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

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<sup>2</sup>We write  $\xi_{v,f}$  to highlight that the quantity is dependent on the initial population vector  $\vec{v}$  and the fertility rates  $f_1, \dots, f_N$

Take power of  $n$  to the both sides of (2.3) and invoke the Binomial Theorem.

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

Use our observation on the powers of  $C$ .

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

Where the second equality follows from the binomial theorem and the approximation from the assumption that  $f_N < f$ . Multiply both sides by the initial population vector  $\vec{v}$ .

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

The vector  $e_N$  is the elementary basis vector, i.e.

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

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

The implication of (2.10) 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.

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

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

Thus the proportion of the two population 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, can be simplified to

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

*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

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

which concludes the proof.  $\square$

**2.2. Bounding dominant eigenvalue.** To determine population dynamics, it is useful to bound the dominant eigenvalues of a Leslie matrix. Using methods from complex analysis, it is possible to derive the following two theorems.

**Theorem 2.5** (Complex Roots of the Characteristic Equation). *The characteristic equation  $\text{ch}_N(z)$  has exactly one dominating real root, that is, an root that is purely real and has the maximum modulus among all complex roots. Furthermore, all other roots lie inside the unit circle.*

*Proof.* We consider the polynomial

$$\tilde{h}(z) := (z-1)\text{ch}_N(z) = z^{N+1} - (f+1)z^N + f \quad (2.13)$$

and show that all the complex roots lie inside the unit circle. It suffices to show that

$$h(z) = \tilde{h}(1/z)z^{N+1} = fz^{N+1} - (f+1)z + 1 \quad (2.14)$$

has only two roots inside the unit circle, including  $z = 1$  and some other unknown root with modulus strictly less than 1. We note that the root  $z = 1$  of  $\tilde{h}(z)$  is an extraneous root added by multiplying  $(z-1)$ ; thus if  $\tilde{h}(z)$  has  $n$  roots,  $\text{ch}_N(z)$  has  $n-1$  roots.

We invoke Rouché's Theorem<sup>3</sup>, applying it to  $h(z)$  and the function

$$g(z) = fz^{N+1} - fz. \quad (2.15)$$

Let  $C_{1-\epsilon}$  be a circular contour centered at the origin with radius  $1-\epsilon$  for some small  $\epsilon$ . On this contour,  $|h(z)| < |g(z)|$ . To verify this, consider

$$|h(z) - g(z)| = |z-1| = \epsilon \geq |h(z)| - |g(z)| \quad (2.16)$$

and choose  $\epsilon$  to be arbitrarily small. It follows that  $|h(z)| < |g(z)|$ .

Therefore, to count the zeros of  $h(z)$  inside the contour  $C_{1-\epsilon}$ , it suffices to count the zeros of  $g(z)$ . We know that the zeros of  $g(z)$  are zero and the roots of unity, with only the former lying inside the contour. Hence, for any arbitrarily small  $\epsilon > 0$ ,  $h(z)$  has one zero inside the contour  $C_{1-\epsilon}$ .

This implies that all the roots of  $h(z)$  except one must have a modulus greater than or equal to 1. Clearly, the only root with modulus 1 is  $z = 1$ . Thus, all roots of  $h(z)$  besides  $z = 1$  and one other root must lie outside the unit circle.

Finally, it remains to show that  $\text{ch}_N(z)$  has one real eigenvalue. We divide into two cases: when  $f \geq 1$  and when  $f < 1$ . Also, trivially

$$\text{ch}_N(0) = -f < 0.$$

<sup>3</sup>Refer to [SS03] p91.

Assuming  $f \geq 1$ , we can write

$$\text{ch}_N(2f) = 2^N f^N - f \left( \frac{(2f)^N - 1}{2f - 1} \right) \geq 2^N f^N - ((2f)^N - 1) = 1 > 0.$$

If  $f < 1$ , we consider  $z = 2/f$ :

$$\text{ch}_N(2/f) = (2/f)^N - f \left( \frac{(2/f)^N - 1}{2/f - 1} \right) \geq 2^N / f^N - ((2/f)^N - 1) = 1 > 0.$$

For both cases, we invoke the Intermediate Value Theorem and find that there exists a real root for  $\text{ch}_N(z)$ . □

We provide a plot of eigenvalues to serve as further evidence for Theorem 2.5.





FIGURE 3. Complex eigenvalues of simple Leslie matrices for varying  $f, N$ .

**Corollary 2.6** (Real Root of the Characteristic Equation). *The real root of the characteristic equation has a magnitude greater than 1 if and only if  $(1 - fN) < 0$ .*

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

$$\text{ch}_N(1) = 1 - fN. \quad (2.17)$$

If this value is less than zero, then the real root lies somewhere in the range  $(1, \infty)$ . Otherwise, since  $f(0) < 0$  and  $\text{ch}_N(z)$  is continuous, by the Intermediate Value Theorem, the dominant root must be less than 1.  $\square$

With a little more analysis, we provide a lower and an upper bound for the dominant eigenvalues of  $L_f$ .

**Theorem 2.7** (Bounds for the dominant eigenvalue). *Given that  $1 - fN \leq 0$ , the dominant eigenvalue of  $L_f$  of order  $N$  is given by*

$$1 + f - \frac{1}{N} \leq \lambda_{\max} < 1 + f. \quad (2.18)$$

*Proof.* The upper bound is trivial:

$$\text{ch}_N(1 + f) = f > 0. \quad (2.19)$$

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

$$\text{ch}_N\left(1 + f - \frac{1}{N}\right) = -\left(1 + f - \frac{1}{N}\right)^N \left[\frac{1}{fN - 1}\right] + \frac{fN}{fN - 1}. \quad (2.20)$$

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

$$fN - \left(1 + f - \frac{1}{N}\right)^N \leq 0, \quad (2.21)$$

which, using the  $\epsilon$  substitution, converts to

$$1 + N\epsilon - (1 + \epsilon)^N \geq 0. \quad (2.22)$$

Expanding the power term by the binomial theorem, we see that inequality indeed holds.  $\square$

### 3. THE LESLIE PREDATOR-PREY MODEL

**3.1. The Classic Lotka-Volterra 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  $[0, 1]$ . The classic predator-prey model is described by a system of differential equations:

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

$r, a > 0$  are reproductive ratio and predation ratio respectively. Studies of the classic model focus on finding the conditions for which the system reaches stability. In [Mer10], 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<sup>4</sup>. 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 the dominant eigenvalue of  $L_\alpha$  is less than  $1/2$  and that the dominant eigenvalue of  $L_\beta$  is greater than  $1/2$ . 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 non-negative. If a population reaches zero at some time  $n \in \mathbb{Z}_{\text{pos}}$ , 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 value  $k$  guarantees exponential growth of the predator population? Moreover, what value of  $k$  ensures maximum growth?*

The real-valued Leslie Predator-Prey model motivates us to study a complex-valued model. By multiplying  $i = \sqrt{-1}$  to one of the summands can be considered as a time-delay in the population change.

**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  $n$ :*

$$\begin{aligned}\vec{\alpha}_n &= (\alpha_n^{(1)}, \dots, \alpha_n^{(N)})^T \\ \vec{\beta}_n &= (\beta_n^{(1)}, \dots, \beta_n^{(N)})^T.\end{aligned}\tag{3.8}$$

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

$$\begin{aligned}\vec{\alpha}_{n+1} &= iL_a \vec{\alpha}_n + km \vec{\beta}_n \\ \vec{\beta}_{n+1} &= iL_b \vec{\beta}_n - k \vec{\alpha}_n,\end{aligned}\tag{3.9}$$

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

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

$$P_{a,n} = \left\| \sum_{k=1}^N \alpha_n^{(k)} \right\| \quad \text{and} \quad P_{b,n} = \left\| \sum_{k=1}^N \beta_n^{(k)} \right\| \quad (3.10)$$

Experimentally speaking, for the complex model, the population grows 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:*

$$\begin{aligned} \vec{\alpha}_n &= (L_a + L_b)\vec{\alpha}_{n-1} - L_b L_a \vec{\alpha}_{n-2} - m k^2 \vec{\alpha}_{n-2} \\ \vec{\beta}_n &= (L_b + L_a)\vec{\beta}_{n-1} - L_a L_b \vec{\beta}_{n-2} - m k^2 \vec{\beta}_{n-2}. \end{aligned} \quad (3.11)$$

For the complex model, we have equivalently

$$\begin{aligned} \vec{\alpha}_n &= i(L_a + L_b)\vec{\alpha}_{n-1} - L_b L_a \vec{\alpha}_{n-2} - m k^2 \vec{\alpha}_{n-2} \\ \vec{\beta}_n &= i(L_b + L_a)\vec{\beta}_{n-1} - L_a L_b \vec{\beta}_{n-2} - m k^2 \vec{\beta}_{n-2}. \end{aligned} \quad (3.12)$$

The coupled second order differences 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<sup>5</sup> of  $\vec{\alpha}_n$  is*

$$G(x) = \frac{(\rho L + m k^2 - (\rho + 1)Lx) \vec{\alpha}_0 + (\rho L + m k^2)x \vec{\alpha}_1}{x^2 - x(\rho + 1)L + \rho L^2 + m k^2}. \quad (3.13)$$

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

$$[x^2 - x(\rho + 1)L + (\rho L^2 + m k^2)] G(x) = -(\rho + 1)L \vec{\alpha}_0 x + (\rho L^2 + m k^2) \vec{\alpha}_0 + (\rho L^2 + m k^2) \vec{\alpha}_1 x. \quad (3.14)$$

This identity can be verified by substituting  $G(x)$  and imposing the appropriate conditions on  $\alpha_n$ . 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  $n > 0$ ,*

$$\vec{\alpha}_n = \frac{(L^2 \rho + k^2 m)^{n-2}}{\sqrt{D}} \left[ ((k^2 m + L^2 \rho) \vec{\alpha}_1 - L(1 + \rho)(k^2 m + L^2 \rho) \vec{\alpha}_0) \delta_{n-1} + (k^2 m + L^2 \rho)^2 \vec{\alpha}_0 \delta_n \right], \quad (3.15)$$

where  $D$  is defined by

$$D = L^2(1 + \rho)^2 - 4(m k^2 + \rho L^2), \quad (3.16)$$

and the sequence  $\delta_n$  is defined by

$$\delta_n = \left(\frac{1}{2}\right)^n (L^2 \rho + k^2 m)^{-n} \left[ \sum_{\substack{l=1 \\ l \text{ odd}}}^{n+1} \binom{n+1}{l} [L(1 + \rho)]^{t+1-l} (\sqrt{D})^l \right]. \quad (3.17)$$

<sup>5</sup>The fraction is an abuse of notation. Precisely, the denominator is a matrix, and dividing by the matrix is by multiplying the inverse of the matrix.

*Proof.* The derivation follows by applying partial fraction decomposition to the previous generating function in Equation 3.13.  $\square$

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:*

$$\begin{bmatrix} l_a + l_b & -l_a l_b - k^2 m \\ 1 & 0 \end{bmatrix}. \quad (3.18)$$

*The eigenvalues of this matrix are purely real if and only if*

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \quad (3.19)$$

*Otherwise, the eigenvalues are complex conjugates of each other.*

*Proof.* The characteristic equation of the companion matrix is

$$\lambda^2 - (l_a + l_b)\lambda + k^2 m + l_a l_b. \quad (3.20)$$

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

$$\frac{D}{4} := \frac{(l_a + l_b)^2}{4} - k^2 m + l_a l_b \geq 0. \quad (3.21)$$

Using elementary algebra, we obtain

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \quad (3.22)$$

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  $n \rightarrow \infty$ :*

$$k \leq \sqrt{\frac{(1 - l_b)(l_a - 1)}{m}}. \quad (3.23)$$

*Proof.* We assume that the discriminant of the companion matrix (Equation 3.18) is a non-negative real value. Then the dominant eigenvalue must be

$$\frac{l_a + l_b}{2} + \frac{\sqrt{D}}{2}, \quad (3.24)$$

which must be greater or equal to 1 for both of the population to not vanish.  $\square$

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

$$k > \frac{l_a - l_b}{2\sqrt{m}}, \quad (3.25)$$

*then the population is guaranteed to go extinct.*

*Proof.* It follows trivially that condition (3.25) 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  $\gamma$  and  $\bar{\gamma}$ , with

$$\gamma = re^{i\theta} \quad \text{and} \quad \bar{\gamma} = re^{-i\theta}, \quad (3.26)$$

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

$$\alpha_n = \nu_1 \gamma^n + \nu_2 (\bar{\gamma})^n. \quad (3.27)$$

We also observe that the populations  $\alpha_0$  and  $\alpha_1$  can be assumed to take positive real values. If  $\alpha_1 \leq 0$ , then the population has gone extinct at time 1. Equation 3.27 for  $n = 0, 1$  is

$$\begin{aligned} \alpha_0 &= \nu_1 + \nu_2 \\ \alpha_1 &= \nu_1 \gamma + \nu_2 \bar{\gamma}. \end{aligned} \quad (3.28)$$

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

$$\alpha_n = \Re(\nu \gamma^n) = \nu r^n \cos(n\theta). \quad (3.29)$$

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.  $\square$

$\square$

**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  $L_\beta$  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*

$$\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2 \quad (3.30)$$

for vectors  $\vec{v}_1$  and  $\vec{v}_2$ .<sup>6</sup> The growth of the predator population is dominated by the dominant eigenvalue of  $\Lambda_1$ . We denote the dominant eigenvalue of  $L_b$  by  $\lambda_{\max}$  and that of  $\Lambda_1$  by  $\Lambda_{\max}$ . Then  $\Lambda_{\max}$  has the following modulus:

$$\|\Lambda_{\max}\| = \frac{(\rho + 1)\lambda_{\max} + \sqrt{(\rho + 1)^2 \lambda_{\max}^2 + 4mk^2}}{2}. \quad (3.31)$$

*Proof.* It is possible to solve for  $\Lambda_1, \Lambda_2$  directly. We wish to find a matrix  $\Lambda$  such that

$$\Lambda^2 - i(\rho + 1)L_b\Lambda + \rho L_b^2 + mk^2 I = 0. \quad (3.32)$$

Applying the quadratic formula yields

$$\begin{aligned} \Lambda_1 &= \frac{(1 + \rho)L_b^2 + \sqrt{(1 - \rho)^2 L_b^2 + 4mk^2}}{2} i \\ \Lambda_2 &= \frac{(1 + \rho)L_b^2 - \sqrt{(1 - \rho)^2 L_b^2 + 4mk^2}}{2} i. \end{aligned} \quad (3.33)$$

Note that the magnitude of  $\Lambda_1$  is greater than that of  $\Lambda_2$ . We approximate the population of the predator species at the limit as  $n \rightarrow \infty$ :

$$P_{a,n} = \|\vec{a}_n\| = \|\Lambda_1\|^n \|\vec{v}_1\| + \|\Lambda_2\|^n \|\vec{v}_2\| \approx \|\Lambda_1\|^n \|\vec{v}_1\|. \quad (3.34)$$

<sup>6</sup> $\vec{v}_1, \vec{v}_2$  are eigenvectors of the system.

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

$$\vec{\alpha}_0 = \vec{v}_2 \quad \text{and} \quad \vec{\alpha}_1 = \Lambda_2 \vec{v}_2, \quad (3.35)$$

which indicates that

$$\vec{\alpha}_1 = \Lambda_2 \vec{\alpha}_0. \quad (3.36)$$

Since  $\Lambda_2$  is purely imaginary,  $\alpha_1$  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

$$\vec{\alpha}_1 = iL_\alpha \vec{\alpha}_0 + km\vec{\beta}_0. \quad (3.37)$$

Therefore,  $\alpha_1$  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, one prey and one predator, with the same growth matrix  $L$ . We assume the two populations are non-vanishing without interaction; that is,  $\lambda_{max}$ , the dominant eigenvalue of  $L$  is greater than or equal to 1.

**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:*

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

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  $\beta$  over  $\alpha$ .

**4.1. Last Species Standing.** A similar analysis used for the predator-prey model can be applied to yield the following result.

**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*

$$D := \alpha_0 - \sqrt{m}\beta_0. \quad (4.2)$$

*In particular, if  $D > 0$ , then the population  $\alpha$  vanishes and population  $\beta$  grows exponentially. If  $D < 0$ , then the population  $\beta$  vanishes and the population  $\alpha$  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

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

we obtain the characteristic equation

$$\Lambda^2 - 2L\Lambda + L^2 - mk^2 = 0, \quad (4.4)$$

and by the quadratic formula, we derive the following roots:

$$\begin{aligned} \Lambda_1 &= L + k\sqrt{m}I \\ \Lambda_2 &= L - k\sqrt{m}I, \end{aligned} \quad (4.5)$$

where  $I$  is the identity matrix. Notice that  $k$  and  $m$  are both non-negative real values, and that  $L$  is assumed to guarantee positive population growth. Hence,  $\Lambda_1$  has a positive eigenvalue.

From (3.11), we characterize the population as

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

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

$$\vec{\alpha}_n \approx \Lambda_1^n \vec{v}_1. \quad (4.7)$$

Thus, the population is non-vanishing if and only if  $\vec{v}_1$  is positive. We compute  $\vec{v}_1$  directly. From 4.6, we obtain two conditions:

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

Solving for  $\vec{v}_1$  yields

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

Similarly, we obtain

$$\beta_n \approx \Lambda_1^n \vec{w}_1, \quad (4.10)$$

where

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

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

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

By induction, it is possible to prove that

$$\vec{\alpha}_n = \sqrt{m} \vec{\beta}_n \quad (4.13)$$

for all nonnegative integers  $n$ . In turn, we obtain

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

and the two populations grow or vanish simultaneously.  $\square$

## 5. APPLICATIONS OF THE COMPETITIVE MODEL

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.



**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 the both populations of the model rely on the same resource with a logistical growth rate.

Let  $r_n(t) : \mathbb{R} \rightarrow [0, 1]$  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  $\tau$  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  $\tau$ . 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  $r(t) = 0$ .

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

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

The quantity  $m$  determines the replenishing rate of the resources. For high values of  $\tau$ , we can estimate the  $r_n(t)$  as the following Iverson bracket.

$$r_{n+1}(\tau) = [T > \alpha_n + \beta_n] \quad (5.3)$$

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 [Bag19]. 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 Exclusion.

**5.3. Competitive Coexistence.** A classical example of competitive coexistence is from the experiment of Gause in the 1930's. The population of *P. Paramecium* and *P. Caudatum* was observed under a controlled environment. Both species shared a resource of *Bacillus pyocyaneus*. P.H. Leslie studied the population dynamics using the Lotka-Euler equations. We carry out a similar analysis using the Leslie model.

## 6. THE MIGRATION MODEL

### 7. POTENTIAL USE OF QUANTUM OPERATORS

### 8. GENERALISED FRAMEWORK: QUANTUM OPERATORS

**8.1. 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.

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 [Bag19b, Bag19c]. 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 [?] (*citation needs fixing*). We use previous work on this subject as a motivation



FIGURE 4.  $r(\tau)$  versus  $\alpha_n + \beta_n$

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.

**8.2. Hermitian of the Leslie Matrix.** In a quantum system, the time evolution of a state  $|\varphi\rangle$  can be described by the Schrodinger Equation:

$$\frac{\partial}{\partial t} i\hbar |\varphi(t)\rangle = iH |\varphi(t)\rangle. \quad (8.1)$$

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

$$|\varphi(t)\rangle = e^{iHt} |\varphi(0)\rangle. \quad (8.2)$$

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 8.1** (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*

$$\|L - I\| \leq 1,$$

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

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

**Proposition 8.2** (Algorithm to Compute the Hamiltonian). *The matrix logarithm of  $L$  is*

$$\log(L) = P \log(D) P^{-1}, \quad (8.3)$$

*where*

$$D = \text{diag}(d_1, \dots, d_N) \quad (8.4)$$

*and*

$$\log(D) = \text{diag}(\log(d_1), \dots, \log(d_N)). \quad (8.5)$$

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

$$\begin{aligned} e^{\log(L)} &= \sum_{k=0}^{\infty} \frac{(\log(L))^k}{k!} = \sum_{k=0}^{\infty} \frac{(P \log(D) P^{-1})^k}{k!} = \sum_{k=0}^{\infty} \frac{P \log(D)^k P^{-1}}{k!} \\ &= P \left( \sum_{k=0}^{\infty} \frac{\log(D)^k}{k!} \right) P^{-1} = P D P^{-1} = L \end{aligned} \quad (8.6)$$

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

$$\vec{p}_{n+1} := \tilde{L} \vec{p}_n = \begin{bmatrix} .2 & .2 & .2 & .5 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -.5 & -.5 & -.5 & 3 \end{bmatrix} \vec{p}_n. \quad (8.7)$$

We obtain

$$\log(\tilde{L}) \approx \begin{bmatrix} -0.3926 & -0.3606 & 0.5079 & 0.2940 \\ 1.9656 & -0.9006 & -0.8685 & -0.2296 \\ -3.2005 & 2.8342 & -0.0320 & 0.4569 \\ -0.5212 & -0.0644 & -0.2940 & 1.1627 \end{bmatrix}, \quad (8.8)$$

and by direct computation via MATLAB, we verify that

$$e^{\log(L)} \approx \begin{bmatrix} .2 & .2 & .2 & .5 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -.5 & -.5 & -.5 & 3 \end{bmatrix} = L. \quad (8.9)$$

□

## 9. FUTURE WORK

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