

**THE NON LINEAR PREY-PREDATOR
MODEL WITH LAGS FOR MATURITY**



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SHEHU ABBA ADAMU**


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**Shehu Abba ADAMU: THE NON-LINEAR PREY-PREDATOR
MODEL WITH LAGS FOR MATURITY**

**Approval of Director of Graduate School of
Applied Sciences**


Prof. Dr. İlkey SALİHOĞLU

**We certify this thesis is satisfactory for the award of the degree of
Masters of Science in Mathematics**

Examining Committee in Charge:



Prof. Dr. Adigüzel Dosiyeve

Committee Chairman
Mathematics Department, NEU



Assoc. Prof. Dr. Evren Hınçal

Supervisor, Mathematics
Department, NEU



Assoc. Prof. Dr. Cem Kaanoğlu

Common Courses Unit, CIU

I hereby declare that all the information in this document has been obtained and presented in accordance with academic rules and ethical conduct. I also declare that, as required by these rules and conduct, I have fully cited and referenced all material and results that are not original to this work.

Name, Last Name : Shelly Abbas Adamu

Signature : Shelly

Date: 25-01-2016

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To my family...

ABSTRACT

Mathematics has always benefited from its involvement with developing science, each successive interaction revitalizes and enhances the field. Biomedical science is clearly the premier science of the foreseeable future. This work introduces a mathematical models for biological systems, and presents the mathematical theory and techniques useful in analyzing those models. Material is organized according to the mathematical theory rather than the biological application. Undergraduate courses in calculus, linear algebra, and differential equations are assumed. In this thesis, We first describe the prey- predator model and how differential equations relates to prey- predator. We consider Lotka-Volterra's model, Lotka-Volterra model as a classical application of mathematics in biology, models based on differential equations for interactions between species, comprising a set of two ordinary differential equations governing the local dynamics present of prey and predator densities.

Analysis of the equations resulting from the introduction of a time lag in the response of the predator to changes in the prey population shows an array of possible solutions . The form of the solution is dependent upon the size of the time lag and the ratio of the equilibrium value for the prey population in the absence of predation to the equilibrium value with predation. While the equations analysed in this thesis were assumed to have terms, It is possible to introduce non linear interactions. Once reasonable values are known for the many parameters, population equations of this degree of complexity are most easily handled by approximation on a computer

Keywords: Prey; Predator; Model; Equilibrium; Maturity; Stability; Analysis and Population

ÖZET

Bilimi geliřtirmede Matematiğin her zaman büyük katkıları olmuřtur. Birbirini izleyen her bir etkileřim canlılık kazandırır ve saha artırır. Biyomedikal bilim gerçekten öngörülebilir gelecekte en önde gelen bilimdir. Bu çalıřma, biyolojik sistemler için matematiksel modeller tanıtmaktadır ve bu modellerin analizinde yararlı matematiksel teori ve teknikleri sunmaktadır. Bu çalıřmanın içerięi biyolojik uygulamadan ziyade matematiksel teoriye göre düzenlenmiřtir. Analiz , lineer cebir ve diferansiyel denklemler dersleri temel olarak alınarak bu tez yazılmıřtır. İlk olarak bu çalıřmada av-avcı modelini tanımladık. Sonra diferansiyel denklemlerle nasıl iliřkili olduęunu açıldık. Av ve avcı yoğunlukları mevcut yerel dinamiklerin yöneten iki adi diferansiyel denklemlerin bir dizi içeren biyoloji, matematik, türler arasındaki etkileřimleri diferansiyel denklemler dayalı modeller, klasik bir uygulama olarak Lotka-Volterra modeli örnek alınarak bu tez geliřtirilmiřtir. Av popölasyonunda deęiřikliklere avcının karřılık olarak bir zaman aralıęı dahil edilmesinden kaynaklanan denklemlerinin analizi ve çözümleri bu tezin ana konusudur. Çözümün formu zaman gecikmesinin boyutu ve avlanma ile denge deęerine avlanma yokluęunda av nüfus için denge deęerinin oranına baęlıdır. Bu tezde analiz edilen denklemlerde kořullar kabul ederken, bu doęrusal olmayan etkileřimlerle karřılařmak mümkündür. Uygun deęerler, birçok parametre için biliniyor olsa da, karmařıklılıęın bu seviyesindeki nüfus denklemleri kolayca bir bilgisayar yardımıyla çözüm bulacaęımızı bu tezde iřlemiř bulunmaktayız.

Anahtar Kelimeler: Av; Avcı; Model; Denge; Olgunluk; Kararlılık; Analiz ve Nüfus

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CHAPTER 1

INTRODUCTION

In this chapter, definition of mathematical model, latest development, limitations and some definitions dealing with the predator-prey models are discussed. Then a description of what the predator-prey model is, and also how differential equations relate to predator-prey.

In chapter 2, focus on the study of the predator-prey model which are Lotka-Volterra models was made, where two species are involved in the interaction. Thus, the differential equations describing the population dynamics must have two unknown variables which are $x(t)$ for prey and $y(t)$ for the predator, creating a system of differential equations. These dynamics present two times. We then study this model and its equilibrium points and also the stability analysis. Finally, the effect of introducing time lags into the equations for the growth of the prey and non linear functions for the prey-predator interaction is considered, it could be seen that these equations swiftly become too difficult for analytical methods. However, the stability analysis for the steady state point is to be considered.

1.1 Some Definitions

1.1.1 What is Mathematical Modeling?

Mathematical modeling is the application of mathematics to describe and investigate an important questions that arise from it in a real-world problems (Banerjee, 2014).

In the 1920's Vito Volterra was asked whether it would be possible to explain the fluctuations that had been observed in the fish population of the Adriatic sea– fluctuations that were of great concern to fishermen in times of low fish populations(Doust & Gholizade, 2014). Volterra in 1926 constructed the model that has become known as the Lotka-Volterra model (because A.J. Lotka (1925) constructed a similar model in a different context about the same time), based on the assumptions that fish and sharks were in a predator–prey relationship(Brauer & Castillo-Chávez, 2012). A mathematical model, as stated, is a mathematical description of a real life situation. So, if a mathematical model can reflect or mimic the behavior of a real life situation, then we can get a better understanding of the system through proper analysis of the model using appropriate mathematical tools. Moreover, in the process of building the model, we discover various factors which govern the system, factors which are most important to the system and that reveal how different aspects of the system are related. Mathematical modeling is an area of great development and research. In recent years, mathematical models have been used to validate hypotheses made from experimental data, and at the same time the designing and testing of these models has led to testable experimental predictions. There are impressive cases in which mathematical models have provided fresh insight into biological systems, physical systems, decision making problems, space models, industrial problems, economical problems and so

forth. The development of mathematical modeling is closely related to significant achievements in the field of computational mathematics(Banerjee, 2014). Real-world systems are complex and a number of inter-related components are involved. Since models are abstractions of reality, a good model must try to incorporate all critical elements and inter-related components of the real-world system. This is not always possible. Looking at a limitations of mathematical model, an important inherent limitation of a model is created by what is left out. Problems arise when key aspects of the real-world system are inadequately treated in a model or are ignored to avoid complications, which may lead to incomplete models. Other limitations of a mathematical model are that they may assume the future will be like the past, input data may be uncertain or the usefulness of a model may be limited by its original purpose.

1.01.2 Modeling cycle;

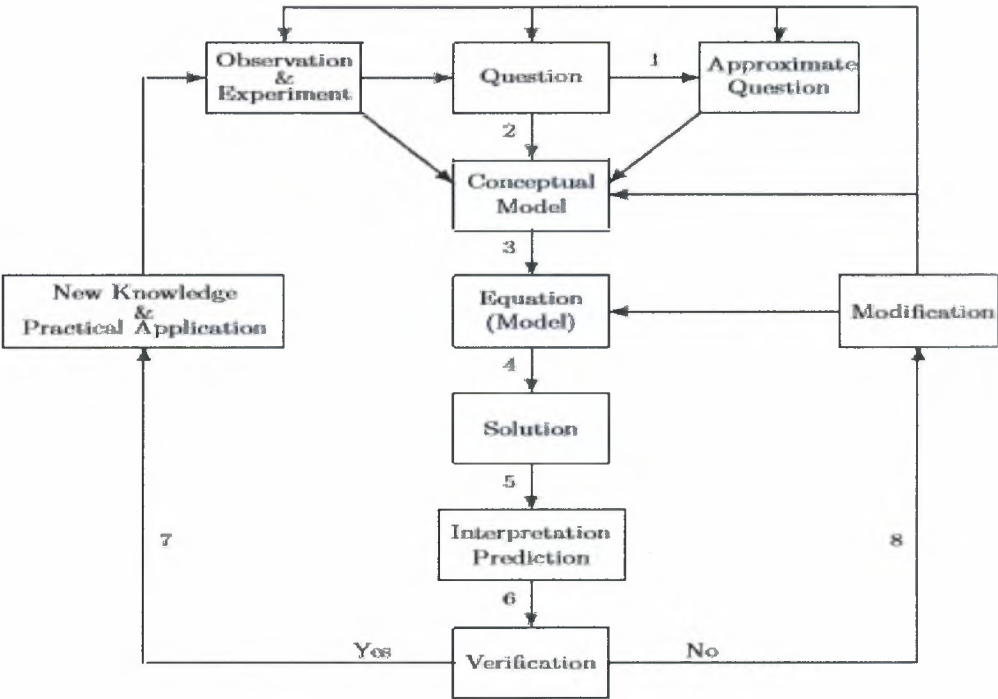


Figure 1.1: Modeling Circle

1.2 What is the Predator-Prey Model ?

There are many instances in nature where one specie of animals feeds on another specie(s) of animal(s), which in turn feeds on other things. The first specie is called the predator and the second is called the prey.

Theoretically, the predator can destroy all the prey so that later it becomes extinct. However, if this happens the predator will also become extinct since, as we assume, it depends on the prey for its existence.

Predator-prey modeling is a population modeling with two distinct populations, one of which is a source of food for the other.

1.3 Differential Equations and how it Relates to Predator-Prey

The differential equations are very much helpful in many areas of science. But most of interesting real life problems involve more than one unknown function. Therefore, the use of system of differential equations is really useful.

One of the most interesting applications of sytems of differential equations is the prey-predator problem. In this thesis without loss of generality, we will concentrate on sytems of two differential equations and we will consider an environment containing two related populations a prey population, such as rabbits and a predator population, such as foxes. Clearly, it is reasonable to expect that the two populations react in such a way as to influence each other's size (Casillas etal., 2002).



1.4 A General Predator-Prey Model

Consider two populations whose sizes at a reference time t are denote by $x(t)$, $y(t)$, respectively. The functions x and y might denote population numbers or concentrations (number per area) or some other scaled measure of the populations sizes, but are taken to be continuous functions. Changes in population size with time area described by the time derivatives $\dot{x} = \frac{dx}{dt}$ and $\dot{y} = \frac{dy}{dt}$, respectively and a general model of interacting populations is written in terms of two autonomous differential equations:

$$\dot{x} = xf(x, y)$$

$$\dot{y} = yg(x, y)$$

(i.e the time t does not appear explicitly in the functions $xf(x, y)$ and $yg(x, y)$). The functions f and g denote the respective “per capita growth rates of two species”. It is assumed that $\frac{df(x,y)}{dy} < 0$ and $\frac{dg(x,y)}{dx} > 0$. This general model is often called Kolmogorov’s prey-predator model (Hoppensteadt, 2006).

1.5 Exponential Growth

Under simplified conditions, such as a constant environment (and with no migration), it can be shown that change in population size (N) through time (t) will depend on the difference between individual birth rate (b_0) and death rate (d_0), and is given by:

$$\frac{dN}{dt} = (b_0 - d_0) N \quad (1.1)$$

where:

b_0 = instantaneous birth rate, births per individual per time period (t).

d_0 = instantaneous death rate, deaths per individual per time period (t) and N = current population size.

The difference between birth and death rates ($b_0 - d_0$) is also called r , the intrinsic rate of natural increase, or the Malthusian parameter. It is the theoretical maximum number of individuals added to the population per individual per time. By solving the differential equation 1.1 we get a formula to estimate a population size at any time:

$$N = N_0 e^{rt} \quad (1.2)$$

where *approximately* $e = 2.718 \dots$

This equation shows us that if birth and death rates are constant, population size will grow exponentially. If you transform the equation to natural logarithms (\ln), the exponential curve becomes linear, and the slope of that line can be shown to be r :

$$\ln(N) = \ln(N_0) + \ln(e^{rt}) \quad (1.3)$$

and

$$r = [\ln(N) - \ln(N_0)] / t \quad (1.4)$$

where $\ln(e) = 1$. The population growth rate, r , is a basic measure in population studies, and it can be used as a basis of comparison for different populations and species.

1.6 Fixed Points or Critical Points (Sometimes Called an Equilibrium Points)

A fixed point of a dynamical system is a state vector x such that if the system is ever in the state x , it will remain in that state for all time (Scheinerman, 2007)

1.7 Stability of an Equilibrium Points

Let λ_1 and λ_2 be the eigenvalues of an equilibrium point (x,y) , then the fixed point is

1.7.1 Stable;

(a) if $\text{Re}(\lambda_1) < 0$ and $\text{Re}(\lambda_2) < 0$ ($\text{Re}(\lambda)$ denotes the real part of λ),

then the trajectories form a stable node.

(b) If λ_1 and λ_2 are complex conjugate pair, the trajectories form a stable focus. (Louzoun & Solomon, 2001)

1.7.2 Node;

If λ_1 and λ_2 are of the same signs.

1.7.3 Spiral;

If both λ_1 and λ_2 are complex conjugate with non zero real parts. The spiral is locally stable if the real parts of the eigenvalues are negative, and unstable if the real parts of the eigenvalues are positive.

1.7.4 Unstable;

If λ_1 and λ_2 are real and positive.

1.7.5 A Saddle Point;

if λ_1 and λ_2 are real and have opposite signs. a saddle is unstable (Louzoun & Solomon, 2001)

1.7.6 A centre;

if λ_1 and λ_2 are purely imaginary (Louzoun & Solomon, 2001).

In other words, for asymptoticity, a fixed point is said to be stable if the system at any point x_0 near x (the fixed point) is converging to x . marginally stable or neutral if for all starting points x_0 near the fixed point x the system stays near it but never converge to it, while it is unstable if it is neither stable nor marginally stable. These are illustrated by figure respectively (Scheinerman, 2007)

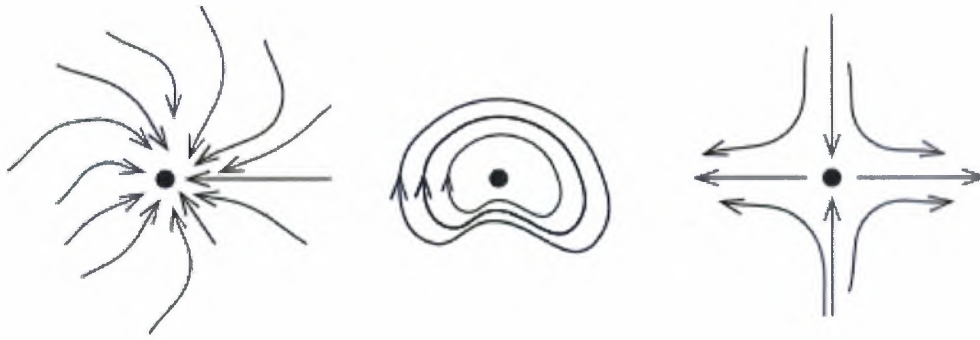


Figure 1.2: Stable, Marginal and unstable

1.7.7 Limit Cycle;

Is a closed trajectory that is eventually reached by a system. It occurs only in a non linear system.

1.8 Logistic Growth

We need to modify the basic equation 1.1 so that birth and death rates are no longer constants through time, but decrease and increase respectively as population size increases :

$$\frac{dN}{dt} = N[(b_0 - k_b N) - (d_0 + k_d N)] \quad (1.5)$$

where k_b and k_d are the density-dependent birth and death rate constant respectively. This equation predicts that a population will stop growing (zero population growth) when birth rate equals death rate, or:

$$b_0 - k_b N = d_0 + k_d N \quad (1.6)$$

This can be converted into an equation showing the size at which the population reaches a steady state:

$$N = \frac{(b_0 - d_0)}{(k_b + k_d)} \quad (1.7)$$

The value of N when the population is at steady state is the carrying capacity of the environment, or K . This can be simplified:

$$K = \frac{r}{(k_b + k_d)} \quad (1.8)$$

Since $b_0 - d_0 = r$. If we combine this new form of the carrying capacity equation with 1.5 we get the familiar form of the logistic growth equation (Toronto, 1997).

$$\frac{dN}{dt} = rN \left[\frac{(K-N)}{K} \right]. \quad (1.9)$$

1.9 Taylor Series:

A Taylor series is a series representation (expansion) of a function about a point. A one dimensional Taylor series expansion of a real function $g(x)$ about a point $x = a$ is given by

$$g(x) = g(a) + (x - a)g'(a) + (x - a)^2 \frac{g''(a)}{2!} + (x - a)^3 \frac{g^{(3)}(a)}{3!} + \dots \\ + (x - a)^n \frac{g^{(n)}(a)}{n!} + \dots \quad (1.10)$$

1.10 Exponential Decay:

If a quantity decreases at a rate proportional to its value, then it is said to be subject to exponential. Symbolically, this process can be modeled by the differential equation below where N is the quantity and λ (lambda) is a positive constant called the decay constant:

$$\frac{dN}{dt} = -\lambda N. \quad (1.11)$$

The solution to this equation is:

$$N(t) = N_0 e^{-\lambda t} \quad (1.12)$$

Here $N(t)$ is the quantity at time t , and $N_0 = N(0)$ is the initial quantity, i.e the quantity at time $t = 0$.

1.11 Delay Model:

In general, if we consider a population to be governed by

$$\frac{dN}{dt} = f(N) \quad (1.13)$$

where typically $f(N)$ is a nonlinear function of N .

One of the deficiencies of single population models like 1.13 is that the birth rate is considered to act instantaneously whereas there may be a time delay to take account of the time to reach maturity, the finite gestation period and so on. We can incorporate such delays by considering delay differential equation models of the form

$$\frac{dN}{dt} = f(N(t), N(t - T)), \quad (1.14)$$

where $T > 0$, the delay is a parameter.

CHAPTER 2

LITERATURE REVIEW

2.1 Models

In this chapter, focus on the study of the predator-prey model which are Lotka-Volterra models was made, where two species are involved in the interaction. Thus, the differential equations describing the population dynamics must have two unknown variables which are $x(t)$ for prey and $y(t)$ for the predator, creating a system of differential equations. These dynamics present two times. We then study this model and its equilibrium points and also the stability analysis.

2.2 Lotka Volterra Model

The Lotka-Volterra equations, in other words the prey-predator equations, are a pair of non-linear first-order, ordinary differential equations usually used to describe the dynamics of biological systems in which two species interact, where one is predator and the other is a prey. The equations were proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926 as stated in the previous chapter.

The model describes the following;

1. How the population of the prey changes
2. Shows the changes in predator population.

All with respect to time according to the pair of equations below:

$$\frac{dx}{dt} = x(\alpha_1 - \beta_1 y)$$

(2.1)

$$\frac{dy}{dt} = y(-\alpha_2 + \beta_2 x)$$

where

x represent the number of prey

y the number of predator

$\frac{dy}{dt}$ and $\frac{dx}{dt}$ represent the growth rate of the two populations with respect to time t .

and also,

$\alpha_1, \alpha_2, \beta_1$ and β_2 are positive constants representing the interaction of the two species.

2.3 The Physical Meanings of the Models

The equations could take more usefull form when multiplied out for interpretation physically, considering the origin from a general framework,

$$\frac{dx}{dt} = xf(x, y)$$

(2.2)

$$\frac{dy}{dt} = yg(x, y)$$

where both functions represent per capita growth rates of the prey and predator respectively.

Because these functions are in general form, a Taylor series approximation is performed to come up with a linearized per capita rates,

$$f(x, y) = P - Qx - Ry$$

(2.3)

$$g(x, y) = S + Tx - Uy$$

The signs of the coefficients were from an assumptions of population regulation, and by choosing non zero coefficients appropriately, an ecologist can obtain prey-predator competition, disease and mutualism models that provide general insight into ecological systems.

The following are some assumptions made:

1. There is an ample food for the prey population at all times

2. The predator population depends entirely on the prey populations for its food

3. The rate of change of population is proportional to its size

4. There is no change in favour of any species and the genetic adaptation is sufficiently slow by the environment during the process.

2.4 Prey

The prey equation becomes

$$\frac{dx}{dt} = \alpha_1 x - \beta_1 xy \quad (2.4)$$

The prey are assumed to have an unlimited food supply and to reproduce exponentially unless subject to predation, this exponential growth is represented in the equation above by the term $\alpha_1 x$. The rate of predation upon the prey is assumed to be proportional to the rate at which the predators and the prey meet this is represented above by $\beta_1 xy$, if either x or y is zero then there can be no predation.

With these two terms the equation 2.4 above, can be interpreted as: the change in the prey's population given by its own growth minus the rate at which it is preyed upon.

2.5 Predators

The predator equation becomes

$$\frac{dy}{dt} = -\alpha_2 y + \beta_2 xy \quad (2.5)$$

In this equation, $\beta_2 xy$ represents the growth of the predator population by interacting with the prey, $\alpha_2 y$ represents the natural death of the predators which is in the absense of the prey, it is an exponential decay.

Hence the equation represents the change in the predator population as the growth of the predator population minus natural death.

2.6 The Dynamics of the System

According to the system, the population of predators increases when there are many prey to feed on, but ultimately, outstrip their food supply and decline. As the population of the predator is low the prey population will be higher. These dynamics continue in a pattern of growth and decline.

2.7 Equilibrium Analysis

When neither of the population levels is changing then the population equilibrium occurs in the model, in other words, when both of the derivatives are equal to 0. Thus, for the prey-predator model above, we equate the derivatives to zero

$$\frac{dx}{dt} = 0 \quad \text{and} \quad \frac{dy}{dt} = 0.$$

It results in a system of non linear algebraic equations to solve.let (\hat{x}, \hat{y}) be the equilibrium solutions for the prey and predator populations respectively, then the system of algebraic equations that need to be solved is given by

$$x(\alpha_1 - \beta_1 y) = 0$$

$$y(-\alpha_2 + \beta_2 x) = 0$$

The solutions are of the forms;

$$(x = 0, y = 0)$$

and

$$(x = \frac{\alpha_2}{\beta_2}, y = \frac{\alpha_1}{\beta_1})$$

Hence, two equilibria exist.The first solution effectively shows the extinction of both the prey and the predator.which means If both populations are at 0, then it will continue to be so indefinitely.And the second solution represents a fixed point at which both populations of the

species sustain a current, non-zero numbers, and in the simplified model, also so indefinitely. The levels of population at which this equilibrium is achieved depend on the chosen values of the parameters $\alpha_1, \alpha_2, \beta_1$ and β_2 .

2.8 Stability of the Fixed Points

By performing a linearization using partial derivatives the stability of the fixed point at the origin is determined. while a more slight sophisticated method could be employed for the other fixed point.

Jacobian matrix is used below for the prey-predator model,

$$J(x, y) = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} \alpha_1 - \beta_1 y & -\beta_1 x \\ \beta_2 y & -\alpha_2 + \beta_2 x \end{bmatrix}.$$

Consider the first fixed point;

When evaluated at the steady state of $(0, 0)$, the Jacobian matrix J becomes

$$J(0,0) = \begin{bmatrix} \alpha_1 & 0 \\ 0 & -\alpha_2 \end{bmatrix}.$$

The eigenvalues of this matrix are $\lambda_1 = \alpha_1$ and $\lambda_2 = -\alpha_2$. In the model α_1 and α_2 are always greater than zero, and as such the sign of the eigenvalues above will always differ. This shows that fixed point at the origin is a saddle point.

This fixed point has a significant stability. If it were stable, non-zero populations might be attracted towards it, and as such the dynamics of the system might lead towards the extinction of both species for so many cases of initial population levels. However, as the fixed point at the origin is a saddle point, and hence unstable, This shows that in the model, the extinction of both species is very hard. (In fact, this is only possible if the prey are completely eradicated artificially, which causes the predators to die of starvation. When the predators are eradicated, there will be a growth in prey's population without bound.

Consider the second fixed point;

Evaluating J at the second fixed point we get

$$J\left(\frac{\alpha_2}{\beta_2}, \frac{\alpha_1}{\beta_1}\right) = \begin{bmatrix} 0 & -\frac{\beta_1\alpha_2}{\beta_2} \\ \frac{\alpha_1\beta_2}{\beta_1} & 0 \end{bmatrix}$$

which yields the two complex conjugate eigenvalues $\lambda_1 = i\sqrt{\alpha_1\alpha_2}$ and $\lambda_2 = -i\sqrt{\alpha_1\alpha_2}$. The real parts of these two eigenvalues are both equal to 0. Thus the linear stability analysis is inconclusive. It turns out that the

equilibrium is neutral stable and this system of equations exhibits neutral oscillations (Wiens, 2010).

2.9 Consumer-Resource Model (a non linear system)

Consider the following non linear, autonomous systems of the form

$$\frac{dx_1}{dt} = f_1(x_1, x_2, \dots, x_n)$$

$$\frac{dx_2}{dt} = f_2(x_1, x_2, \dots, x_n)$$

$$\vdots$$

$$\frac{dx_n}{dt} = f_n(x_1, x_2, \dots, x_n)$$

where each of the functions f_i $i=1,2,3,\dots,n$ are real-valued functions in n variables. in the analysis the restriction is on system of two variables..

2.10 The Stability Analysis Of The Equilibria

Consider the system of two autonomous differential equations

$$\frac{dx}{dt} = f(x, y)$$
$$(2.6)$$

$$\frac{dy}{dt} = g(x, y)$$

The first step is to find the equations of the *zero isoclines* (for finding the equilibrium point), which are defined as the set of points that satisfy

$$0 = f(x, y)$$

$$0 = g(x, y)$$

Each equation results in a curve in the x-y space. *Point equilibria* occur where the two isoclines intersect Figure 2.1. A point equilibrium (\hat{x}, \hat{y}) of 2.6 therefore simultaneously satisfies the two equations

$$f(\hat{x}, \hat{y}) = 0 \quad \text{and} \quad g(\hat{x}, \hat{y}) = 0$$

The equilibrium is simply called “equilibria”.

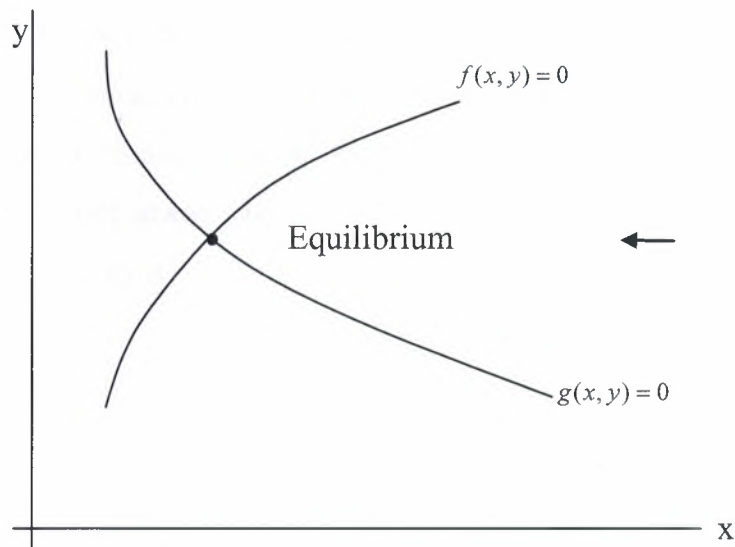


Figure 2.1: Zero isoclines corresponding to the two differential equations. Equilibria occur where the isoclines intersect.

The stability from an analytical approach relies on analysis of the effects of small perturbations. If the system returns to (\hat{x}, \hat{y}) after a small perturbation then the equilibrium (\hat{x}, \hat{y}) is locally stable, otherwise unstable. Mathematically, the analysis can be made through linearization of the right-hand side of each the two differential equations in 2.6 about the equilibrium.

The equations 2.6 can be written in matrix form as follows

$$\frac{d}{dt} \begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = \begin{bmatrix} f(x, y) \\ g(x, y) \end{bmatrix}$$

The right-hand side is a vector-valued function that maps a point in \mathbf{R}^2 into a point in \mathbf{R}^2 . Linearizing a vector-valued function means linearizing each component separately. Also linearizing a function of two variables about a specific point means finding the tangent plane at that point (which, of course, may not always be possible). The equation of a tangent plane of $f(x, y)$ about (\hat{x}, \hat{y}) is;

$$\alpha(x, y) = f(\hat{x}, \hat{y}) + \frac{\partial f(\hat{x}, \hat{y})}{\partial x} (x - \hat{x}) + \frac{\partial f(\hat{x}, \hat{y})}{\partial y} (y - \hat{y})$$

We thus find for the linearization of the vector-valued function $\begin{bmatrix} f(x, y) \\ g(x, y) \end{bmatrix}$

$$\begin{bmatrix} \alpha(x, y) \\ \beta(x, y) \end{bmatrix} = \begin{bmatrix} f(x, y) \\ g(x, y) \end{bmatrix} + \begin{bmatrix} \frac{\partial f(\hat{x}, \hat{y})}{\partial x} & \frac{\partial f(\hat{x}, \hat{y})}{\partial y} \\ \frac{\partial g(\hat{x}, \hat{y})}{\partial x} & \frac{\partial g(\hat{x}, \hat{y})}{\partial y} \end{bmatrix} \begin{bmatrix} (x - \hat{x}) \\ (y - \hat{y}) \end{bmatrix}$$

Now, considering $\zeta = x - \hat{x}$ and $\eta = y - \hat{y}$ the perturbations, then with $f(\hat{x}, \hat{y}) = 0$ and $g(\hat{x}, \hat{y}) = 0$, we find

$$\begin{bmatrix} \frac{d\zeta}{dt} \\ \frac{d\eta}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f(\hat{x}, \hat{y})}{\partial x} & \frac{\partial f(\hat{x}, \hat{y})}{\partial y} \\ \frac{\partial g(\hat{x}, \hat{y})}{\partial x} & \frac{\partial g(\hat{x}, \hat{y})}{\partial y} \end{bmatrix} \begin{bmatrix} \zeta \\ \eta \end{bmatrix} \quad (2.7)$$

The matrix

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

is called the *Jacobian matrix*.

The system 2.7 is a linear system of two equations, and we can use the results from linear systems of two differential equations to determine the stability of the equilibria.

2.11 The Density Model:– Dependent Growth of the Prey

To stabilize the prey-predator model a density-dependant growth of the prey in the form of logistic growth can be included. Which takes the form

$$\frac{dx}{dt} = Rx \left(1 - \frac{x}{K}\right) - Sxy \quad (2.8)$$

$$\frac{dy}{dt} = Txy - Uy$$

where all parameters are positive. In the absence of the predator, the prey dynamics reduce to logistic growth in 2.8. Namely, if we set $y = 0$, then

$$\frac{dx}{dt} = Rx \left(1 - \frac{x}{K}\right)$$

The system of equations 2.8 has the nontrivial equilibrium $(0,0)$, which is always unstable. In addition, it has the prey only equilibrium $(K, 0)$, which is locally stable provided $K < \frac{U}{TS}$. If $K > \frac{U}{TS}$, an additional nontrivial equilibrium in the first quadrant appears, which is locally stable. If $K > \frac{U}{TS}$, the prey only equilibrium is unstable.

CHAPTER 3

THE REACTION TIME LAG

3.1 The Time Lags In Prey-Predator Population Models

The conventional set of differential equations used to describe the relationship in a prey predator population model are;

$$\frac{dx(t)}{dt} = \lambda(x)x(t) - \mu(x)y(t)x(t) \quad (3.1)$$

$$\frac{dy(t)}{dt} = -\mu(y)y(t) + \lambda(y)x(t)y(t)$$

Where

$x(t)$ = number of matured prey

$y(t)$ = number of matured predator

$\lambda(x)$ = rate of increase of prey

$\mu(x)$ = coefficient of effect of predation on $x(t)$

$\lambda(y)$ = coefficient of effect of predation on $y(t)$

$\mu(y)$ = death rate of $y(t)$

Thus, the term $\mu(x)y(t)x(t)$ states that the cause of death of the prey is predation alone and that this predation is linearly proportional to the product of prey and predator, in the same manner the growth of the predator population is considered to be linearly proportional to the product of the population and the only limitation on the growth of the predator population is the number of prey. These equations give rise to the familiar Lotka-Volterra prey predator cycles.

3.2 The Equations

The defect in this mathematical treatment of population have been discussed by many ecologists. Most notably by F. E Smith (1952). The equations describe ideal populations whose members can react instantaneously to any change in the environment. In real population both prey and predator require reaction time lags. However, in order to keep the equations simple enough for mathematical analysis, the effect of introducing a time lag into the predator's reaction to change in the prey population will be the only one considered in this thesis. The equations in this form become

$$\frac{dx(t)}{dt} = \lambda(x)x(t - \tau_x) - \mu(x)x(t)y(t) \quad (3.2)$$

$$\frac{dy(t)}{dt} = -\mu(y)y(t) + \lambda(y)y(t - \tau_y)x(t - \tau_y)$$

That is to say the change in the number of matured predators depends on the number of prey and matured predator present at same previous time.

This type of equations was found to have no stable solutions as long as the term $\mu(x)y(t)x(t)$ was considered to be linear.

In biological terms, If prey and predator interact in a linear fashion, then predation can not be the only limit on the growth of the prey in a stable system. This would seem to confirm the theory of Nicholson and Balley.

In order to consider prey predator system with linear interaction as well as those systems where a limitations upon the growth of the prey other than predation is evident, it is necessary to include a density dependant term in the equation of the prey. The equations then become

$$\frac{dx(t)}{dt} = \lambda(x)x(t - \tau_x) \left\{ 1 - \frac{x(t - \tau_x)}{K_x} \right\} - \mu(x)x(t)y(t) \quad (3.3)$$

$$\frac{dy(t)}{dt} = -\mu(y)y(t) + \lambda(y)x(t - \tau_y)y(t - \tau_y)$$

Where $K_x > 0$

And simplifying by combining terms

$$\frac{dx(t)}{dt} = \lambda(x)x(t - \tau_x) - cx^2(t - \tau_x) - \mu(x)x(t)y(t) \quad (3.4)$$

$$\frac{dy(t)}{dt} = -\mu(y)y(t) + \lambda(y)x(t - \tau_y)y(t - \tau_y) \quad (3.5)$$

Where

$$c = \frac{\lambda(x)}{K_x}$$

For these equations there are equilibrium conditions or steady state at which both $\frac{dx(t)}{dt}$ and $\frac{dy(t)}{dt}$ are equal to zero simultaneously.

These are;

$$1. \quad x(t) = x_1 = 0 \qquad y(t) = y_1 = 0$$

$$2. \quad x(t) = x_2 = \frac{\lambda(x)}{c} = K_x \qquad y(t) = y_2 = 0$$

$$3. \quad x(t) = x_3 = \frac{\mu(y)}{\lambda(y)} \qquad y(t) = y_3 = \lambda(x) \left\{ \frac{\left[\frac{1-x_3}{K_x} \right]}{\mu(x)} \right\}$$

The kinds of solutions near each steady state can be found by studying equations 3.4 and 3.5. It is simplest to nomalize the equations by introducing the following definitions

$$p = \frac{t}{\tau} \quad r = \frac{x(t)}{x_3} \quad s = \frac{y(t)}{y_3} \quad z = \frac{x_2}{x_3}$$

If the coefficients are all positive as assumed and if the requirement is made that y_3 be positive, as it must be , to be biologically meaningfull, then x_2 exceeds x_3 and the ratio z is greater than unity.

If the coefficient C is made smaller than x_2 and an increase in the ratio z towards infinity occurs, C goes to zero.

By using these definitions, equatimons 3.4 and 3.5 can be put into the form

$$r'(p) = \mu(x)\tau y_3 \left[\frac{z}{(z-1)} - s(p) - \frac{1}{(z-1)} r(p) \right] r(p) \quad (3.6)$$

$$s'(p) = \mu(y)\tau(r(p-1)s(p-1) - s(p)) \quad (3.7)$$

Where primes indicates differenciatioin with respect to p .

The steady states now occur at

1.	$r_1 = 0$	$s_1 = 0$
2.	$r_2 = z$	$s_2 = 0$
3.	$r_3 = 1$	$s_3 = 1$

Table 3.1: Steady State Points

The region of particular interest is that where the solutions are near steady state 3 as in table 3.1. This region can be explored by studying the variational equations formed by replacing r by $(1+u)$ and s by $(1+v)$ where u and v are small compared with unity. The equations 3.6 and 3.7 become

$$u'(p) = \mu(x)\tau y_3 \left[\frac{-u(p)}{(z-1)} - v(p) \right] \quad (3.8)$$

$$v'(p) = \mu(y)\tau [u(p-1) + v(p-1) - v(p)] \quad (3.9)$$

Where only linear terms are retained.

Because the algebra gets involved from this point on, it is well to use the definitions,

$$A = \mu(y)\tau \quad B = \mu(x)\tau y_3 \quad \text{and} \quad C = \frac{B}{(z-1)}$$

All of which are dimensionless numbers. It is possible to eliminate v from equations 3.8 and 3.9 to give

$$u''(p) + (A + C)u'(p) - Au'(p - 1) + ACu(p) + A(B - C)u(p - 1) = 0 \quad (3.10)$$

This differential equation is difficult to solve directly, However, some knowledge of its solutions indicates that the delay of one unit in variable p is in many cases of interest relatively small compared with the interval of p necessary for significant changes to occur in the solution.

This observation allows just the first three terms of a Taylor's series to be used as

$$u(p - 1) = u(p) - u'(p) + \frac{u''(p)}{2} + \dots \quad (3.11)$$

$$u'(p - 1) = u'(p) - u''(p) + \dots \quad (3.12)$$

Where derivatives only to the second order are retained. Putting this series into equation 3.10 gives the pure differential equations featured in equation 3.13

$$[1 + A + (\frac{A}{2})(B - C)]u'' + \{C - A(B - C)\}u' + ABu = 0 \quad (3.13)$$

Where all terms are evaluated at p .

3.3 Stability Analysis

A number of conclusion can be drawn from equation 3.13 regarding solutions near steady state 3 in table 3.1. The possible solutions depend upon values of z and τ with the relations being illustrated in figure 3.1.

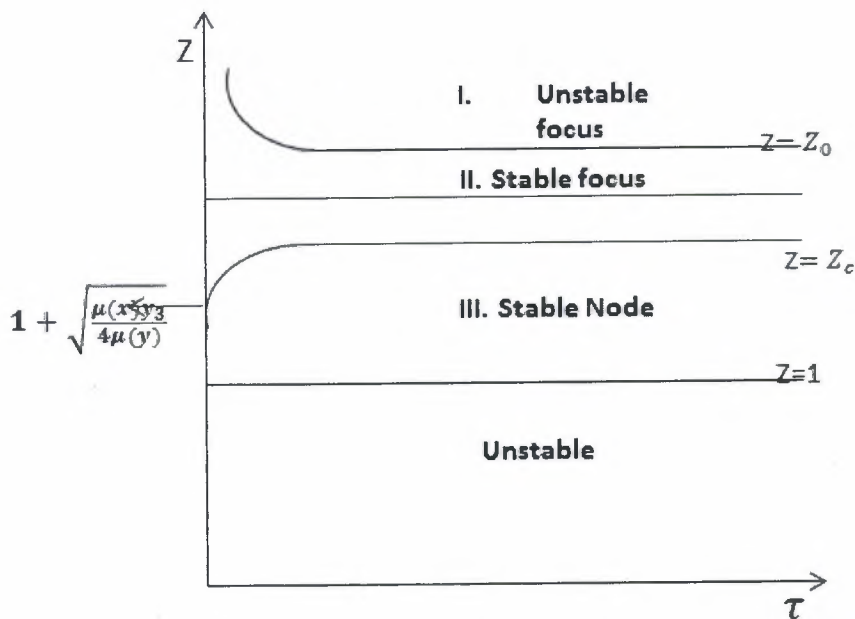


Figure 3.1: : Types of solution for equation 3.13

Figure 3.1: Types of solution for equation 3.13 or equation 3.4 and equation 3.5 near (x_3, y_3) as determined by values of $z = \frac{x_2}{x_3}$ and τ . Three particular values of z are chosen for a single value of τ .

A. If $0 < z < 1$, then there are no stable solutions.

B. If $1 < z < z_c$ a monotonic approach to equilibrium occurs. This is illustrated by I in both figures. The boundary z_c is found by the complicated relationship

$$z_c = 1 + \frac{(-A + \sqrt{A^2 + (1+A)^2 (4\frac{A}{B} + 4\frac{A^2}{B} + A^2)})}{(4\frac{A}{B} + 4\frac{A^2}{B} + A^2)}$$

The point of intersection of this boundary with the z axis is at

$$z = 1 + \sqrt{\frac{\mu(x)y_3}{4\mu(y)}}$$

It evidently depends upon exact values of the parameters and could occur at a value of z larger than that shown in figure 3.1. Figure 3.1 is intended to be typical of a biologically reasonable situation.

C. if $z_c < z < z_0$ where $z_0 = (2 + \frac{1}{A})$ a damped oscillation about x_3 occurs. This is illustrated by II in both figures

D. If $z = z_0$ then, it occurs about the steady state, a steady state oscillation with angular frequency in terms of time variable p that can be written

$$\Omega = \sqrt{\frac{AB}{1+A+\frac{C}{2}}}$$

The period in terms of real time t is

$$T = \frac{2\pi\tau}{\Omega}$$

In certain cases of practical interest, the coefficients in the original equations are of such value that

$$\left(\frac{b}{d} - \frac{c}{\lambda(y)}\right) \ll 1$$

And as a result, typically $B \ll A$, If this is so, $C \ll A$ and approximately

$$\Omega = \sqrt{\frac{AB}{(1+A)}}$$

E. If $z > z_0$, a growing oscillation about steady state 3 exists featured in table 3.1. A limit cycle representing a steady state oscillation appears to arise. This is illustrated by III in both figures.

F. If z becomes infinite, corresponding to $c = 0$ in equation 3.4, the system is unstable and the solutions ultimately becomes infinite.

G. If $\tau = 0$, a growing oscillation is possible and only stable solutions may exist. These solutions are of the Lotka-Volterra type.

H. If z is held constant and τ increased, then the outcome depends upon the value of z chosen. If $z_c < z < 2$ at $\tau = 0$, an increase in τ may change the solution from a damped oscillation to a monotonic approach to equilibrium. If $2 < z < z_0$ at $\tau = 0$ an increase in τ may change the damped oscillation to a growing oscillation and finally to limit cycle.

The work clearly indicates that there is not just one solution for the mathematical prey-predator population model. But a whole array of solutions. The proper solution in a given case depends upon the type of prey-predator interaction. The density-dependant limitation on the growth of the prey and the reaction time lag of the predator. The type of oscillation proposed by Lotka-Volterra for $\tau = 0$ is also for $\tau > 0$ but only for a very narrow range of values for the parameters as represented in figure 3.1 by the line $z = z_0$.

This type of solution does not seem likely to occur in nature, since it is to be expected that in any natural population the value $C > 0$ holds true. The growing oscillation assumed by Nicholson-Bailey, for some prey parasite populations should eventually give rise to a limit cycle. The three main types of solution to be expected are described in b,c and e as illustrated in figure 3.1.

Figure 3.1

Figure 3.2 : Types of solution for equations 3.3 and 3.4

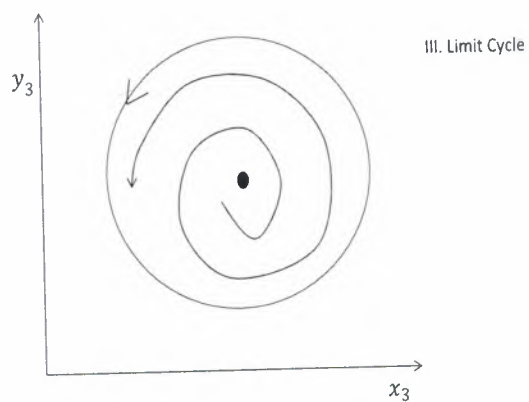
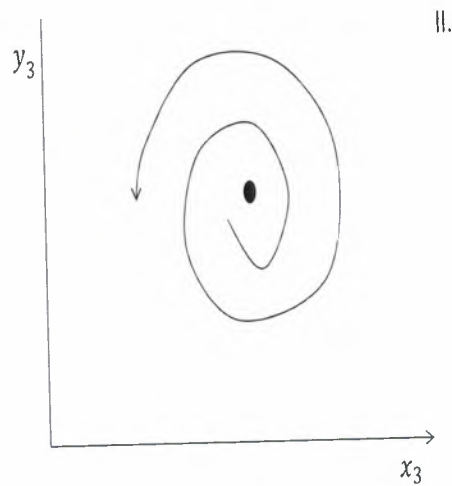
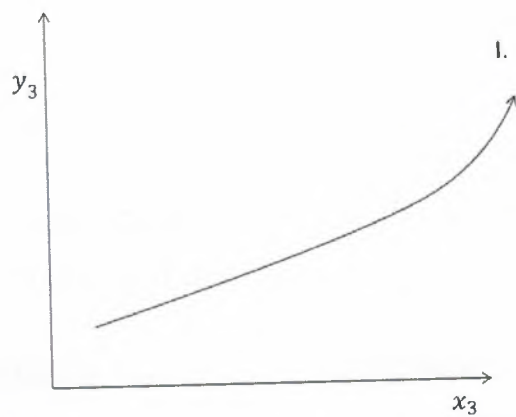


Figure 3.2 : Types of solution for equations 3.3 and 3.4

Figure 3.2; types of solutions for equations 3.4 and 3.5. Showing the relation between x and y as t increases in the direction of the arrows. The steady state at (x_1, y_1) and delay time τ are fixed, while z and thus x_2 varied. Three fundamentally different kinds of solutions are shown corresponding to points I, II and III of figure 3.1.

If the effect of introducing time lags into the equation for the growth of the prey and non linear functions for the prey-predator interaction is considered, it can be seen that these equations swiftly become too difficult for analytical methods. Even the simplified equations presented here are of sufficient complexity to make numerical calculations impossible. However, if there are reasonably good estimate of the several parameters available it is possible to set up equations of this type on a computer and thus drive some idea of the type of solution.

This technique of handling populations can be expanded to three or more interacting populations and is limited mainly by the size of the computer programme and by the accuracy of the biologist in selecting and evaluating the important parameters in a population.

CHAPTER 4

CONCLUSION

4.1: Conclusion

Lotka-Volterra Predator-Prey Model is a rudimentary model of the global complex ecology. It assumes just one prey for the predator, and vice versa. It also assumes no outside influences like disease, changing conditions, pollution and so on. However, the model can be expanded to include other variables, and we have Lotka-Volterra Competition Model, which models two competing species and the resources that they need to survive.

We can modify the equations by adding more variables and get a better picture of the ecology. But with more variables, the model becomes more complex and would require more brains or computer resources.

This model is an excellent tool to teach the principles involved in ecology, and to show some rather counter-intuitive results. It also shows a special relationship between biology and mathematics.

Analysis of the equations resulting from the introduction of a time lag in the response of the predator to changes in the prey population shows an array of possible solutions. The form of the solution is dependant upon the size of the time lag and the ratio of the equilibrium value for the prey population in the absence of predation to the equilibrium value with predation. While the equations analysed in this thesis were assumed to have terms, it is possible to introduce non linear interactions. Once reasonable values are known for the many parameters, population equations of this

degree of complexity are most easily handled by approximation on a computer.

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