ANALYSIS ON LESLIE POPULATION MODELS: PREDATOR-PREY MODEL, COMPETETIVE MODEL, AND THE MIGRATION MODEL

STEVEN J. MILLER, DANIEL SON, JANINE WANG

ABSTRACT. Blah blah
  *Thm 2.5 *Thm 3.7 (Add that the complexity of the equation leads us to consider an alternate approach)
*Thm 3.11 *Thm 4.2

CONTENTS

1. INTRODUCTION

A Leslie matrix describes a time evolution of a homogeneous population with multiple age groups. Consider a population of Whales with three age groups. We wish to model the population of the whales in discrete time. Let $a^{(i)} : \mathbb{Z}_{\mathrm{pos}} \to \mathbb{R}$ for $1 \le i \le 3$ be the time dependent population. We use the sequence notation to denote the population at a specific time. e.g. $a_n^{(1)}$ denotes the population of the newborns at time n. For convenience, define the population vector as

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

Also, the total population is the sum of the population of all age groups, which is $a^{(1)} + a^{(2)} + a^{(3)}$.

Email addresses: `sjm1@williams.edu` (Steven J. Miller), `ds15@williams.edu` (Daeyoung Son), `jjw3@williams.edu` (Janine Wang)

We set the fertility of the whales to be $f > 0$ constantly among all age groups. Also, it is reasonable to assume that Whales have a survival rate of 1. That is, the whales do not die other than natural causes. Taking these facts into account, we obtain a set of equations that describe the time evolution of the population.

$$
\begin{aligned}
a_{n+1}^{(1)} &= f(a_n^{(1)} + a_n^{(2)} + a_n^{(3)}) \\
a_{n+1}^{(2)} &= a^{(1)}(t) \quad \text{and} \quad a_{n+1}^{(2)} = a^{(1)}(t)
\end{aligned}
\tag{1.2}
$$

This equation can be rewritten in matrix form. Define L, the Leslie matrix.

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

It is possible to use the same technique used to describe homogenous populations to describe hetrogenous populations. We move on to the predator-prey model. Suppose the whales consume plankton as food, which has a single population group. Denote $b : \mathbb{Z}_{\mathrm{pos}} \to \mathbb{R}$ to be the population of the plankton. Introduce a predation rate $k > 0$, predator population multiplier $m > 0$ along with the fertility rate of the plankton $F > 0$. Writing the new population vector as

$$
\vec{p}_n := (a_n^{(1)}, a_n^{(2)}, a_n^{(3)}, b_n)
\tag{1.4}
$$

we introduce a new model

$$
\vec{p}_{n+1} := \widetilde{L}\vec{p}_n = \begin{pmatrix} f & f & f & m \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ -k & -k & -k & 1+F \end{pmatrix} \vec{a}_n
\tag{1.5}
$$

Depending on the parameters (f, F, m, k), the model can describe the population where the predator exhausts the prey or consumes an appropriate amount such that both the predator and prey population grows mutually. In specific, if the predation rate is too high, the prey population is exhausted, and an adequete predation rate guarantees mutual population growth. Note that if the prey population is exhausted, the predator population will startve and eventually become distinct too.

(A) Case with low predation and mutual population growth

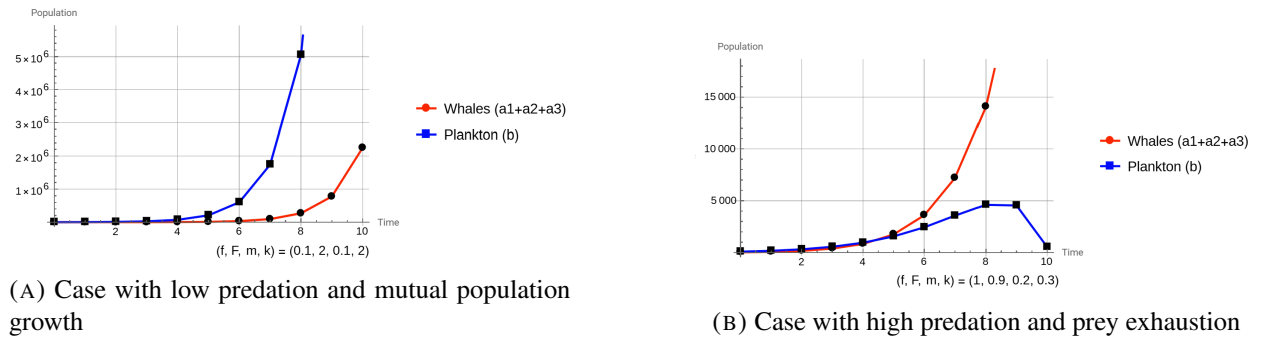(B) Case with high predation and prey exhaustion

FIGURE 1. Plot of model 1.5 for varying parameters

In the following sections, we define and study the eigenvalues of a simple leslie matrix (Section 2). Then, we present the Leslie Predator-Prey model for both real and imaginary values along with the Competitive population model. We present a closed form formula for the population using a generating function approach (Section 3.2). The complexity of the closed form formula motivates us to study the model for lower dimensions (Section 3.3). Finally, 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).

Saad, please edit this part according to your own whim, this is me hallucinating. We observe that the model described in 1.5 also displays oscillatory behavior. To study such oscillatory behavior in a coherent biological system, we define the migration model.
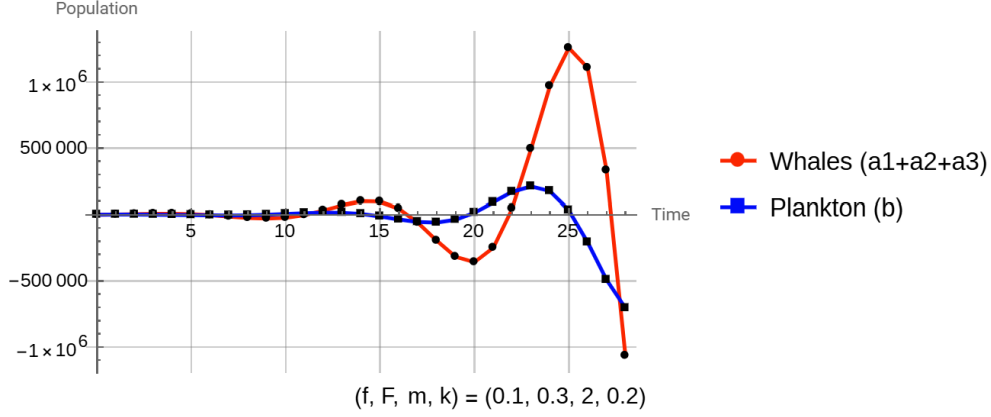

FIGURE 2. Figure of ocillatory population with high predtion

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 of the system under the assumption that the population obeys the Schrodinger's equation.

2. SINGLE SPECIES POPULATION

2.1. **Definition of Simple Leslie Matrices and the Lotka-Euler Equation.** Leslie Matrices characterize
the change of population with different age groups, given the survival rate and the fertility rate of the species.

We focus on a specific class of Leslie matrices with a fixed fertility rate f and a survival rate 1.

Definition 2.1 (Simple Leslie Matrices). *Suppose $N \in \mathbb{Z}_{\mathrm{pos}}$. A simple Leslie matrix that characterizes the population evolution is defined as follows.*

$$(L_f)_{ij} = \begin{cases} f & (i = 0) \\ 1 & (i \neq 0 \wedge j = i + 1) \\ 0 & otherwise; \end{cases}$$

or writing the matrix out,

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

.

The maximum eigenvalue of this matrix describes the asymptotic behavior of the population. The first approach is to compute the characteristic equation and find the roots to derive properties about the eigenvalues.

3

Theorem 2.2 (Lotka-Euler Equation). *The characteristic equation of a simple Leslie matrix L_f of order N greater than 1 is*

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

which, using the geometric series formula, can be simplified as

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

Proof. 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.

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

Expand the determinant 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

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

which concludes the proof. $\qquad\square$

2.2. **Bounding Maximum Eigenvalue.** To determine population strategies, it is useful to bound the maximum eigenvalues. Using methods from Complex Analysis, it is possible to derive the following two theorems.

Theorem 2.3 (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 the all the complex roots. Also, all the other roots lie inside the unit circle.*

Proof. We consider the polynomial

$$\widetilde{h}(z) = (z - 1)\text{ch}_N(z) = z^{N+1} - (f + 1)z^N + f \tag{2.1}$$

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

$$h(z) = \widetilde{h}(1/z)z^{N+1} := fz^{N+1} - (f + 1)z + 1 \tag{2.2}$$

has only two roots inside the unit circle, including $z = 1$ and some other unknown root that has a modulus strictly less than 1. We also note that the root $z = 1$ of $\widetilde{h}(z)$ is an extraneous root added by multiplying $(z - 1)$.

We invoke Rouche's Theorem.[1] Compare $h(z)$ with the function

$$g(z) = fz^{N+1} - fz. \tag{2.3}$$

Take a circular contour centered at the origin with radius $1 - \epsilon$ for some small ϵ. Call it $C_{1-\epsilon}$. At this contour, $|h(z)| < |g(z)|$. To verify, consider the following:

$$|h(z)| - |g(z)| \geq |h(z)| - |h(z)| - |g(z) - h(z)| = -|z - 1| < 0. \tag{2.4}$$

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. The only zeros included within the contour is $z = 0$. Hence, for any arbitrarily small $\epsilon > 0$, $h(z)$ has one zero inside the contour $C_{1-\epsilon}$

---

[1] Refer to [SS03] p91.

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

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

$$\mathrm{ch}_N(0) = -f < 0.$$
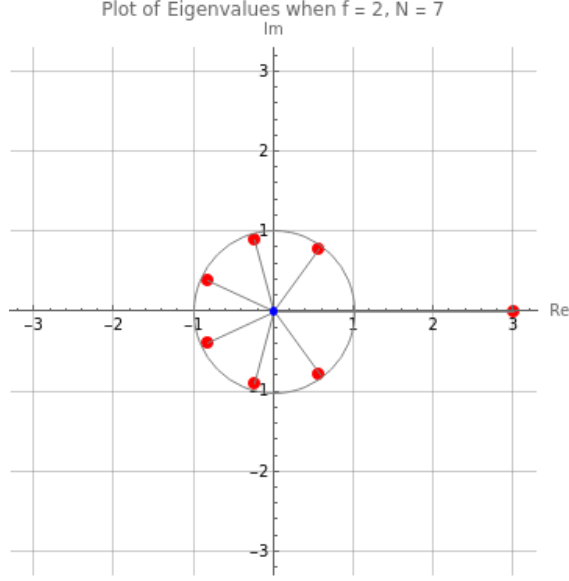
Assuming $f \geq 1$, we can write

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

If $f < 1$, then try $z = 2/f$.

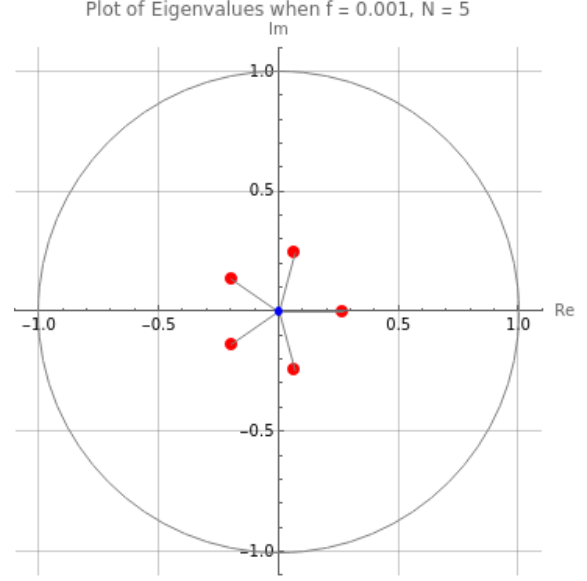$$\mathrm{ch}_N(2/f) = (2/f)^N - f\left(\frac{(2/f)^N - 1}{2/f - 1}\right) \geq 2^N/f^N - ((2/f)^N - 1) = 1 > 0$$

For both cases, invoke the Intermediate Value Theorem. Thus, there exists a real root for $\mathrm{ch}_N(z)$.
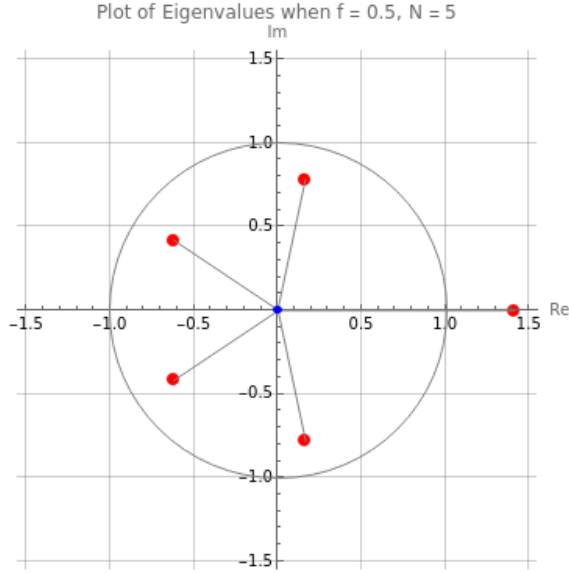
$\square$

We provide a plot of eigenvalues to provide further evidence for Theorem 2.3.

(A) $f > 1$, N odd

(B) Small fertility rate

(C) $f < 1$
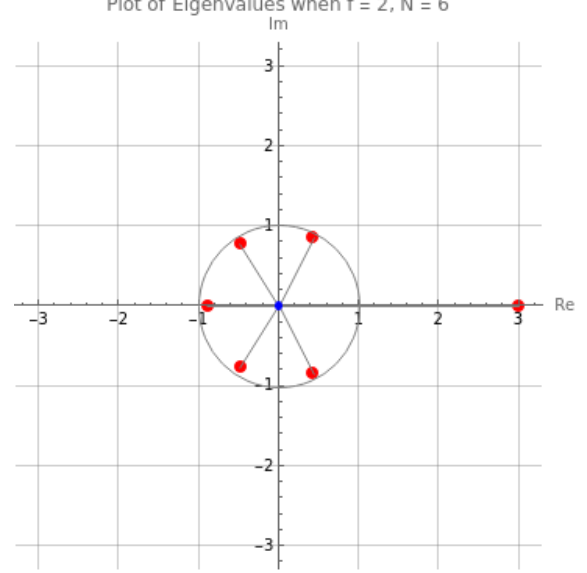
(D) $f > 1$, N even

FIGURE 3. Complex Eigenvalues of Simple Leslie Matrices for varying f, N.

Corollary 2.4 (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 $\mathrm{ch}_{(z)}$ can be evaluated somewhere in the interval $[1, \infty)$ to be positive. Evaluate the following:

$$\mathrm{ch}_N(1) \;=\; 1 - fN. \tag{2.5}$$

If this value is less than zero, than the real root lies somewhere in the range $(1, \infty)$. Otherwise, since $f(0) < 0$, the dominant root must be less than 1. $\qquad \square$

With a little more analysis, we provide a lower bound and the upper bound of the maximum eigenvalues of L_f.

Theorem 2.5 (Bounds for the maximum eigenvalue). *Given that $1 - fN \leq 0$, the maximum eigenvalue of L_f of order N is given by*

$$1 + f - \frac{1}{N} \leq \lambda_{\max} < 1 + f.$$

Proof. The upper bound is trivial:

$$\mathrm{ch}_N(1 + f) = f > 0.$$

We have $\mathrm{ch}_N(0) = -f < 0$, 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, we compute $\mathrm{ch}_N(z)$ at the 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

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

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

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

Which, using the ϵ substitution converts to

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

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

3. THE LESLIE PREDATOR-PREY MODEL

3.1. **The Classic Lotka-Volterra Model.** Let $x(t), y(t)$ be continuous functions that describe the density of the prey and predator. That is, the range of x, y are in the interval $[0, 1]$. The classical Predator-Prey Model is described by a system of differential equations.

$$\frac{dx}{dt} = rx(1 - x) - axy$$
$$\frac{dy}{dt} = ay(x - y) \tag{3.1}$$

The focus of study for the classical model is to find out the conditions for when the system reaches stability. In [Mer10], Merdan studies a similar system that accounts for the Allee effect, described by the equations below.

$$\frac{dx}{dt} = r\alpha(x)x(1 - x) - axy$$
$$\frac{dy}{dt} = ay(x - y) \tag{3.2}$$

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

$$r - \alpha\beta > 0 \tag{3.3}$$

the population converges to a positive stable state

$$(x_*, y_*) := ((r - \alpha\beta)/(a + r), (r - \alpha\beta)/(a + r)) \tag{3.4}$$

3.2. **The Predator-Prey Model with Leslie Matrices.** We wish to account for the different age groups in the predator and prey population. Hence, we replace the population density, which was a scalar function, into a vector. Also, we replace the reproductive and predation constants by a Leslie matrix.

Definition 3.1 (Leslie Predator-Prey). *Let $\vec{\alpha}_n, \vec{\beta}_n \in \mathbb{R}^N_{\text{pos}}$ be the population vectors of the predator and prey at timestep n. Set the number of age groups of both population to be N, so the population vectors will have entries.*

$$\vec{\alpha}_n = (\alpha_n^{(1)}, \ldots, \alpha_n^{(N)})$$
$$\vec{\beta}_n = (\beta_n^{(1)}, \ldots, \beta_n^{(N)}). \tag{3.5}$$

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

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

The constants k, m are predation ratio and nurturing ratios, both greater than zero. We set the population of predator and prey to be the sum of all entries. In symbols, we write $P_{a,n}, P_{b,n}$ the population of the predator and prey by the following sums.

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

We assume that the x-value of L_α is less than $1/2$ and that the x-value of L_β is greater than $1/2$. In other words, the predator population decays in absense of the prey and the prey populatin explodes in absence of the predator. Moreover, the population is fixed to be nonnegative.

If the population reaches zero at some time $n \in \mathbb{Z}_{\text{pos}}$, we say that the population has gone extinct. Notice that if the predation rate is too high, the prey population will be exhausted. In the absence of the prey, the predator population will become extinct. On the other hand, if the predation rate is too low, the predator population will not be able to maintain itself, and will become extinct. Hence, it is natural to ask the following question.

Problem 3.2 (Optimal Predation Strategy). *What ranges of the real value k guarantees exponential growth of the predator? Moreover, what value of k is necessary to guarantee maximum growth?*

Furthermore the real-valued formula motivates us to study the complex-valued model.

Definition 3.3 (Complex Predator-Prey). *Let $\alpha_n, \beta_n \in \mathbb{R}^N_{\text{pos}}$ for $n = 0$ $\alpha_n, \beta_n \in \mathbb{C}^N$ for $n > 0$ be the population vectors of the predator and prey at timestep n. The population vectors are defined by the following system of matrix differences.*

$$\vec{\alpha}_n = (\alpha_n^{(1)}, \ldots, \alpha_n^{(N)})$$
$$\vec{\beta}_n = (\beta_n^{(1)}, \ldots, \beta_n^{(N)}). \tag{3.8}$$

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

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

where k, m are predation ratio and nurturing ratios, both greater than zero, for we set the population of predator and prey to be the sum of all entries. In symbols, we write $P_{a,n}, P_{b,n}$ the population of the predator and prey by the following sums:

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

8

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 the following.

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

By elementary substitutions, we obtain the following proposition.

Proposition 3.5 (Coupled 1st order to 2nd order). *Assuming both the prey and predator population are nonextinct within a given period of time, the predator population satisfies the following second order difference equation:*

$$\begin{aligned}
\alpha_n &= (L_a + L_b)\alpha_{n-1} - L_b L_a \alpha_{n-2} - mk^2 \alpha_{n-2} \\
\beta_n &= (L_b + L_a)\beta_{n-1} - L_a L_b \beta_{n-2} - mk^2 \beta_{n-2}.
\end{aligned} \tag{3.11}$$

For the complex model,

$$\begin{aligned}
\alpha_n &= i(L_a + L_b)\alpha_{n-1} + L_b L_a \alpha_{n-2} - mk^2 \alpha_{n-2} \\
\beta_n &= i(L_b + L_a)\beta_{n-1} + L_a L_b \beta_{n-2} - mk^2 \beta_{n-2}.
\end{aligned} \tag{3.12}$$

The coupled second order difference equation can be solved using generating function 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 for the real case). *Suppose $\vec{\alpha}_n$ is the population vector of the predator in a real Leslie Predator-Prey model where $L = \rho L$ and $L_b = L$. The generating function of $\vec{\alpha}_n$ is*

$$G(x) = \frac{\left(\rho L + mk^2 - (\rho+1)Lx\right)\vec{\alpha}_0 + (\rho L + mk^2)x\vec{\alpha}_1}{x^2 - x(\rho+1)L + \rho L^2 + mk^2}. \tag{3.13}$$

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

$$\begin{aligned}
&\left[x^2 - x(\rho+1)L + (\rho L^2 + mk^2)\right]G(x) \\
&= -(\rho+1)L\vec{\alpha}_0 x + (\rho L^2 + mk^2)\vec{\alpha}_0 + (\rho L^2 + mk^2)\vec{\alpha}_1 x
\end{aligned} \tag{3.14}$$

This identity can be verified by substituting $G(x)$ and imposing the conditions on α_n. The expansion on the lefthand side has residues for terms that have an x power less than or equal to 2. Solve for $G(x)$ to obtain the result. $\qquad\square$

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

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

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

where D is defined by

$$D = L^2(1+\rho)^2 - 4(mk^2 + \rho L^2) \tag{3.16}$$

and the sequence δ_n is defined by

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

Proof. The derivation follows by applying partial fraction decomposition on the Generating Function. $\qquad\square$

Though the theorem gives a closed-form equation for the population, the complexity of the formula poses difficulties to determine the optimal predation rate for maximal growth.

3.3. **Real-Valued Model with Scalar** L. The following three propositions properly model the populations where 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 the scalarness, we write $l_a < 1$ and $l_b > 1$ instead of L_a, L_b.

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

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

The eigenvalues of this matrix is purely real if and only if

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \tag{3.18}$$

Otherwise, the eigenvalues of these matrices are complex conjugates of each other.

Proof. The characteristic equation of the companion matrix is

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

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

$$\frac{D}{4} := \frac{(l_a + l_b)^2}{4} - k^2 m + l_a l_b \geq 0 \tag{3.19}$$

With elementary algebra, we obtain

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}. \tag{3.20}$$

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

Theorem 3.9 (Exponential growth of population for small predation). *The following condition guarantees that the predator and prey population do not vanish as $n \to \infty$:*

$$k \leq \sqrt{\frac{(1 - l_b)(l_a - 1)}{m}}. \tag{3.21}$$

Proof. Assume that the discriminant is a nonnegative real value. Then the maximum eigenvalue must be

$$\frac{l_a + l_b}{2} + \frac{\sqrt{D}}{2}, \tag{3.22}$$

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

Theorem 3.10 (Complex eigenvalue implies extinction). *If*

$$k > \frac{l_a - l_b}{2\sqrt{m}} \tag{3.23}$$

then the population is guaranteed to go extinct.

Proof. It follows trivially that the condition (3.23) implies that the eigenvalue is complex. Also, the real part of the root will be $(l_a + l_b)/2$ which is guaranteed to be positive. Let the two eigenvalues of the companion matrix be γ and $\gamma*$ with

$$\gamma = r e^{i\theta}, \ \gamma* = r e^{-i\theta} \tag{3.24}$$

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

$$\alpha_n = \nu_1 \gamma^n + \nu_2 (\gamma*)^n. \tag{3.25}$$

We also observe that the population α_0, α_1 can be assumed to be a positive real value. If $\alpha_1 \leq 0$, then the population has gone extinct at time 1. Equation 3.25 for $n = 0, 1$ is

$$
\begin{aligned}
\alpha_0 &= \nu_1 + \nu_2 \\
a_1 &= \nu_1 \gamma + \nu_2 \gamma*
\end{aligned}
\tag{3.26}
$$

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

$$
\alpha_n = \Re(\nu \gamma^n) = \nu r^n \cos(n\theta)
\tag{3.27}
$$

We know that $\theta \in (0, \pi/2)$. Thus, there exists an integer n such that $\cos(n\theta) < 0$. We have shown that the predator population must go extinct. $\qquad\square$

$$\square$$

3.4. **The Complex-Valued 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 where the coefficients are Matrices. Since the only Matrices involved on this equation are I and L_β which commute, we can use the quadratic equation to solve this equation.

Theorem 3.11 (Maximum Eigenvalue for the general case). *The population vector of the predator in (2.1) can be characterized as*

$$
\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2
\tag{3.28}
$$

for some vectors $\vec{v}_1$ and $\vec{v}_2$. The growth of the predator population is dominated by the maximum eigenvalue of Λ_1. Call the maximum eigenvalue of L_b as $\lambda_{\max}$. Then, the maximum eigenvalue of Λ_1, denoted by $\Lambda_{\max}$ has the following modulus.

$$
\|\Lambda_{\max}\| = \frac{(\rho + 1)\lambda_{\max} + \sqrt{(\rho + 1)^2 \lambda_{\max}^2 + 4mk^2}}{2}
\tag{3.29}
$$

.

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

$$
\Lambda^2 - i(\rho + 1)L_b\Lambda + \rho L_b^2 + mk^2 I = 0
\tag{3.30}
$$

Apply the quadratic formula.

$$
\begin{aligned}
\Lambda_1 &= \frac{(1 + \rho)L_b^2 + \sqrt{(1 - \rho)^2 L_b^2 + 4mk^2}}{2}i \\
\Lambda_2 &= \frac{(1 + \rho)L_b^2 - \sqrt{(1 - \rho)^2 L_b^2 + 4mk^2}}{2}i.
\end{aligned}
\tag{3.31}
$$

The magnitude of Λ_1 is greater than that of Λ_2. We approximate the population of the predator at the limit $n \to \infty$.

$$
P_{a,n} = \|\vec{a}_n\| = \|\Lambda_1\|^n \|\vec{v}_1\| + \|\Lambda_2\|^n \|\vec{v}_2\| \approx \|\Lambda_1\|^n \|\vec{v}_1\|
\tag{3.32}
$$

It remains to show that the vector $\vec{v}_1$ is nonzero. Assume for a contradiction that $\vec{v}_1 = (0, \ldots, 0)$. Then we can write out the predator population at time 0, 1 as

$$
\vec{\alpha}_0 = \vec{v}_2, \ \vec{\alpha}_1 = \Lambda_2 \vec{v}_2
\tag{3.33}
$$

which indicates that

$$
\vec{\alpha}_1 = \Lambda_2 \vec{\alpha}_0
\tag{3.34}
$$

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

$$
\vec{\alpha}_1 = iL_\alpha \vec{\alpha}_n + km\vec{\beta}_n.
\tag{3.35}
$$

Therefore α_1 cannot be purely imaginary, which is a contradiction. □

4. THE COMPETITIVE MODEL

We can slightly modify one of the sign of the model and study the following system. Suppose there exists two identical population that has a same growth matrix L. Also, assume that the population is nonvanishing without interaction. That is, λ_{max}, the maximum eigenvalue of L is greater than or equal to 1.

Definition 4.1 (Leslie Competitive Model). *Let α_n, β_n be the population vectors of the predator and prey at timestep n. The competitive model is defined by the following system of matrix differences.*

$$
\begin{aligned}
\alpha_{n+1} &= \max(L\alpha_n - km\beta_n, \vec{0}) \\
\beta_{n+1} &= \max(L\beta_n - k\alpha_n, \vec{0})
\end{aligned}
\tag{4.1}
$$

k, m are interaction ratio and competitive advantage, both between $0, 1$.

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 $\vec{\alpha}_0 = \alpha_0(1, \dots, 1)$ and $\vec{\beta}_0 = \beta_0(1, \dots, 1)$. In a Leslie competetive model, one of the two species is likely to vanish as $n \to \infty$ The fate of the 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 grow exponentially together.

Proof. Proposition 3.5 can be simply 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 eqation

$$
\Lambda^2 - 2L\Lambda + L^2 - mk^2 = 0
\tag{4.4}
$$

and by the quadratic formula, we derive the root.

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

where I is the identity matrix. Notice that k, m are both nonnegative real values, and 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 $n \to \infty$,

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

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 $\vec{v}_1$, obtain

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

Similarly, we obtain

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

where

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

. If $D \neq 0$, plugging in the appropriate value of D yields the result. Suppose $D = 0$ or $\alpha_0 = \sqrt{m}\beta_0$. The conditions of 4.1 imply

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

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

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

and the population grows or vanishes simultaneously. $\qquad\square$

5. THE MIGRATION MODEL

6. POTENTIAL USE OF QUANTUM OPERATORS

7. FUTURE WORK

REFERENCES

[ArG89] R. Arditi and L. R. Ginzburg, *Coupling in predator-prey dynamics: Ratio-Dependence*, Journal of Theoretical Biology **139** (1989), no. 3, 311–326. https://doi.org/10.1016/S0022-5193(89)80211-5.

[Bag19] F. Bagarello, *Some Preliminaries*, in *Quantum Concepts in the Social, Ecological and Biological Sciences*, Cambridge University Press (2019), 7–56.

[Bag19b] F. Bagarello, *Closed Ecosystems*, in *Quantum Concepts in the Social, Ecological and Biological Sciences*, Cambridge University Press (2019), 168–193.

[Bag19c] F. Bagarello, *More on Biological Systems*, in *Quantum Concepts in the Social, Ecological and Biological Sciences*, Cambridge University Press (2019), 194–205.

[Gar21] F. Gargano, *Population dynamics based on ladder bosonic operators*, Applied Mathematical Modelling **96** (2021), 39–52. https://doi.org/10.1016/j.apm.2021.02.013.

[MeD09] H. Merdan, O. Duman, Ö. Akın, and C. Çelik, *Allee effects on population dynamics in continuous (overlapping) case*, Chaos, Solitons & Fractals **39** (2009), no. 4, 1994–2001. https://doi.org/10.1016/j.chaos.2007.06.062.

[Mer10] H. Merdan, *Stability Analysis of a Lotka–Volterra Type Predator–Prey System Involving Allee Effects*, The ANZIAM Journal **52** (2010), no. 2, 139–145. https://doi.org/10.1017/S1446181111000630.

[ZhL05] S.-R. Zhou, Y.-F. Liu, and G. Wang, *The stability of predator–prey systems subject to the Allee effects*, Theoretical Population Biology **67** (2005), no. 1, 23–31. https://doi.org/10.1016/j.tpb.2004.06.007.

[SS03] E. M. Stein and R. Shakarchi, *Complex Analysis*, Princeton University Press (2003).