BILKENT UNIVERSITY FACULTY OF MATHEMATICS



Introduction to Applied Mathematics

Class Project

Analysis on Prey-Predator Models, Lotka-Volterra Equations

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1 Introduction

Understanding ecological system dynamics is essential for understanding species interactions and how they affect the overall stability and biodiversity of an ecosystem. The Lotka-Volterra equations, developed in the early 20th century by Alfred J. Lotka and Vito Volterra, transformed the study of predator-prey interactions in ecological systems. These equations formed a set of coupled differential equations that might be used to scientifically explain the oscillations and connectedness observed in natural ecosystems. They have a significant influence on the discipline of mathematical biology and have sparked further investigation and modeling in a number of domains.

1.1 Structure

We will start by introducing the reader with both the non-linear and linear models for the Lotka-Volterra equations. Then we will proceed by showing how perturbation can be used to analyze and find an analytical solution for the non-linear model. Afterwards we will analyze and visualize the linear model in search of extracting valuable information about the ecological systems.

2 Models

2.1 Linear Model

Linear model for the Lotka Volterra equations consists of two coupled differential equations. First of them represents the change in the prey population at a given time and the second one is the change in the predator population.

$$\frac{\partial x}{\partial t} = \alpha x - \beta x y \tag{2.1}$$

$$\frac{\partial y}{\partial t} = \delta xy - \gamma y \tag{2.2}$$

where x represents the population density of the prey, y represents the population density of the predator, $\frac{\partial x}{\partial t}$ and $\frac{\partial y}{\partial t}$ represent the growth rates of the populations. α represents the maximum prey per capita. β represents the effect of predators on the prey growth rate. δ represents the predator's per capita death rate. γ represents the effect of the presence of

the prey on the growth of the predator and α , β , δ , $\gamma > 0$.^[4]

2.2 Non-Linear Model

Like the linear non-linear model consists of two equations that represent the changes in the population sizes of preys and predators. But both impose that as the population density increases its effect to the size will be negative and it is proportional with the square of the population at that point.

$$x_1' = (a_1 - b_1 x_1 - c_1 x_2) x_1 (2.3)$$

$$x_2' = (-a_2 + b_2 x_1 - c_2 x_2) x_2 (2.4)$$

where x'_1 and x'_2 represent the growth rates of the populations. [2]

3 Perturbation Methods

Now that we have presented the reader with the non-linear model in this section we will continue by showing how perturbation methods can be used to approximate the non-linear part and find analytical solutions.^[1]

3.1 Analysis

$$x_1' = (a_1 - b_1 x_1 - c_1 x_2) x_1 (3.1)$$

$$x_2' = (-a_2 + b_2 x_1 - c_2 x_2) x_2 (3.2)$$

First to analyze the system the changes in the population sizes are set to zero and the equilibrium points of the system are found. These are (0,0), $\left(0,\frac{-a_2}{c_2}\right)$, $\left(\frac{a_1}{b_1},0\right)$ and (α,β) where,

$$\alpha = \frac{a_1c_2 + a_2c_1}{b_1c_2 + b_2c_1}, \quad \beta = \frac{a_1b_2 - a_2b_1}{b_1c_2 + b_2c_1}$$

Afterward to setup the perturbation on the non-linear part observe the alternative forms of the equations,

$$\frac{\partial x}{\partial t} = f_1(x, y, t) + \epsilon g_1(x, y, t) \tag{3.3}$$



$$\frac{\partial y}{\partial t} = f_2(x, y, t) + \epsilon g_2(x, y, t) \tag{3.4}$$

and let $x(0) = P_0$ and $y(0) = P_1$ be the initial conditions. Where the non-linear and linear parts of the equations are grouped and ϵ is put in front of the non-linear part to use in the perturbation.

Then in order to represent the deviations from the equilibrium point (α, β) two new variables are defined. $y_1 = x_1 - \alpha$ and $y_2 = x_2 - \beta$. Afterwards substitution into (3.1), (3.2) yields the following.

$$y_2' = b_2 \beta y_1 - c_2 \beta y_2 + b_2 y_1 y_2 - c_2 y_2^2 \tag{3.5}$$

$$y_2' = b_2 \beta y_1 - c_2 \beta y_2 + b_2 y_1 y_2 - c_2 y_2^2 \tag{3.6}$$

After the substation both x and y terms are expanded

$$y_1(t) = y_{10}(t) + \epsilon y_{11}(t) + \epsilon^2 y_{12}(t) + \dots$$
(3.7)

$$y_2(t) = y_{20}(t) + \epsilon y_{21}(t) + \epsilon^2 y_{22}(t) + \dots$$
(3.8)

and ϵ is put in front of the components of respected $g_i(x, y, t)$

$$y_1' = -b_1 \alpha y_1 - c_1 \alpha y_2 - c_1 \epsilon y_1 y_2 - b_1 \epsilon y_1^2 \tag{3.9}$$

$$y_2' = b_2 \beta y_1 - c_2 \beta y_2 + b_2 \epsilon y_1 y_2 - c_2 \epsilon y_2^2$$
(3.10)

Substituting (3.7) and (3.8) into (3.9) and (3.10). And equating equal orders of ϵ yields the following differential equations

$$y'_{10} = -b_1 \alpha y_{10} - c_1 \alpha y_{20} \tag{3.11}$$

$$y_{20}' = -c_2 \beta y_{20} + b_2 \beta y_{10} \tag{3.12}$$

$$y'_{11} = -b_1 y_{10}^2 - b_1 \alpha y_{11} - c_1 \alpha y_{21} - c_1 y_{10} y_{20}$$
(3.13)

$$y_{21}' = -c_2 y_{20}^2 - c_2 \beta y_{21} + b_2 \beta y_{11} + b_2 y_{10} y_{20}$$
(3.14)

Hence the solutions for the equation (3.9) and (3.10), with the initial conditions $y_{10}(0) = p_0$, $y_{20}(0) = p_1$ to generate solutions for $y_{10}(t)$ and $y_{20}(t)$.

$$y_{10}(t) = \frac{1}{r_1 - r_2} \left[\left(r_1 e^{r_1 t} - r_2 e^{r_2 t} \right) p_0 + \left(p_0 c_2 \beta - p_1 c_1 \alpha \right) \left(e^{r_1 t} - e^{r_2 t} \right) \right]$$
(3.15)



$$y_{20}(t) = \frac{1}{r_1 - r_2} \left[\left(r_1 e^{r_1 t} - r_2 e^{r_2 t} \right) p_1 + \left(p_1 b_1 \alpha + p_0 b_2 \beta \right) \left(e^{r_1 t} - e^{r_2 t} \right) \right]$$
(3.16)

where r_1 and r_2 from discriminant of quadratic equation, with $r_1 - r_2 \neq 0$ $r_1 = \frac{-(\alpha b_1 + c_2 \beta) + \sqrt{(\alpha b_1 + c_2 \beta)^2 - 4\alpha \beta (c_1 b_2 + c_2 b_1)}}{2}, r_2 = \frac{-(\alpha b_1 + c_2 \beta) - \sqrt{(\alpha b_1 + c_2 \beta)^2 - 4\alpha \beta (c_1 b_2 + c_2 b_1)}}{2}$ and α , β as mentioned above.

$$y_{11}(t) = A_1 e^{r_1 t} + A_2 e^{r_2 t} + A_3 e^{2r_1 t} + A_4 e^{2r_2 t} + A_5 e^{(r_1 + r_2)t}$$

$$y_{21}(t) = B_1 e^{r_1 t} + B_2 e^{r_2 t} + B_3 e^{2r_1 t} + B_4 e^{2r_2 t} + B_5 e^{(r_1 + r_2)t}$$
(3.17)

We calculated all the coefficients A_i 's and B_i 's but did not add them here cause they are long and complicated, we mentioned them at the end of the paper. Let's look at the appropriate solution of (3.9) and (3.10) in terms of the first correction terms.

$$y_1(t) \cong y_{10} + y_{11}(t)$$

 $y_2(t) \cong y_{20} + y_{21}(t)$
(3.18)

Hence the solutions of the $x_1(t)$ and $x_2(t)$, original prey and predator populations, with substituting back, we the the followings;

$$x_{1}(t) = \frac{a_{1}c_{1} + a_{2}c_{1}}{b_{1}c_{2} + b_{2}c_{1}} + \left[\frac{(r_{1} + \beta c_{2}) p_{0} - p_{1}c_{1}\alpha}{r_{1} - r_{2}} + A_{1} \right] e^{r_{1}t}$$

$$- \left[\frac{(r_{2} + \beta c_{2}) - p_{1}c_{1}\alpha}{r_{1} - r_{2}} - A_{2} \right] e^{r_{2}t} + A_{3}e^{2r_{1}t} + A_{4}e^{2r_{2}t} + A_{5}e^{(r_{1} + r_{2})t}$$

$$x_{2}(t) = \frac{a_{1}b_{2} - a_{2}b_{1}}{b_{1}c_{2} + b_{2}c_{1}} + \left[\frac{(r_{1} + \alpha b_{1}) p_{1} + p_{1}b_{2}\beta}{r_{1} - r_{2}} + B_{1} \right] e^{r_{1}t}$$

$$- \left[\frac{(r_{2} + \alpha b_{1}) p_{1} + p_{0}b_{2}\beta}{r_{1} - r_{2}} - B_{2} \right] e^{r_{2}t} + B_{3}e^{2r_{1}t} + B_{4}e^{2r_{2}t} + B_{5}e^{(r_{1} + r_{2})t}$$

Thus we finally get the approximation solutions of the general form of Lotka-Volterra equations (3.1) and $(3.2)^{[1]}$

4 Analysis on the Linear Model

Now that we have examined the non-linear model for the Lotka-Volterra equations in this section we will introduce the reader to a simpler version which was used by Vito Volterra in the early 20th century. This version offers us with a better understanding of the inner workings of the model and enables us to extract valuable insights for researching



predator-prey interactions.

$$\frac{\partial x}{\partial t} = \alpha x - \beta x y \tag{4.1}$$

$$\frac{\partial y}{\partial t} = \delta xy - \gamma y \tag{4.2}$$

[4]

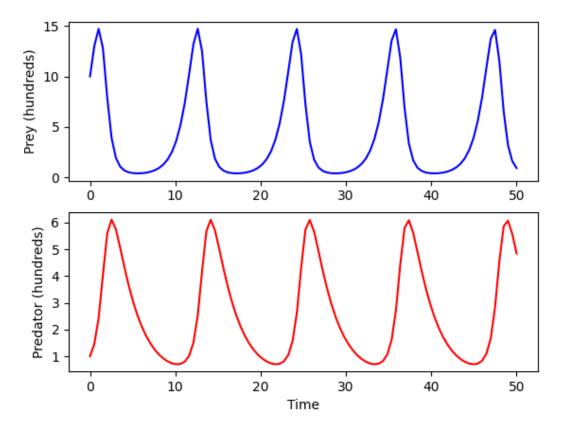


Figure 4.1: Prey - Predator

The python code to generate this graph can be found at the end of the document.

- 1. Population sizes are directly correlated to each other.
- 2. Predators over hunt and cause the food supply to decrease which result in a decrease in the predator's population.
- 3. As soon as the predator population decreases. Suitable grounds for preys to repopulate forms and prey population starts a steep increase.

4. Due to the reasons above there is a cyclical correlation between the populations of prey and predator.

4.1 Alternative Visualization

We can also represent these equations without time. Which would provide a visual representation that would show the correlation between the sizes of populations.

$$\frac{\partial y}{\partial x} = -\frac{y}{x} \frac{\gamma x - \delta}{\beta y - \alpha}$$

Rearranged using the separation of variables yields the following equation,

$$\frac{\beta y - \alpha}{y} dy + \frac{\delta x - \gamma}{x} dx = 0 \tag{4.3}$$

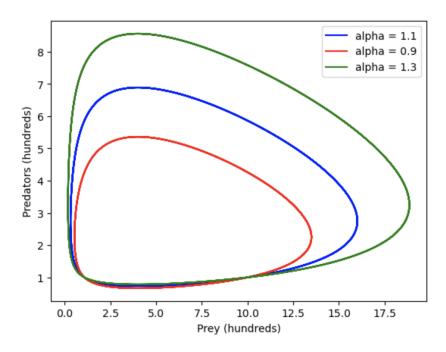


Figure 4.2: Prey - Predator (Without Time)

We see that this alternative way of representing the system of equations gives us insights about the effects of different values of α where higher values of alpha generally correspond to faster growth of the prey population, which can result in increased oscillations and more frequent predator-prey cycles. And lower values of alpha, can lead to more stable equilibria and slower population dynamics.

4.2 Equilibrium

Equilibrium occurs when neither population level is changing hence to find the desired points we set up and solve the following equations,

$$x(\alpha - \beta y) = 0$$

$$-y(\gamma - \delta y) = 0$$

Which results in two fixed points where the change in both population sizes is zero. (x, y) = (0, 0) and (x, y) = $(\frac{\alpha}{\beta}, \frac{\gamma}{\delta})$

4.3 Stability

Now that we have found the fixed points we can find the Jacobi matrix of this model and analyze stability near these fixed points. With that purpose we first continue by finding the Jacobian matrix. Let $f_1(x, y) = \alpha x - \beta xy \wedge f_2(x, y) = \gamma xy - y\delta$ and observe the 2 x 2 formula for the Jacobi matrix given bellow.

$$J(x,y) = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} \end{bmatrix}$$

Using the information above we calculate the required derivatives which yields the corresponding matrix.

$$J(x,y) = \begin{bmatrix} \alpha - \beta y & -\beta x \\ \gamma y & \delta \end{bmatrix}$$

Now that we have the Jacobian matrix we can analyze the first steady state at (0, 0). To do so we calculate J(0, 0) which yields,

$$J(0,0) = \begin{bmatrix} \alpha & 0 \\ 0 & -\gamma \end{bmatrix}$$

calculating its eigenvalues result in,

$$\lambda_1 = \alpha$$

$$\lambda_2 = -\gamma$$

First observe that the both eigenvalues values are real hence we can use the linear stability

test from the course book^[4]. Then observe that from the assumption made on the model. We know that both α , $\gamma > 0$. Hence the signs of λ_1 and λ_2 will always differ. Hence we see that the fixed point at the origin is a saddle point and is unstable. Now we continue by examining the behavior near the second fixed point. For $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$ we have the following Jacobi matrix and eigenvalues.

$$J(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}) = \begin{bmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ \frac{\alpha\gamma}{\beta} & -0 \end{bmatrix}$$
$$\lambda_1 = i\sqrt{\alpha\gamma}$$
$$\lambda_2 = -i\sqrt{\alpha\gamma}$$

Since both of the eigenvalues are purely imaginary the linear stability test^[4] is inconclusive for determining the stability of $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$. Hence we cant conclude anything.

5 Conclusion

In summary, the Lotka-Volterra equations have made substantial contributions to our knowledge of population dynamics and predator-prey interactions in ecological systems. Alfred J. Lotka and Vito Volterra developed a mathematical framework that makes it possible to analyze the intricate oscillations and interconnections seen in natural ecosystems. The equations have been widely utilized to predict and study predator-prey relationships in a variety of domains, from population biology to epidemiology. They have provided insightful information on the coexistence of species, species stability, and the impact of environmental conditions on population dynamics. The Lotka-Volterra equations, despite being straightforward, remain a key tool in mathematical biology, inspiring additional study and aiding in our growing understanding of the complex dynamics governing the natural world.

6 Appendix

6.1 Codes

```
# Importing the required libraries
  import numpy as np
  import matplotlib
   import matplotlib.pyplot as plt
  from scipy.integrate import odeint
  matplotlib.use('tkagg')
  y0 = [10, 1]
   # Creating a linear space of ... ...
  t = np.linspace(0, 50, num = 100)
  params = [1.0, 0.4, 0.1, 0.4]
13
   def sim(variables, t, params):
       # Setting up the data in the inner scope of the function
       x = variables[0]
       y = variables[1]
       alpha = params[0]
       beta = params[1]
       delta = params[2]
       gamma = params[3]
       # Setting up the linear-model
       dxdt = alpha * x - beta * x * y
       dydt = delta * x * y - gamma * y
       return ([dxdt, dydt])
30
```



```
# Solving the model
y = odeint(sim, y0, t, args = (params,))

f, (ax1, ax2) = plt.subplots(2)

# Plotting the model
line1 = ax1.plot(t, y[:, 0], color = "b")
line2 = ax2.plot(t, y[:, 1], color = "r")

ax1.set_ylabel("Prey (hundreds)")
ax2.set_ylabel("Predator (hundreds)")
ax2.set_xlabel("Time")

plt.show()
```

6.2 Coefficients at Perturbation Method

$$A_{1} = \frac{1}{(r_{1} - r_{2})^{3}} \left[\frac{1}{2r_{2} - r_{1}} \left\{ (2r_{2} + \alpha c_{1}c_{2}) \left(c_{1}M + b_{1}Q \right) + \left(b_{2}M - c_{2}F \right) b_{1}c_{1}\alpha \right\} \right.$$

$$- \frac{1}{r_{2}} \left\{ \left(r_{1} + r_{2} + \alpha c_{1}c_{2} \right) \left(c_{1}N + 2b_{1}R \right) + \left(b_{2}N - 2c_{2}G \right) b_{1}c_{1}\alpha \right\}$$

$$+ \frac{1}{r_{1}} \left\{ \left(2r_{1} + \alpha c_{1}c_{2} \right) \left(c_{1}L + b_{1}P \right) + \left(b_{2}L - c_{2}E \right) b_{1}c_{1}\alpha \right\} \right]$$

$$A_{2} = \frac{1}{(r_{1} - r_{2})^{3}} \left[-\frac{1}{2r_{1} - r_{2}} \left\{ \left(2r_{1} + \alpha c_{1}c_{2} \right) \left(c_{1}L + b_{1}P \right) + \left(b_{2}L - c_{2}E \right) b_{1}c_{1}\alpha \right\}$$

$$+ \frac{1}{r_{1}} \left\{ \left(r_{1} + r_{2} + \alpha c_{1}c_{2} \right) \left(c_{1}N + 2b_{1}R \right) + \left(b_{2}N - 2c_{2}G \right) b_{1}c_{1}\alpha \right\}$$



$$\begin{split} &-\frac{1}{r_2}\left\{(2r_2+\alpha c_1c_2)\left(c_1M+b_1Q\right)+(b_2M-c_2F)\,b_1c_1\alpha\right\}\right]\\ &A_3=\frac{1}{(r_1-r_2)^2}\left[-\frac{1}{r_1\left(2r_1-r_2\right)}\left\{(2r_1+\alpha c_1c_2)\left(c_1L+b_1P\right)+(b_2L-c_2E)\,b_1c_1\alpha\right\}\right]\\ &A_4=\frac{1}{(r_1-r_2)^2}\left[-\frac{1}{r_1\left(2r_2-r_1\right)}\left\{(2r_2+\alpha c_1c_2)\left(c_1M+b_1Q\right)+(b_2M-c_2F)\,b_1c_1\alpha\right\}\right]\\ &A_5=\frac{1}{(r_1-r_2)^2}\left[\frac{1}{2r_2}\left\{(r_1+r_2+\alpha c_1c_2)\left(2b_1R+c_1N\right)+(b_2N-2c_2G)\,b_1c_1\alpha\right\}\right]\\ &B_1=\frac{-1}{(r_1-r_2)^3}\left[\frac{1}{2r_2-r_1}\left\{\left(b_1^2\alpha+2r_2\right)\left(b_2M-c_2F\right)-\left(c_1M+b_1Q\right)\right\}\right.\\ &+\frac{1}{r_1}\left\{\left(b_1^2\alpha+2r_1\right)\left(b_2L-c_2E\right)-\left(c_1L+b_1P\right)b_2c_1\alpha\right\}\right.\\ &+\frac{1}{r_2}\left\{\left(b_1^2\alpha+r_1+r_2\right)\left(2c_2G-b_2N\right)+\left(c_1N+2b_1R\right)b_2c_1\alpha\right\}\right]\\ &B_2=\frac{1}{(r_1-r_2)^3}\left[\frac{1}{2r_1-r_2}\left\{\left(b_1^2\alpha+2r_1\right)\left(b_2L-c_2E\right)-\left(c_1L+b_1P\right)b_2c_1\alpha\right\}\right.\\ &+\frac{1}{r_1}\left\{\left(b_1^2\alpha+2r_2\right)\left(b_2M-c_2F\right)-\left(c_1M+b_1Q\right)b_2c_1\alpha\right\}\right]\\ &B_3=\frac{1}{(r_1-r_2)^2}\left[\frac{1}{r_1\left(2r_1-r_2\right)}\left\{\left(b_1^2\alpha+2r_1\right)\left(b_2L-c_2E\right)-\left(c_1L+b_1P\right)b_2c_1\alpha\right\}\right]\\ &B_4=\frac{1}{(r_1-r_2)^2}\left[\frac{1}{r_1\left(2r_1-r_2\right)}\left\{\left(b_1^2\alpha+2r_1\right)\left(b_2L-c_2E\right)-\left(c_1L+b_1P\right)b_2c_1\alpha\right\}\right]\\ &B_5=\frac{1}{(r_1-r_2)^2}\left[\frac{1}{r_1\left(2r_1-r_2\right)}\left\{\left(b_1^2\alpha+2r_1\right)\left(b_2M-c_2F\right)-\left(c_1M+b_1Q\right)b_2c_1\alpha\right\}\right]\\ &B_5=\frac{1}{(r_1-r_2)^2}\left[\frac{1}{r_1r_2}\left\{\left(b_1^2\alpha+r_1+r_2\right)\left(2c_2G-b_2N\right)+\left(2b_1R+c_1N\right)b_2c_1\alpha\right\}\right]\\ ∧\\ &P=\left(\left(r_1+\beta c_2\right)p_0-p_1c_1\alpha\right)\\ &Q=\left(\left(r_2+\beta c_2\right)p_0-p_1c_1\alpha\right)\\ &L=\left(\left(r_1+\beta c_2\right)p_0-p_1c_1\alpha\right)\left(\left(r_2+\beta c_2\right)p_0-p_1c_1\alpha\right)\\ &L=\left(\left(r_1+\beta c_2\right)p_0-p_1c_1\alpha\right)\left(\left(r_2+\alpha b_1\right)p_1-p_0b_2\beta\right)\\ \end{aligned}$$



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$$N = ((r_1 + \beta c_2) p_0 - p_1 c_1 \alpha) (r_2 + \alpha b_1) p_1 + p_0 b_2 \beta)$$

$$+ ((r_2 + \beta c_2) p_0 - p_1 c_1 \alpha)) ((r_2 + \alpha b_1) p_1 + p_0 b_2 \beta)$$

$$M = ((r_2 + \beta c_2) p_0 - p_1 c_1 \alpha) (r_2 + \alpha b_1) p_1 + p_0 b_2 \beta)$$

$$E = ((r_1 + \alpha b_1) p_1 + p_0 b_2 \beta)^2$$

$$F = ((r_2 + \alpha b_1) p_1 + p_0 b_2 \beta)^2$$

$$G = ((r_1 + \alpha b_1) p_1 + p_0 b_2 \beta) ((r_2 + \alpha b_1) p_1 + p_0 b_2 \beta)$$

[1]

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