Predator-Prey Model using Leslie matricies and optimal predation strategies

PP Group

Contents

1 Abstract

In this paper, we introduce a new predator-prey model based the Lotka-Voltera model. Extensive study have been conducted on the stability of the equation for the simple model which considers an homogenous population . For example, Merdan carries out a stability analysis by computing the Jacobian and drawing from methods of differential calculus.

We replace the population evolution constants to 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.

Moreover, we analyze an open population where migration is allowed. We first study population under constant migration provide conditions for harmonic fluctuations of the model. Also, expanding on the work of Arditi and Ginzburg, we study the case where migration considered as a response to the environment, i.e. dependent on the population.

2 Single Species Population

2.1 Definition of Simple Leslie Matricies and the Lotka-Euler Equation

Leslie matricies 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 matricies with a fixed fertility rate f and a survival rate 1.

Definition 2.1 (Simple Leslie Matricies). *Suppose $N \in \mathbb{Z}_{pos}$. 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 apporach is to compute the characteristic equation and find the roots to derive properties about the eigenvalues.

Theorem 2.1 (Lotka-Euler Equation). *The characteristic equation of a simple leslie matrix L_f of order N greater than 1 is*

$$ch_N(x) := x^N - f(x^{N-1} + \cdots + x + 1)$$

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 $N > 2$. We write out the characteristic polynomial as a determinant expansion.

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

Expand the determinant with respect to the last column.

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

By the inductive hypothesis, we write

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

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 2.2 (Complex Roots of the Characteristic Equation)**.** *The characteristic equation* $\text{ch}_N(z)$ *has exactly one dominating real eigenvalue. All other roots lie inside the unit circle.*

Proof. We consider the polynomial

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

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

$$h(z) \;:=\; \bar{h}(1/z)z^{N+1} \;:=\; fz^{N+1} - (f+1)z + 1$$

has only two roots inside the unit circle, including $z = 1$ and some other unknown root that has a modullus strictly less than 1.

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

$$g(z) \;:=\; fz^{N+1} - fz$$

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.

$$|h(z)| - |g(z)| \;\geq\; |h(z)| - |h(z)| - |g(z) - h(z)| \;=\; -|z-1| \;<\; 0$$

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 $C_{1-\epsilon}$

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 $\text{ch}_N(z)$ has one real eigenvalue. Divide into two cases when $f \geq 1$ and $f < 1$. Also, trivially

$$\text{ch}_N(0) \;=\; -f < 0$$
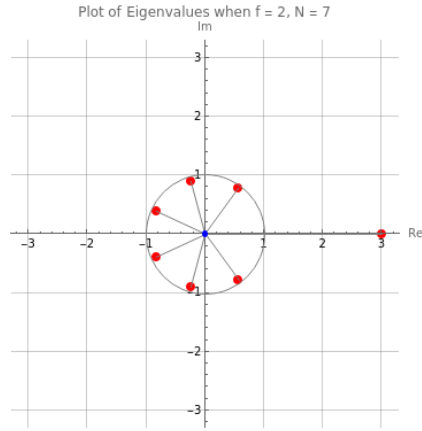
3

. Assuming $f \geq 1$, we can write

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

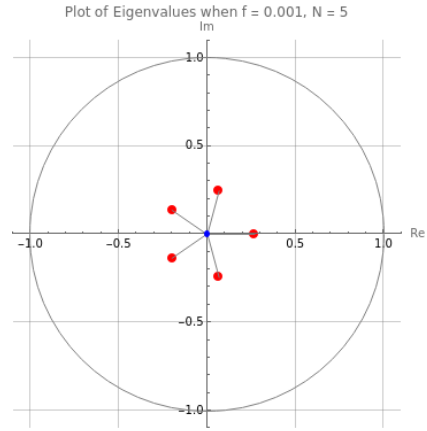If $f < 1$, then try $z = 2/f$.

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

For both cases, invoke the intermediate value theorem. There exists a real root for $\mathrm{ch}_N(z)$.
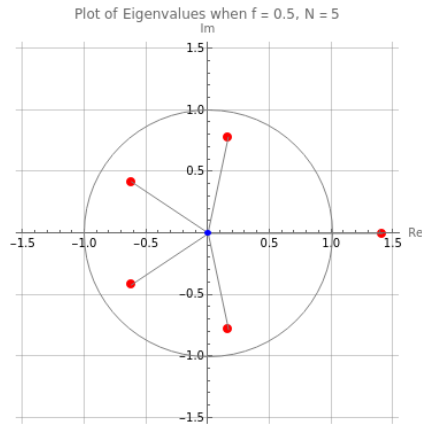
$\square$

We provide a plot of eigenvalues to provide further evidence for theorem (2.2).
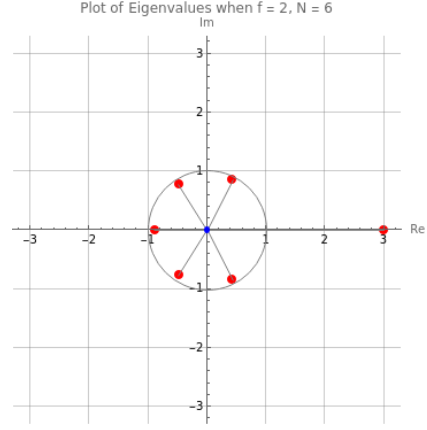
(a) $f > 1$, N odd

(b) Small fertility rate

(c) $f < 1$

(d) $f > 1$, N even

Figure 1: Complex Eigenvalues of Simple Leslie Matricies for varying f, N

Corollary 2.1 (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 $\text{ch}_{(}z)$ can be evaluated somewhere in the interval $[1, \infty)$ to be positive. Evaluate the following.

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

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. $\square$

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

Theorem 2.3 (Bounds for the maximum eigenvalue). *Given that* $1 - fN \leq 0$, *the maximum eigenvalue of* L_f *of order* N *is given by*

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

Proof. The upper bound is trivial.

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

$\text{ch}_N(0) = -f < 0$ and by the intermediate value theorem, the maximum root is bounded.

To obtain the lower bound, we write $f = 1/N + \epsilon$ for some $\epsilon > 0$. With some algebra, we compute $\text{ch}_N(z)$ 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.

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

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

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

Which, using the ϵ substitution converts to

$$1 + N\epsilon - (1 + \epsilon)^N \ < \ 0$$

And expanding the power term by the binomial theorem, the inequality must hold. $\square$

3 The predator-prey model

3.1 The predator-prey model with Leslie Matricies

Definition 3.1 (Leslie Predator-Prey). *Let $\vec{\alpha}_n$, $\vec{\beta}_n$ 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.*

$$\begin{aligned}
\vec{\alpha}_n &= (\alpha_n^{(1)}, \ldots, \alpha_n^{(N)}) \\
\vec{\beta}_n &= (\beta_n^{(1)}, \ldots, \beta_n^{(N)})
\end{aligned} \tag{3.1}$$

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

$$\begin{aligned}
\vec{\alpha}_{n-1} &= L_a \vec{\alpha}_n + km\vec{\beta}_n \\
\vec{\beta}_{n-1} &= L_b \vec{\beta}_n - k\vec{\alpha}_n
\end{aligned} \tag{3.2}$$

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.

$$P_{a,n} = \sum_{k=1}^{N} \alpha_n^{(k)} \quad and \quad P_{b,n} = \sum_{k=1}^{N} \beta_n^{(k)} \tag{3.3}$$

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 $n \in \mathbb{Z}_{pos}$, 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 be extinct. On the other hand, if the predation rate is too low, the predator population will not be able to maintain itself, and hence will go extinct. Hence, it is natural to ask the following question.

Question 3.1 (Optimal Predation Strategy). *For 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 introduce an extra factor of i in the recurrence.

Definition 3.2 (Complex Predator-Prey). *Let α_n, β_n be the population vectors of the predator and prey at timestep n. The population vectors are defined by the following system of matrix differences.*

$$\begin{aligned}
\vec{\alpha}_n &= (\alpha_n^{(1)}, \ldots, \alpha_n^{(N)}) \\
\vec{\beta}_n &= (\beta_n^{(1)}, \ldots, \beta_n^{(N)})
\end{aligned} \tag{3.4}$$

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

$$\vec{\alpha}_{n-1} = iL_a\vec{\alpha}_n + km\vec{\beta}_n$$
$$\vec{\beta}_{n-1} = iL_b\vec{\beta}_n - k\vec{\alpha}_n \qquad (3.5)$$

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.

$$P_{a,n} = \left\| \sum_{k=1}^{N} \alpha_n^{(k)} \right\| \quad and \quad P_{b,n} = \left\| \sum_{k=1}^{N} \beta_n^{(k)} \right\| \qquad (3.6)$$

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.

Question 3.2 (Modeling Predator Growth). *What is the growth rate of the predator as $n \to \infty$*

By elementary substitutions, we obtain the follwoing proposition.

Proposition 3.1 (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.*

$$\alpha_n = (L_a + L_b)\alpha_{n-1} - L_b L_a \alpha_{n-2} - mk^2\alpha_{n-2}$$
$$\beta_n = (L_b + L_a)\beta_{n-1} - L_a L_b \beta_{n-2} - mk^2\beta_{n-2} \qquad (3.7)$$

For the complex model,

$$\alpha_n = i(L_a + L_b)\alpha_{n-1} + L_b L_a \alpha_{n-2} - mk^2\alpha_{n-2}$$
$$\beta_n = i(L_b + L_a)\beta_{n-1} + L_a L_b \beta_{n-2} - mk^2\beta_{n-2} \qquad (3.8)$$

.

The coupled second order difference equation can be solved using generating function under the assumption that the leslie matricies of the two populations are constant multiples of each other.

Theorem 3.1 (Generating Function of the predator population for 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*

$$G(x) = \frac{\left(\rho L + mk^2 - (\rho + 1)Lx\right)\vec{\alpha}_0 + (\rho L + mk^2)x\vec{\alpha}_1}{x^2 - x(\rho + 1)L + \rho L^2 + mk^2} \qquad (3.9)$$

Proof. From the recurrence relation provided in proposition 3.1, we have the following identity.

$$\left[x^2 - x(\rho + 1)L + (\rho L^2 + mk^2)\right]G(x)$$
$$= -(\rho + 1)L\vec{\alpha}_0 x + (\rho L^2 + mk^2)\vec{\alpha}_0 + (\rho L^2 + mk^2)\vec{\alpha}_1 x \qquad (3.10)$$

8

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 a x power less than or equal to 2. Solve for $G(x)$ to obtain the result. $\square$

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

Theorem 3.2 (Formula for $\vec{\alpha}_n$). *For $\vec{\alpha}_n$ where $n > 0$,*

$$\vec{\alpha}_n = \frac{(L^2\rho + k^2m)^{n-2}}{\sqrt{D}} \left[\left((k^2m + L^2\rho)\vec{\alpha}_1 - L(1+\rho)\left(k^2m + L^2\rho\right)\vec{\alpha}_0\right)\delta_{n-1} + \left(k^2m + L^2\rho\right)^2 \vec{\alpha}_0\delta_n \right]$$
(3.11)

where D is defined as

$$D = L^2(1+\rho)^2 - 4(mk^2 + \rho L^2)$$
(3.12)

and sequence δ_n defined as

$$\delta_n = \left(\frac{1}{2}\right)^n \left(\frac{1}{L^2\rho + k^2m}\right)^n \left[\sum_{\substack{l=1 \\ l \text{ odd}}}^{n+1} \binom{n+1}{l} [L(1+\rho)]^{t+1-l}(\sqrt{D})^l \right]$$
(3.13)

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

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

3.2   Real-valued model where L is a scalar

The following three propositions properly models the population where the dimension of the Leslie matrix is 1. That is, the population growth is characterized by a exponential of a scalar without interaction. To emphasize the scalarness, write $l_a < 1$ and $l_b > 1$ instead of L_a, L_b.

Theorem 3.3 (Eigenvalues of the companion matrix). *Using proposition (3.1), it is possible to obtain a companion matrix that describes the population.*

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

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

$$k \leq \frac{l_a - l_b}{2\sqrt{m}}$$
(3.14)

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

9

Proof. The coefficient matrix of the companion matrix is

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

. The discriminant of this polynomial must be a nonnegative value. In symbols,

$$\frac{D}{4} = \frac{(l_a + l_b)^2}{4} - k^2 m + l_a l_b \geq 0 \tag{3.15}$$

With elementary algebra, we obtain

$$k \leq \frac{l_a - l_b}{2\sqrt{m}} \tag{3.16}$$

$\square$

Theorem 3.4 (Exponential growth of population for small predation). *The following condition guarantees that the predator and prey population to not vanish as $n \to \infty$.*

$$k \leq \sqrt{\frac{(1 - l_b)(l_a - 1)}{m}} \tag{3.17}$$

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

$$\frac{l_a + l_b}{2} + \frac{\sqrt{D}}{2}$$

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

Theorem 3.5 (Complex eigenvalue implies extinction). *If*

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

then the population is guaranteed to be extinct.

Proof. It follows trivially that the condition (3.18) implies that the eigenvalue is complex. Consider powers of the complex eigenvalues as rotation along the complex plane. There exists some arbitrary rotation that guarantees the real part of the power to be negative. $\square$

$\square$

3.3 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 matricies. Since the only matricies involved on this equation are I and L_β which commute, we can use the quadratic equation to solve this equation.

Theorem 3.6 (Maximum Eigenvalue for the general case)**.** *The population vector of the predator in (2.1) can be characterized as*

$$\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2 \tag{3.19}$$

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 λ_{max}. Then, the maximum eigenvalue of Λ_1, denoted by Λ_{max} has the following modullus.

$$\|\Lambda_{max}\| = \frac{(\rho + 1)\lambda_{max} + \sqrt{(\rho + 1)^2 \lambda_{max}^2 + 4mk^2}}{2} \tag{3.20}$$

.

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

$$\Lambda^2 - i(\rho + 1)L_b\Lambda + \rho L_b^2 + mk^2 I = 0 \tag{3.21}$$

Apply the quadratic formula.

$$\Lambda_1 = \frac{(1 + \rho)L_b^2 + \sqrt{(1 - \rho)^2 L_b^2 + mk^2}}{2} i$$

$$\Lambda_2 = \frac{(1 + \rho)L_b^2 - \sqrt{(1 - \rho)^2 L_b^2 + mk^2}}{2} i \tag{3.22}$$

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

$$P_{a,n} = \|\vec{a}_n\| = \|\Lambda_1\|^n \|\vec{v}_1\| + \|\Lambda_2\|^n \|\vec{v}_2\| \approx \|\Lambda_1\|^n \|\vec{v}_1\| \tag{3.23}$$

$\square$

With some more analysis, we provide a bound for k that guarantees the survival of both the predator and k.

4   The Competetive 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 Competetive Model)**.** *Let α_n, β_n be the population vectors of the predator and prey at timestep n. The competetive model is defined by the following system of matrix differences.*

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

k, m are interaction ratio and competetive 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 4.1 (Last Species Standing). *Suppose $\vec{\alpha}_0 = \alpha_0(1, \cdots, 1)$ and $\vec{\beta}_0 = \beta_0(1, \cdots, 1)$. In a Leslie competetive model, one of the two species are likely to vanish as $n \to \infty$ The fate of the species is determined by the sign of the term*

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

. To qualify, 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 (3.1) can be simply generalized by the substitution $m \mapsto -m$. From the recursive relation

$$\alpha_n = (2L)\alpha_{n-1} - L^2\alpha_{n-2} + mk^2\alpha_{n-2} \tag{4.2}$$

we obtain the characteristic eqation

$$\Lambda^2 - 2L\Lambda + L^2 - mk^2 = 0 \tag{4.3}$$

and by the quadratic formula, we derive the root.

$$\Lambda_1 = L + k\sqrt{m}I \quad \text{and} \quad \Lambda_2 = L - k\sqrt{m}I \tag{4.4}$$

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 (3.6), we characterize the population as

$$\vec{\alpha}_n = \Lambda_1^n \vec{v}_1 + \Lambda_2^n \vec{v}_2 \tag{4.5}$$

In the far limit, as $n \to \infty$,

$$\vec{\alpha}_n \approx \Lambda_1^n \vec{v}_1 \tag{4.6}$$

Thus, the population is nonvanishing if and only if $\vec{v}_1$ is positive. Compute $\vec{v}_1$ directly. We have the following conditions from (4.5), we obtain two conditions.

$$\vec{\alpha}_0 = \vec{v}_1 + \vec{v}_2$$
$$\vec{\alpha}_1 = \Lambda_1 \vec{v}_1 + \Lambda_2 \vec{v}_2 \tag{4.7}$$

Solving for $\vec{v}_1$, obtain

$$\vec{v}_1 = \frac{\Lambda_2 \vec{\alpha}_0 - \vec{\alpha}_1}{\Lambda_2 - \Lambda_1} = \frac{L\vec{\alpha}_0 - k\sqrt{m}\vec{\alpha}_0 - L\vec{\alpha}_0 + km\beta_0}{2mk} = \frac{\sqrt{m}\vec{\beta}_0 - \vec{\alpha}_0}{2\sqrt{m}}$$
$$= \frac{\sqrt{m}\beta_0 - \alpha_0}{2\sqrt{m}}(1, \ldots, 1) = -\frac{D}{2\sqrt{m}}(1, \ldots, 1) \tag{4.8}$$

12

Similarly, we obtain

$$\beta_n \approx \Lambda_1 \vec{w}_1 \tag{4.9}$$

where

$$\vec{w}_1 = \frac{\alpha_0 - \sqrt{m}\beta_0}{2\sqrt{m}}(1,\ldots,1) = \frac{D}{2\sqrt{m}}(1,\ldots,1) \tag{4.10}$$

. 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 the following.

$$\begin{aligned}
\vec{\alpha}_1 &= L\vec{\alpha}_0 - k\sqrt{m}\vec{\alpha}_0 \\
\vec{\beta}_1 &= L\vec{\beta}_0 - k\sqrt{m}\vec{\beta}_0
\end{aligned} \tag{4.11}$$

By induction, it is possible to prove that

$$\vec{\alpha}_n = \sqrt{m}\vec{\beta}_n \tag{4.12}$$

for all nonnegative integers n. In turn, we obtain

$$\begin{aligned}
\vec{\alpha}_{n+1} &= \left(L - k\sqrt{m}\right)^n \vec{\alpha}_0 \\
\vec{\beta}_{n+1} &= \left(L - k\sqrt{m}\right)^n \vec{\beta}_0
\end{aligned} \tag{4.13}$$

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