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*“Mathematical Modeling in
Biology”*

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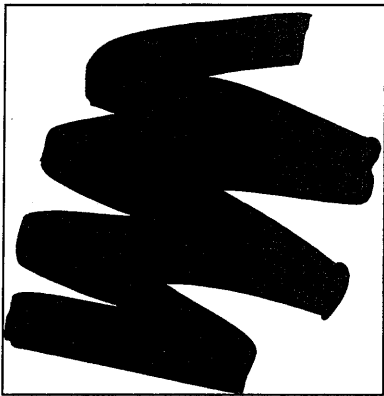
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***Dedicated to
my dear parents who
have been patient
to bring me up, also to
dear husband and
family.***



A Mathematical Study to Predator-prey Model

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Abstract

In this thesis, it develops mathematical models which describing one aspect of the biological world, the mutual relationships among plants, animals and their environment. It constructs a small part of the biological universe by considering the interactions of just two species. The relationship may be one of mutual aid, of competition for limited sources, or of predation of one upon other. The mathematical modeling of two species interactions is as following.

$$\left. \begin{aligned} \frac{dx}{dt} &= x(a_0 + a_1x + a_2y) \\ \frac{dy}{dt} &= y(b_0 + b_1x + b_2y) \end{aligned} \right\} \quad (1)$$

where $x(t)$ and $y(t)$ denoted the respective populations at time t of two species which form a closed interacting community and a 's and b 's are constants. If $a_1 = a_2 = b_1 = b_2 = 0$ then **Malthusian model** is obtained which involves the simplest birth and death process of a species ecosystem. On the other hand, if $a_2 = b_1 = 0$, then (1) models a pair of noninteracting species, each of which follows generalized **Logistic law**.

The steady-state orbits which correspond to the constant and the periodic solutions of (1) and which are portrayed in the population quadrant (first quadrant) by points and simple closed curves (**No cycles Theorem**) is studied. The results appear to be contradictory.

Specific predator – prey model accounts. It constructs a simple mathematical model of a predator – prey community. This model was developed independently by Lotka – Volterra in 1920s who set the system.

$$\left. \begin{aligned} \frac{dx}{dt} &= x(a - cy) \\ \frac{dy}{dt} &= y(-k + \lambda x) \end{aligned} \right\} \quad (2)$$

where x and y are the prey and predator populations respectively, at time t and a, c, k, λ are positive constants. Throughout the study it focuses the attention on qualitative behavior, explicit solutions, and the resulting ecological interpretations. It found that the solution trajectories in the phase plane of (2) model is closed and represents a periodic motion.

Then the effect of an indiscriminate harvester or poison that kills both predator and prey is determined and is found that the average of prey is $(k + H_2)/\lambda$ and for predator is $(a - H_1)/c$, where H_1, H_2 are positive constants, H_1 represents the effect of harvesting on the prey and H_2 represents the effect of harvesting on the predator. Harvesting of this type has surprising consequence with important ecological implication (**Volterra's Principle**) and then it is presented a discussion of this implication. It is concluded with a discussion of some limitations of this model since its formulation.

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In closing, I wish to avail this opportunity to record my sincer thanks to my family.

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Introduction

In the past, mathematics has not been successful a tool in the biological science as it has been in the physical sciences. There are probably many reasons for this. Plants and animals are complex, made up of many components. Thus scientific community is along way from understanding cause– effect relationships in the biological world.

In the following chapters mathematical models are developed which describes the relationships of the biological world. In the dynamics of life no species is alone. The survival or the flourishing of a species rests on strategies of cooperation, competition, and predation. It constructs a small part of the biological universe by considering the interactions of just two species. The relationship may be one of mutual aid, of competition for limited resources, or of predation of the one upon other.

In Chapter 1:

It begins to give a general model of ecosystems involving the interaction of two species, pausing to discuss some necessary mathematics. Fundamentals concepts, such as phase plane, equilibrium and their stability are discussed in this text.

In Chapter 2:

It develops mathematical models describing the relationships between plants, animals and their environment. The first model involves the simplest birth and death process of one species ecosystems (***Malthusian model***) which must be modified to model more realistic environmental influences (***Logistic law***). Then it begins to model more complex ecosystems involving the interaction of two species and to look for cyclical steady states in these models. The results appear to be contradictory.

In chapter 3:

The predator – prey relationship is explored for concluding parts of the discussion of population dynamics. It constructs a simple mathematical model of predator – prey community (***Lotka- Volterra equations***). Then it determines the average population of predator and prey. The influence of man on predator – prey ecosystems is studied (***Volterra's principle***). Then it gives a discussion of these implications, follow by a conclusion of a discussion some objects which are taken on this model.



Chapter One

**Introduction to
Two - Species
Models**

Chapter One

Introduction to Two – Species Models

1.1 Introduction

Interactive situations occur in the study of economics, ecology, electrical circuits, mechanical systems, celestial mechanics, control systems, and so forth. For example, the study of the dynamics of population growth of various plants and animals is an important ecological application of mathematics. Different species interact in a variety of ways. One animal may serve as the primary food sources for another, commonly referred to as a “predator - prey” relationship such that the interaction between the sharks and the small fish who are eaten by them.

Two species may depend upon one another for mutual support, such as bee's using a plant's nectar as food while simultaneously pollinating that plant; such a relationship is referred to as “mutualism”. Another possibility occurs when two or more species compete against one another for a common food sources or even compete for survival, such a relationship occurs in forests which are dominated by two similar trees.

In this chapter, the general model for complex ecosystems involving the interaction of two species is discussed. Then the result equations are changed to the linear systems by using perturbation

method. Two methods, elimination method and systems method, are used to obtain solutions.

The solutions of linear systems are used to investigate the linearized stability of the equilibrium solutions. Finally, the phase plane of such linear systems will be studied

1.2 Differential Systems – Phase Plane, Equilibrium, and Linearization.

In this section, the general model for the interaction of two-species is developed. Considering a small ecosystem with two species, their respective populations, that is the numbers of individual, being N_1 and N_2 . Assuming that the rates of change of each species depend only on the populations of each species, not other environmental factors. Thus;

$$\frac{dN_1}{dt} = g(N_1, N_2) \quad (1.2.1)$$

$$\frac{dN_2}{dt} = f(N_1, N_2)$$

The mathematical model consists of a system of two first order (possibly nonlinear) ordinary differential equations. The solution of equation (1.2.1) satisfies any given initial value of both populations, $N_1(t_0)$ and $N_2(t_0)$. Since t does not appear explicitly in the system (1.2.1), i.e autonomous system, it is certainly tempting to divide the two equations, using chain rule.

$$\frac{dN_2}{dN_1} = \frac{dN_2 / dt}{dN_1 / dt}$$

Considering the single first order differential equation

$$\frac{dN_2}{dN_1} = \frac{f(N_1, N_2)}{g(N_1, N_2)} \quad (1.2.2)$$

Equation (1.2.2) is called the phase plane equation. The two population are called the phases of the ecosystem. The solution of the phase plane equation is said to give the trajectories of the populations and the N_1N_2 - plane is called to as the phase plane. The solution of the resulting first order equation can be sketched by the method of isoclines, since neither $g(N_1, N_2)$ nor $f(N_1, N_2)$ depend explicitly on time.

To study the interaction of the two populations, either the time - dependent systems of equations, or the phase plane equation must be analyzed. A pair of functions, $N_1(t)$ and $N_2(t)$, is a solution of (1.2.1) if:

(a) $N_1(t)$ and $N_2(t)$ are defined on a common open interval I :
 $a < t < b$ (a may be $-\infty$, b may be $+\infty$)

(b) $N_1(t)$ and $N_2(t)$ satisfy (1.2.1) for every $t \in I$:

$$\frac{dN_1}{dt} = g(N_1(t), N_2(t))$$

$$\frac{dN_2}{dt} = f(N_1(t), N_2(t))$$

(c) There are no functions, $N_1^*(t)$ and $N_2^*(t)$, defined on an interval $I^* \supset I$, which coincide with $N_1(t)$ and $N_2(t)$, respectively, on I and satisfy (1.2.1) for all $t \in I^*$.

It is often the case that finding all solutions to the systems (1.2.1) is an impossible task. But it is relatively easy to find constant solutions: $N_1 = N_{1e}$ and $N_2 = N_{2e}$, such that.

$$f(N_{1e}, N_{2e}) = 0$$

$$g(N_{1e}, N_{2e}) = 0$$

The constant solution $N_1 = N_{1e}$ and $N_2 = N_{2e}$ is called an equilibrium solution or an equilibrium population. It is defined as a possible population of both species such that both populations will not vary in time. The births and deaths of species N_1 must balance, and similarly those of N_2 must balance.

To investigate what happens in time if both populations are near their respective equilibrium populations, the Perturbation method is used as follows:

$$N_1 = N_{1e} + \varepsilon N_{11}(t) \quad (1.2.3)$$

$$N_2 = N_{2e} + \varepsilon N_{21}(t)$$

Where ε is small number $0 < |\varepsilon| < 1$. N_{1e} and N_{2e} are an equilibrium population. εN_{11} and εN_{21} are the differences between the total population and the equilibrium population or the population displacement from equilibrium. Substituting this into the time dependent population equations yields,

$$\varepsilon \frac{dN_{11}}{dt} = g[N_{1e} + \varepsilon N_{11}(t), N_{2e} + \varepsilon N_{21}(t)]$$

$$\varepsilon \frac{dN_{21}}{dt} = f[N_{1e} + \varepsilon N_{11}(t), N_{2e} + \varepsilon N_{21}(t)]$$

Using the Taylor expansion for a function of two variables

$$F(x_0 + h, y_0 + h) = F(x_0, y_0) + h \frac{\partial F}{\partial x}(x_0, y_0) + k \frac{\partial F}{\partial y}(x_0, y_0) + \dots$$

In this manner,

$$\varepsilon \frac{dN_{11}}{dt} = g(N_{1e}, N_{2e}) + \varepsilon N_{11} \frac{\partial g}{\partial N_1}(N_{1e}, N_{2e}) + \varepsilon N_{21} \frac{\partial g}{\partial N_2}(N_{1e}, N_{2e}) + O(\varepsilon^2)$$

(1.2.4)

$$\varepsilon \frac{dN_{21}}{dt} = f(N_{1e}, N_{2e}) + \varepsilon N_{11} \frac{\partial f}{\partial N_1}(N_{1e}, N_{2e}) + \varepsilon N_{21} \frac{\partial f}{\partial N_2}(N_{1e}, N_{2e}) + O(\varepsilon^2)$$

Neglecting the $O(\varepsilon^2)$ terms (corresponding to the non linear terms in the neighborhood of the equilibrium populations) and if recalling that N_{1e} and N_{2e} is an equilibrium populations, then the following is obtained:

$$\frac{dN_{11}}{dt} = \frac{\partial g}{\partial N_1}(N_{1e}, N_{2e})N_{11} + \frac{\partial g}{\partial N_2}(N_{1e}, N_{2e})N_{21}$$

(1.2.5)

$$\frac{dN_{21}}{dt} = \frac{\partial f}{\partial N_1}(N_{1e}, N_{2e})N_{11} + \frac{\partial f}{\partial N_2}(N_{1e}, N_{2e})N_{21}$$

This is a linear system of differential equations with constant coefficients. Knowing the solution of the linearized equation will only indicate the behavior of each species in the immediate vicinity of an equilibrium population. In order to describe growth far away from an equilibrium population, it uses the phase plane equation. If equation (1.2.3) is substituted into the phase plane equation, equation (1.2.2) expanded via Taylor's theorem, and the nonlinear terms are neglected, then it is derived

$$\frac{dN_2}{dN_1} = \frac{\frac{\partial f}{\partial N_1} N_{11} + \frac{\partial f}{\partial N_2} N_{21}}{\frac{\partial g}{\partial N_1} N_{11} + \frac{\partial g}{\partial N_2} N_{21}}$$

Comparing this with equation (1.2.5) the slopes of the phase plane are approximated in the vicinity of an equilibrium population by the slopes of the phase plane of the linear system. Knowing and understanding the phase plane of all possible linear systems are necessary in the investigation of the phase plane corresponding to non-linear systems.

1.3 System of Two Constant Coefficient First Order Differential Equations

This section discusses the solution of a system of two coupled first – order homogenous liner differential equations with constant coefficients,

$$\frac{dx}{dt} = ax + by \quad (1.3.1a)$$

$$\frac{dy}{dt} = cx + dy \quad (1.3.1b)$$

Here x and y are the displacements from an equilibrium population. Two methods to solve these equations will be discussed.

1. Method of Elimination

Case (1): if $c \neq 0$, then x can be eliminated from equation (1.3.1a) using equation (1.3.1b)

$$x = \frac{1}{c} \frac{dy}{dt} - \frac{d}{c} y$$

The system of equation is reduced to one second – order differential equation,

$$\frac{1}{c} \frac{d^2 y}{dt^2} - \frac{d}{c} \frac{dy}{dt} = \frac{a}{c} \frac{dy}{dt} - \frac{ad}{c} y + by,$$

So after some algebra,

$$\frac{d^2 y}{dt^2} - (a + d) \frac{dy}{dt} + (ad - bc)y = 0$$

Seeking solution in the form e^{rt} , yield the characteristic polynomial

$$r^2 - (a + d)r + (ad - bc) = 0$$

the two roots being

$$r = \frac{a + d \pm \sqrt{(a + d)^2 - 4(ad - bc)}}{2}$$

Thus

$$y = c_1 e^{r_1 t} + c_2 e^{r_2 t}$$

$$x = c_1 \frac{r_1 - d}{c} e^{r_1 t} + c_2 \frac{r_2 - d}{c} e^{r_2 t}$$

Case (2): if $c = 0$, then from equation (1.3.1b) is obtained $y = Be^{dt}$. Thus x can be solved from equation (1.3.1a) as following.

$$\frac{dx}{dt} = ax + bBe^{dt}$$

(1.3.2)

$$\frac{dx}{dt} - ax = bBe^{dt}$$

1. if $a \neq d$ the integrating factor is:

$$\mu(t) = e^{\int -at} = e^{-at}$$

Multiplying equation (1.2.3) by $\mu(t)$ yields

$$\begin{aligned} e^{-at} \frac{dx}{dt} - ae^{-at} x &= bBe^{(d-a)t} \\ \frac{d}{dt}(e^{-at} x) &= \int bBe^{(d-a)t} \end{aligned} \quad (1.3.3)$$

Integrating both sides and solve for x to find

$$\begin{aligned} e^{-at} x &= \int bBe^{(d-a)t} \\ &= \frac{bB}{d-a} e^{(d-a)t} + A \\ x &= \frac{bB}{d-a} e^{(d-a)t} + Ae^{at} \end{aligned}$$

2. If $a = d$ then it is obtained from (1.3.3)

$$\begin{aligned} \frac{d}{dt}(e^{-at} x) &= bB \\ e^{-at} x &= bBt + A \\ x &= bBte^{at} + Ae^{at} \end{aligned}$$

So the general solution for x is

$$x = \begin{cases} Ae^{at} + \frac{bB}{d-a} e^{dt} & \text{if } d \neq a \\ Ae^{at} + bBte^{at} & \text{if } d = a \end{cases}$$

2. System Methods (using Matrix Theory)

An alternative to the method of elimination is to solve the linear system, equations(1.3.1a)and (1.3.1b), using the matrix and vector notation:

$$\left. \begin{aligned} \frac{d}{dt} \begin{bmatrix} x \\ y \end{bmatrix} &= \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} \\ \frac{dv}{dt} &= Av \end{aligned} \right\} \quad (1.3.3)$$

where

$$v = \begin{bmatrix} x \\ y \end{bmatrix} \text{ and } A = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

Solutions are sought in terms of exponentials

$$v = v_0 e^{rt} \quad (1.3.4)$$

or equivalently

$$\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} x_0 \\ y_0 \end{bmatrix} e^{rt}$$

Where $v_0 = \begin{bmatrix} x_0 \\ y_0 \end{bmatrix}$ is a constant vector to be determined. The substitution of equation (1.3.4) into equation (1.3.3) yields,

$$Av_0 = rv_0 \quad (1.3.5)$$

Or equivalently,

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} x_0 \\ y_0 \end{bmatrix} = r \begin{bmatrix} x_0 \\ y_0 \end{bmatrix}$$

Nontrivial solutions of equation (1.3.5) (i.e., $v_o \neq 0$) exist only for certain values of r , called the eigenvalues of the matrix A . Equation (1.3.5) can be written as a homogeneous system (using the identity matrix I):

$$(A - rI)v_o = 0 \quad (1.3.6)$$

$$\begin{bmatrix} a - r & b \\ c & d - r \end{bmatrix} \begin{bmatrix} x_o \\ y_o \end{bmatrix} = 0$$

There are nontrivial solutions to a homogenous liner system if and only if the determinant of the coefficients equal zero. Thus

$$|A - rI| = 0$$

Or

$$\begin{vmatrix} a - r & b \\ c & d - r \end{vmatrix} = 0$$

Solving this determinate, obtaining

$$(a - r)(d - r) - bc = 0$$

This yields two values for the exponent

$$r = \frac{a + d \pm \sqrt{(a + d)^2 - 4(ad - bc)}}{2}$$

the same result as obtained by elimination.

If the roots are distinct, then the nontrivial value of $v_0 = \begin{bmatrix} x_0 \\ y_0 \end{bmatrix}$ corresponding to each eigenvalue (called the eigenvector corresponding to that eigenvalue) must be determined. If an eigenvalue is designated r_i and its corresponding eigenvector

$v_i = \begin{bmatrix} x_i \\ y_i \end{bmatrix}$ then the solution is given by

$$v = \sum_{i=1}^2 c_i v_i e^{r_i t}$$

where c_i are arbitrary constants or

$$\begin{bmatrix} x \\ y \end{bmatrix} = \sum_{i=1}^2 c_i \begin{bmatrix} x_i \\ y_i \end{bmatrix} e^{r_i t}$$

1.4 Stability of Two – species Equilibrium Populations

The concept of the stability of solutions is considered to be one of the fundamental aspects of applied mathematics. In this section, a mathematical method to distinguish between stable and unstable equilibrium solution is given. The behavior of population near equilibrium is governed by a system of constant coefficient differential equations.

$$\frac{dx}{dt} = ax + by$$

$$\frac{dy}{dt} = cx + dy$$

the solution consist of liner combination of exponentials, e^{rt} , where.

$$r = \frac{a + d \pm \sqrt{(a + d)^2 - 4(ad - bc)}}{2}$$

are the roots of the characteristic polynomial. The equilibrium solution is said to stable if for all initial conditions sufficiently near the equilibrium solution, the solution stays close to the equilibrium solution that is the displacement from equilibrium does not grow. Otherwise the equilibrium solution is said to be unstable.

Thus the stability of the equilibrium solution is determined by the time dependence of the displacement from equilibrium. That is, it is determined by the signs of two values of real parts of the roots.

An equilibrium solution is stable if the real parts of both roots are less than zero, unstable if at least one is greater than zero, neutrally stable if the real part of one roots equal zero and the other is less than or equal zero except if both roots are identically zero in which case the solution is algebraically unstable. Letting

$$p \equiv a + d$$

$$q \equiv ad - bc$$

$$\Delta \equiv (a + d)^2 - 4(ad - bc) = p^2 - 4q$$

The Following table indicates the behavior of the equilibrium solution:

Table 1		1. real and unequal $\Delta > 0$	
A	same sign $q > 0$	both positive $p > 0$	unstable
		both negative $p < 0$	stable
B	different signs $q < 0$		unstable
C	One root zero $q = 0$	Other root positive $p > 0$	unstable
		other root negative $p < 0$	neutrally stable

Table2		2. real and equal $\Delta = 0$	
A	same sign	both positive $p > 0$	unstable
		both negative $p < 0$	stable
B	both zero $p = 0$	algebraically unstable	

Table3		3. Complex conjugates $\Delta < 0$	
A	real part has same sign	real part positive $p > 0$	unstable
		real part negative $p < 0$	stable
B	real part zero $p = 0$	naturally stable	

Tables 1.4.1, 2 and 3 The behavior of the equilibrium solution

These results are summarized in Fig. 1.4.1. The ideal of stability is central to any discussion of the behavior of trajectories near equilibrium point. The equilibrium point (x_0, y_0) is stable if any trajectory that starts close to the point stays close to it for all future time. It is asymptotically stable if it is stable and if any trajectory that starts close to (x_0, y_0) approaches that point as t tends to infinity. If it is unstable then the trajectories move away from it.

Example:

Considering the following system:

$$\begin{aligned}\frac{dx}{dt} &= x(a - 4 + 2y) - a \\ \frac{dy}{dt} &= y(a + 1 - x) - 2a,\end{aligned}$$

Letting:

$$f(x, y) = x(a - 4 + 2y) - a$$

$$g(x, y) = y(a + 1 - x) - 2a$$

$x = 1, y = 2$ is an equilibrium solution since $f(1, 2) = 0, g(1, 2) = 0$

Linearizing this system near this equilibrium by using perturbation methods, so it obtained:

$$\begin{aligned}\frac{dx_1}{dt} &= ax_1 + 2y_1 \\ \frac{dy_1}{dt} &= -2x_1 + ay_1\end{aligned}$$

Where x_1 and y_1 are respective displacements from equilibrium.

$x = 1, y = 2$ is stable for $a < 0$

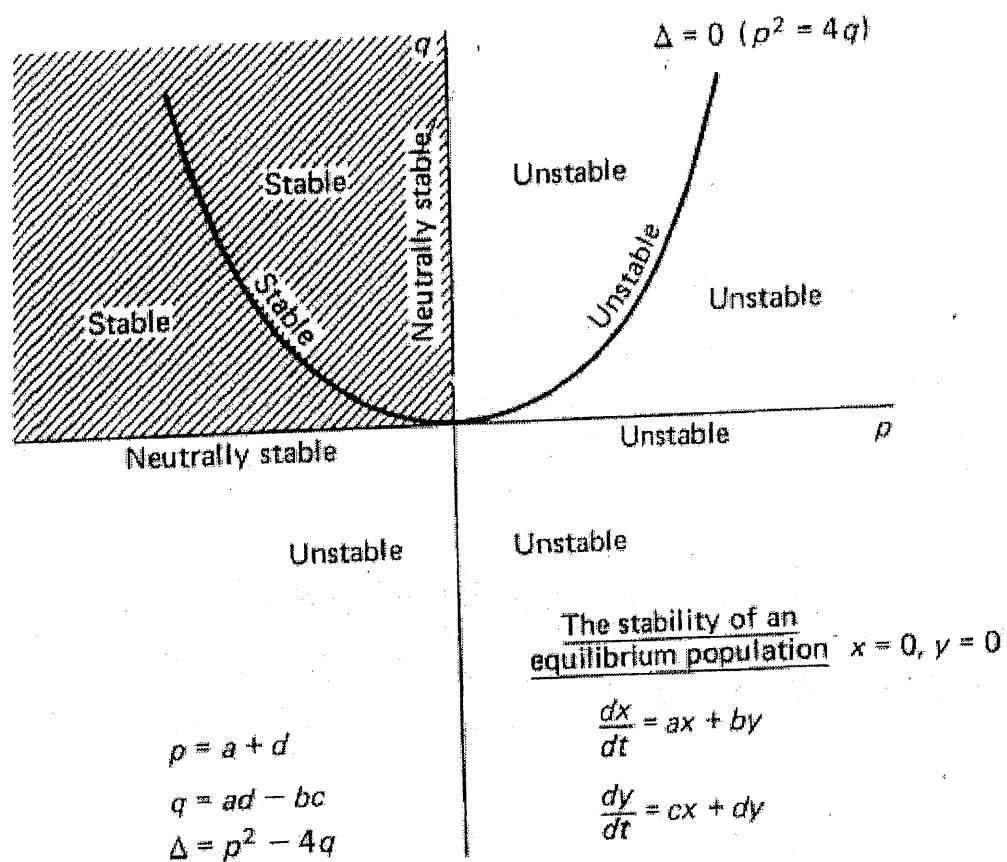


Figure 1.4.1 Stability Diagram (the shaded region is stable).

1.5 Phase Plane of Linear Systems:

Note only does analysis of the linear systems determine the stability or instability of an equilibrium population, but the resulting phase plane of the linear systems will yield an approximation to the phase plane of the non linear systems valid in the neighborhood of the equilibrium population.

It will show that to each different case of table (1.4.1,2,3) there corresponds only one qualitative behavior in the phase plane. It will consider only the two cases. **(1) B** ($\Delta > 0, q < 0$), and **(3) A** ($\Delta < 0$).

A. saddle points ($\Delta > 0, q < 0$)

The case in which the roots of the characteristic polynomial are of opposite signs [**(1) B** $\Delta > 0, q < 0$] is analyzed first. Considering the time dependent equations,

$$\frac{dx}{dt} = ax + by \quad (1.5.1)$$

$$\frac{dy}{dt} = cx + dy$$

It was shown in sec. 1.3 that if $c \neq 0$, then

$$x = c_1 \frac{r_1 - d}{c} e^{r_1 t} + c_2 \frac{r_2 - d}{c} e^{r_2 t}$$

$$y = c_1 e^{r_1 t} + c_2 e^{r_2 t}$$

It may assume that

$$r_1 < 0 < r_2,$$

since the roots are real and of opposite signs. To sketch the trajectories in the phase plane, t must be eliminated. Some specific trajectories are sketched. For example, if $c_1 = 0$ then

$$\begin{aligned} x &= c_2 \frac{r_2 - d}{c} e^{r_2 t} \\ y &= c_2 e^{r_2 t} \end{aligned}$$

and t is easily eliminated

$$\frac{x}{y} = \frac{r_2 - d}{c}$$

This straight line represents two trajectories emanating from the origin (as $t \rightarrow -\infty$, $x \rightarrow 0$ and $y \rightarrow 0$ since $r_2 > 0$) and going toward infinity in a particular direction depending on the signs of $(r_2 - d)/c$ and c_2 . A trajectory which starts at a finite point and goes in a straight line to infinity is called a ray. These two rays are sketched in Fig 1.5. 1 (assuming that $(r_2 - d)/c > 0$). Two other simple trajectories occur if $c_2 = 0$, since then

$$\begin{aligned} x &= c_1 \frac{r_1 - d}{c} e^{r_1 t} \\ y &= c_1 e^{r_1 t} \end{aligned}$$

Thus again, t is eliminated easily

$$\frac{x}{y} = \frac{r_1 - d}{c}$$

Although this also represents two trajectories emanating from the origin, these trajectories are tending to the origin as $t \rightarrow \infty$ since $r_1 < 0$ (and tend towards, infinity as $t \rightarrow -\infty$).

The direction of these trajectories are determined by the sign of c_1 and the sign of $(r_1 - d)/c$. Thus if $(r_1 - d)/c > 0$ and $(r_2 - d)/c > 0$, then Fig 1.5.1 is obtained,

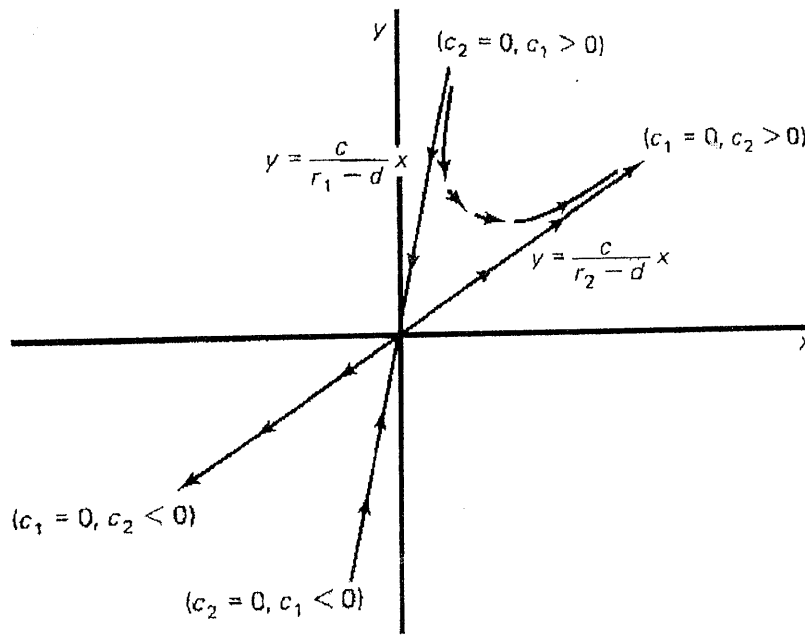


Figure 1.5.1 Some important trajectories

It will show that the other trajectories ($c_1 \neq 0$ and $c_2 \neq 0$) do not go through the origin. Of more significance to the phase plane sketch is to notice that these curves do not tend towards the origin as $t \rightarrow \pm\infty$. As $t \rightarrow +\infty$, since $r_1 < 0 < r_2$,

$$x \rightarrow c_2 \frac{r_2 - d}{c} e^{r_2 t}$$

$$y \rightarrow c_2 e^{r_2 t}$$

Thus all trajectories ($c_2 \neq 0$) tend towards infinity as $t \rightarrow +\infty$, in the direction.

$$\frac{x}{y} \rightarrow \frac{r_2 - d}{c}$$

i.e tending towards being parallel to the outward going ray. Similarly as $t \rightarrow -\infty$,

$$\begin{aligned} x &\rightarrow c_1 \frac{r_1 - d}{c} e^{\eta t} \\ y &\rightarrow c_1 e^{\eta t} \end{aligned}$$

If $c_1 \neq 0$, these trajectories also tend towards infinity $t \rightarrow -\infty$, in the direction

$$\frac{x}{y} \rightarrow \frac{r_1 - d}{c}$$

this time parallel to the inward going rays. The trajectory corresponding to one value of c_1 and c_2 (in addition, assuming $c_1 > 0$ and $c_2 > 0$) is sketched in Fig. 1.5.1 in partially dotted lines (other cases will be sketched in an analogous fashion). The curves is dotted, indicating the general behavior the curve must have for values of t which are not either large and positive or large and negative as shown in Fig1.5.2.

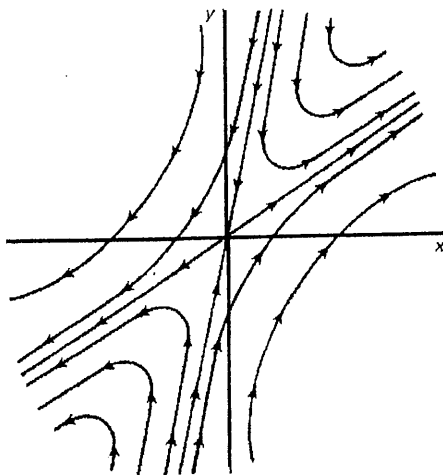


Figure 1.5.2 Sketch of trajectories in the vicinity of a saddle point

The equilibrium point $(x = 0, y = 0)$ is unstable as most trajectories near point eventually tend away from the equilibrium point as shown in Fig . Imagine the phase plane trajectories of this example as the paths of a person moving along some hills $Z = f(x,y)$ as viewed from above. If the person moves down the hill in some manner, then certain regions correspond to high ground and others to low ground. The resulting hill as illustrated in Fig. 1.5.3 resembles the shape of a saddle with a seat at $(x = 0, y = 0)$ For this reason this type of equilibrium points is called a saddle point an unstable equilibrium point

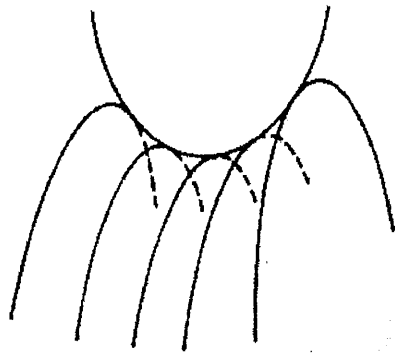


Figure 1.5.3

B. Spirals ($\Delta < 0$, $P \neq 0$)

When the two roots of the characteristic equation are complex conjugates of each other the analysis is more complicated than in other cases. If the roots are purely imaginary, then the solution exhibits a pure oscillation. A simple example of equation (1.5.1) corresponding to imaginary roots is the equation of spring-mass systems without friction.

$$\begin{aligned}\frac{dx}{dt} &= v \\ \frac{dy}{dt} &= -\frac{k}{m}x.\end{aligned}$$

The phase plane for this example consists of closed curves (in general ellipses) encircling the equilibrium point called a center. However, if the roots have both nonzero real and imaginary parts, then it would expect an oscillation with the amplitude either growing or decaying. In the phase plane the resulting trajectories are spirals, as it is proceed to show.

A simple example of system of equations whose roots are complex numbers is

$$\begin{aligned}\frac{dx}{dt} &= ax + by \\ \frac{dy}{dt} &= -bx + ay\end{aligned}$$

The roots of the characteristic polynomial are determined by

$$\begin{vmatrix} a - r & + b \\ - b & a - r \end{vmatrix} = 0$$

yielding,

$$(a - r)^2 + b^2 = 0$$

or equivalently the complex conjugates pair

$$r = a \pm ib$$

The trajectories in the phase plane can be obtained from

$$\frac{dy}{dx} = \frac{-bx + ay}{ax + by}$$

The first order differential equation is not separable. The alternate form (obtained by dividing the numerator and denominator by x),

$$\frac{dy}{dx} = \frac{-b + a \frac{y}{x}}{a + b \frac{y}{x}}$$

Suggests that the change of variables,

$$\frac{y}{x} = v \quad \text{or} \quad y = xv$$

will enables its explicit integration. Since $\frac{dy}{dx} = x \left(\frac{dv}{dx} \right) + v$ it follows that

$$x \frac{dv}{dx} = -v + \frac{-b + av}{a + bv}$$

The equation is now separable, after some algebra

$$\frac{(a + bv) dv}{-b(1 + v^2)} = \frac{dx}{x}$$

Integration yields

$$-\frac{a}{b} \tan^{-1} v - \frac{1}{2} \ln(1 + v^2) = \ln|x| + c$$

where c is the constant of integration. Returning to the x, y variables ($v = y/x$) yields

$$-\frac{a}{b} \tan^{-1} \frac{y}{x} = \frac{1}{2} \ln\left(1 + \frac{y^2}{x^2}\right) + \ln|x| + c$$

or

$$-\frac{a}{b} \tan^{-1} \frac{y}{x} = \ln(x^2 + y^2)^{1/2} + c.$$

This form suggests the introduction of polar coordinates,

$$\begin{aligned} \theta &= \tan^{-1} \frac{y}{x} \\ r &= (x^2 + y^2)^{1/2} \end{aligned}$$

In which case after exponentiating it has that

$$r = r_0 e^{-(a/b)\theta}$$

Such curves are called exponential spirals (if $a \neq 0$). If $a = 0$, the curves become the closed curves $r = r_0$ circles.

If $a/b < 0$, then as θ increase, r increases, as shown in Fig. 1.5.4. If $a/b > 0$, then as θ increases, r decreases as shown in the Fig. 1.5. 5. the stability or instability also follow from the exponential term e^{rt} , where $r = a \pm ib$. There is an unstable spiral if $a > 0$ and a stable spiral if $a < 0$.

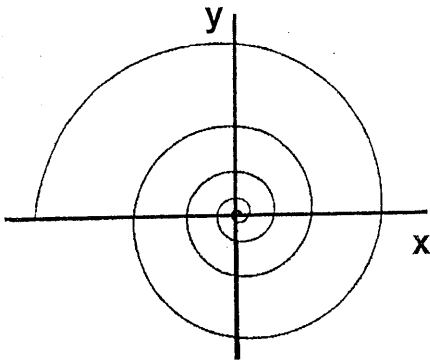


Figure 1.5.4 Left-hand spiral

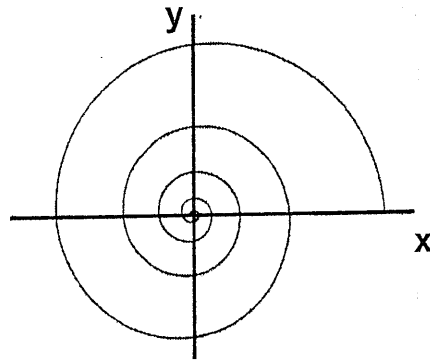


Figure 1.5.5 Right-hand spiral

In general case of complex conjugates roots, it is also convenient to introduce the polar angle θ

$$\theta = \tan^{-1} \frac{y}{x}$$

$$\frac{d\theta}{dt} = \frac{x \frac{dy}{dt} - y \frac{dx}{dt}}{x^2 + y^2}$$

Eliminating dx/dt and dy/dt from the differential equations,

$$\frac{dx}{dt} = ax + by$$

$$\frac{dy}{dt} = cx + dy$$

yields,

$$\frac{d\theta}{dt} = \frac{cx^2 + xy(d - a) - by^2}{x^2 + y^2}$$

It shows that $\frac{d\theta}{dt} \neq 0$, the angle continually either increase or decrease. Suppose $\frac{d\theta}{dt} = 0$. Then, by dividing by y^2

$$c\left(\frac{x}{y}\right)^2 + \frac{x}{y}(d - a) - b = 0$$

or

$$\frac{x}{y} = \frac{a - d \pm \sqrt{(d - a)^2 + 4bc}}{2c}.$$

However, the criteria for complex conjugate roots is

$$(a + d)^2 - 4(ad - bc) < 0$$

Or equivalently

$$(a - d)^2 + 4bc < 0$$

Thus there are no values of x and y for which $\frac{d\theta}{dt} = 0$. The solution either spirals into the origin or spirals out from the origin.

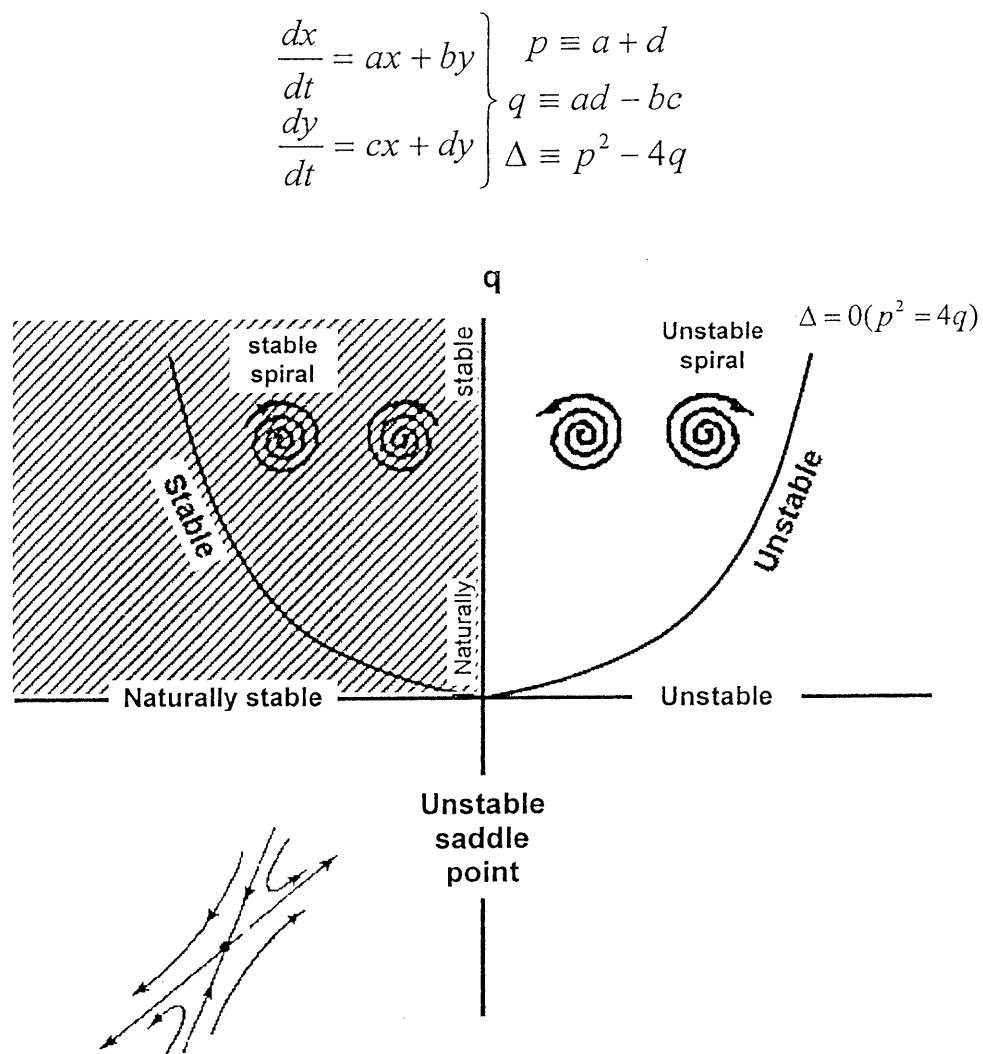


Figure 1.5.6 Stability diagram including typical trajectory in the neighborhood of equilibrium (shaded region indicates a stable equilibrium point).

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Chapter Two

**Mathematical
Modeling in
Ecology (Population
Models)**

Chapter Two

Mathematical Modeling in Ecology

(Population Models)

2.1 Introduction

This chapter develops mathematical models, which describe the mutual relationships among plants, animals and their environment. Starting the study of mathematical ecology by formulate models based on observed population data of various species, such as human population in a specified area or the population of fish and algae in a lake. The first model, Malthusian model or Exponential model, which assumes that the rate of change of a parameter, negative (decay) or positive (growth) is directly proportional to the instantaneous value of the parameter.

The Malthusian model considered only death by natural causes. Thus Malthusian model is expanded to reflect the effects of environment (Logistic law)

Then more complex ecosystems involving the interaction of two species are modeled. There are three types of the biological interaction. The interaction may be one of mutual aid, of competition for same food sources or of predation which threaten the very existence of the prey. Finally, cyclical steady state is studied in these models. The results appear to be contradictory.

2.2 Population Growth

Interest in how populations tend to grow was stimulated in late 18th century by Thomas Malthus. He put forth an exponential growth model for human population and concluded that eventually the population would exceed the capacity to grow an adequate food supply.

Although the assumptions of this model leave out factors important to population growth, but it is instructive to examine this model as a basis for later refinement. In this section the models of population growth of a species are developed.

There are some factors that pertain to population growth, the birth rate and death rate. The birthrate and death rate are determined by different factors. The birthrate is influenced by infant mortality rate, attitudes toward and availability of contraceptives, attitudes toward abortion, health care during pregnancy and so forth. The death rate is affected by sanitation and public health, wars, pollution, medicines, diet, psychological stress and anxiety and so forth. Other factors that influence population growth in a given region are immigration and emigration, living space restrictions, availability of food and water, epidemics and so forth. Now it will consider only the birth rate and death rate.

Letting $N(t)$ denote the population function and it is assumed to be continuous and differentiable function. Assuming that during a small unit time period a percentage b of the population is newly born. Similarly, a percentage c of the population dies. In other word, the new population $N(t + \Delta t)$ is the old population $N(t)$ plus the number of births minus the number of death during the time period Δt . Symbolically,

$$N(t + \Delta t) = N(t) + bN(t)\Delta t - cN(t)\Delta t$$

$$N(t + \Delta t) = N(t) + \Delta t(b - c)N(t)$$

Letting $R = b - c$, and the growth rate R ,

$$R(t) = \left(\frac{N(t + \Delta t) - N(t)}{\Delta t N(t)} \right)$$

In general, this growth rate can depend on time and on the measuring time interval. The instantaneous growth rate:

$$R(t) = \lim_{\Delta t \rightarrow 0} \left(\frac{N(t + \Delta t) - N(t)}{\Delta t N(t)} \right) = \frac{1}{N} \frac{dN}{dt} \quad (2.2.1)$$

Equation (2.2.1) can be rewriting

$$\frac{dN}{dt} = RN$$

Assuming the growth rate is a constant R_0 , the population growth is described by the solution to the first order linear differential equation with constant coefficients.

$$\frac{dN}{dt} = R_0 N \quad (2.2.2)$$

which satisfies the initial condition

$$N(t_0) = N_0$$

A solution to this differential equation can be obtained since the equation is separable.

$$\frac{dN}{N} = R_0 dt$$

Integration of both sides of this last equation yields,

$$\ln N(t) = R_0 t + c \quad (2.2.3)$$

For some constant c . applying the condition $N(t_0) = N_0$ to equation (2.2.3) to find c , result in

$$\ln N_0 = R_0 t_0 + c$$

Or

$$c = \ln N_0 - R_0 t_0$$

Then substitution for c in to (2.2.3) gives

$$\ln N(t) = R_0 t + \ln N_0 - R_0 t_0$$

or simplifying algebraically,

$$\ln \frac{N}{N_0} = R_0 (t - t_0)$$

Finally, by taking the exponential of both sides of the preceding equation and multiplying the result by N_0 , it obtaining the solution,

$$N(t) = N_0 e^{R_0 (t - t_0)} \quad (2.2.4)$$

Equation (2.2.4) is known as the Malthusian model of population or exponential model, predicts that population grows exponentially with time.

As sketched in Fig. (2.2.1) for $R_0 > 0$, a population grows exponentially if the grow rate is positive constant. Similarly, a population decays exponentially if its growth rate is a negative constant as shown in Fig. (2.2.2)

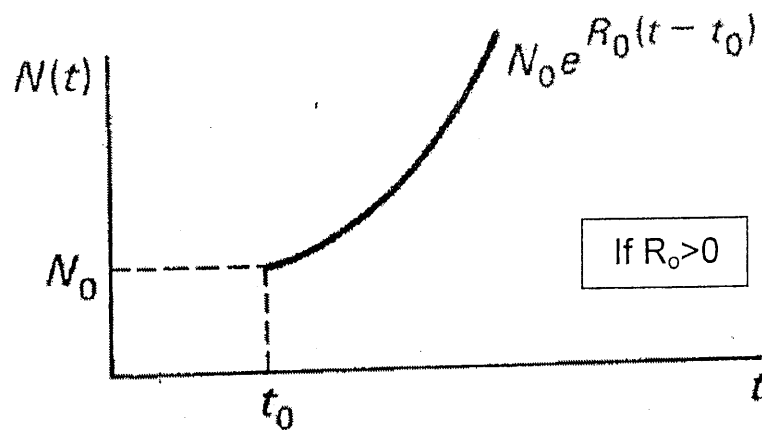


Figure 2.2.1 Exponential growth

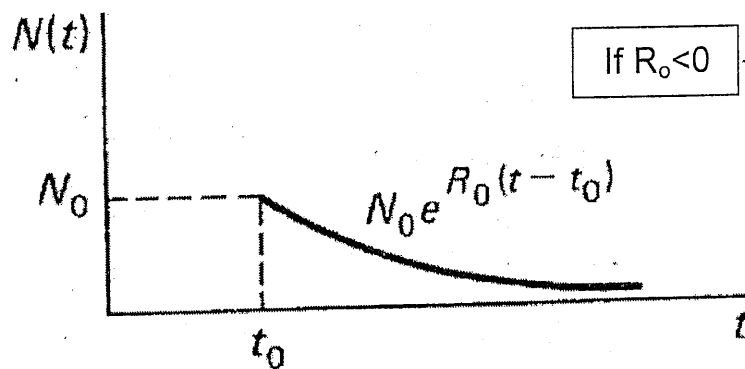


Figure 2.2.2 Exponential decay

Of interest is the time necessary for a population to double if the growth rate is a positive constant. The length of time, $t_1 - t_0$, such that the population doubles, $N(t_1) = 2N(t_0)$, is obtained from the expression.

$$2N_0 = N_0 e^{R_0(t_1 - t_0)}$$

N_0 cancel. Hence the time to double population is,

$$t_1 - t_0 = \frac{\ln 2}{R_o}$$

This results can be applied to the following problem if the population grows continually at the instantaneous rate of two percent a year ($R_o = .02$) then the required time to double population is

$$t_1 - t_0 \approx \frac{0.69315}{0.02} \approx 0.35$$

Thus, the population doubles in approximately 35 years.

Some populations do grow exponentially. However, when the population gets extremely large though, this model cannot be very accurate, since it does not reflect the fact that individual members are competing with each other for food supplies, availability of water, living space restriction and other natural resources. Thus, Malthusian model must be refined to reflect this competition. Letting attempt to mathematically model this process. It can go at this model construction in two ways. In General, the growth rate

$\frac{1}{N} \frac{dN}{dt}$ may not be constant, but might depend on the population.

$$\frac{1}{N} \frac{dN}{dt} = R(N) \quad \text{or} \quad \frac{dN}{dt} = NR(N) \quad (2.2.5)$$

For moderate size populations, growth occurs with only slight limitations from the species total environment as N diminishes $R(N)$ should approach the growth rate without environmental influences. As the population increase, it still expects it to grow, but at a smaller rate due to the limitation on growth caused by increased population. Thus $R(N)$ decrease as N increase for a much larger population, experiments show the growth rate to be negative, more deaths than births. If assuming that the growth rate is continuous, then there is a population at which the growth rate is zero. The simplest function with this property is the straight line.

$$R(N) = a - bN$$

is sketched in Fig. 2.2.3, yielding the non linear first order differential equation known as the logistic equation.

$$\frac{dN}{dt} = N(a - bN) \quad (2.2.6)$$

a is the growth rate without environmental influences, and b represents the effect of increased population, a and b are positive constants.

This model was first investigated by Verhulst in the 1830 s and later rediscovered by Peal and Reed in 1920s.

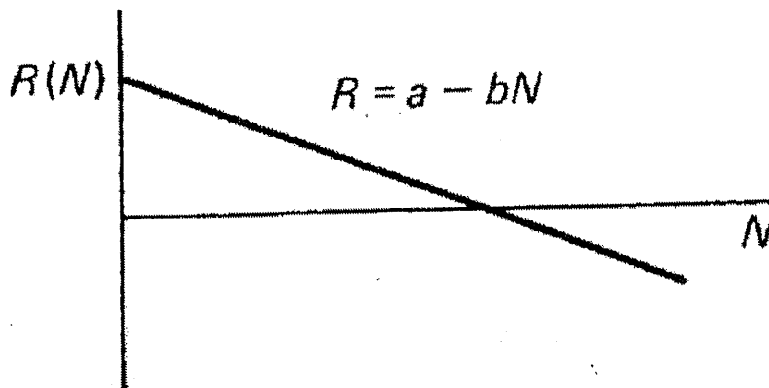


Figure 2.2.3 Logistics growth rate

The other way is to assume that the growth rate on the right hand side of Eq. (2.2.2) can be expanded in to a series, as

$$\frac{1}{N} \frac{dN}{dt} = c_0 + c_1 N + \dots$$

The constant c_0 would obviously be our potential growth rate a . Then the constant c_1 can be evaluated in much the same way as it evaluated b in Eq (2.2.6).

The population at which the growth rate is zero is an equilibrium population in the sense that if the population was initially at that value it would stay there. That is, the number of births would exactly offset the number of deaths.

Using the logistic model, equation (2.2.5), the equilibrium populations are

$$N = 0 \quad \text{and} \quad N = a/b$$

To investigate the stability of the equilibrium population $N = a/b$, the differential equation (2.2.6) may be linearized in the neighborhood of the equilibrium population by using perturbation methods as follows.

$$N = a/b + \varepsilon N_1$$

Where N_1 is the displacement from equilibrium and must be small. Substituting this into the logistic equation yields,

$$\varepsilon \frac{dN_1}{dt} = (a/b + \varepsilon N_1)(a - a - \varepsilon b N_1)$$

Or equivalently

$$\frac{dN_1}{dt} = -b N_1 (a/b + \varepsilon N_1)$$

since εN_1 is small, neglecting the non linear term. Thus

$$\frac{dN_1}{dt} = -a N_1$$

the solution of this differential equation

$$N_1 = ce^{-at}$$

it shows that the equilibrium population is stable. Explicitly as $t \rightarrow \infty$, $N \rightarrow a/b$, but it never reaches it in a finite time. For the equilibrium population $N = 0$, by using the perturbation methods it obtains:

$$N_1 = c_1 e^{at}$$

where N_1 is the displacement from equilibrium. Thus the equilibrium population $N = 0$ is unstable any population not starting at that level tends to move away from it.

An explicit solution to the logistic equation can be obtained since the equation is separable.

$$\frac{dN}{N(a - bN)} = dt$$

Using the methods of partial fractions

$$\frac{1}{N(a - bN)} = \frac{1/a}{N} + \frac{b/a}{a - bN}$$

Integration yields;

$$\frac{1}{a} \ln |N| - \frac{1}{a} \ln |a - bN| = t + c$$

the arbitrary constant c enables the initial value problems $N(0) = N_0$ to be solved. Eliminating c yields,

$$\frac{1}{a} \ln |N| - \frac{1}{a} \ln |a - bN| = t + \frac{1}{a} \ln |N_0| - \frac{1}{a} \ln |a - bN_0|$$

since both N and N_0 must be positive,

$$\frac{1}{a} \ln \frac{N}{N_0} + \frac{1}{a} \ln \left| \frac{a - bN_0}{a - bN} \right| = t$$

Multiplying a and exponentiating, yields;

$$\frac{N}{N_0} \left| \frac{a - bN_0}{a - bN} \right| = e^{at}$$

$a - bN$ and $a - bN_0$ have the same sign and hence

$$\frac{N}{N_0} \left(\frac{a - bN_0}{a - bN} \right) = e^{at}$$

or equivalently

$$N(a - bN_0) = (a - bN)N_0 e^{at}$$

this equation can be solved for N

$$N = \frac{aN_0 e^{at}}{a - bN_0 + bN_0 e^{at}}$$

or

$$N = \frac{a/b}{1 + \left(\frac{a - bN_0}{bN_0} \right) e^{-at}} \quad (2.2.7)$$

Notice from equation (2.2.7) that $N(t)$ approaches a/b as t tend to infinity, but never reaches it in a finite time. While for $t = 0$, Eq (2.2.6) yields the appropriate initial condition.

N increases if $dN/dt > 0$ and vice versa. For populations less than the equilibrium population, $N = a/b$, the population increase and for the population more than the equilibrium the population decrease. If initially less than the equilibrium population, the population continually grows, but it never reaches the equilibrium population. If initially greater than the equilibrium population, the population continually diminishes towards the equilibrium population, as shown in Fig 2.2.4.

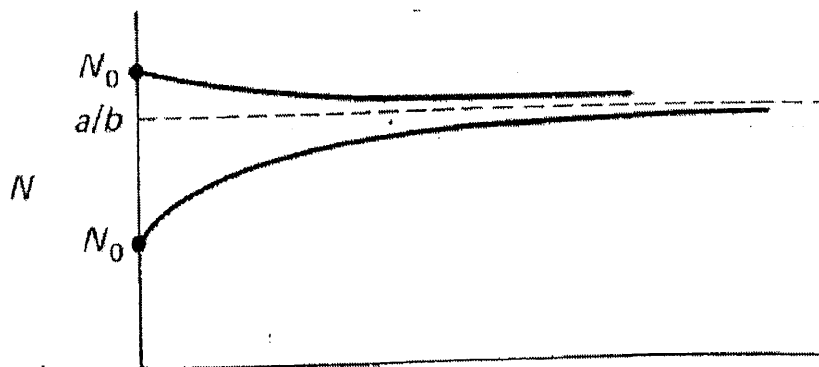


Figure 2.2.4 Logistics growth model: approach to equilibrium.

2.3 Quadratic Population Models

The population of lynx and here in the Canadian North woods wax and wane together in a mysterious. The number of sharks and of food fish in the Adriatic jointly oscillates in a curious way.

The aim of this section is to construct mathematical models for the interaction of any pair of species.

Letting $N_1(t)$ and $N_2(t)$ denote the respective populations, that is the number of individuals at time t of two species. The values of $N_1(t)$ and $N_2(t)$ are integers and change by integer amount as time goes on. Assuming that $N_1(t)$ and $N_2(t)$ are continuous, smooth off any corners on the graphs of $N_1(t)$ and $N_2(t)$ and assuming that both function are differentiable. Fig. 2.3.1 shows this smoothing process for $N_1(t)$.

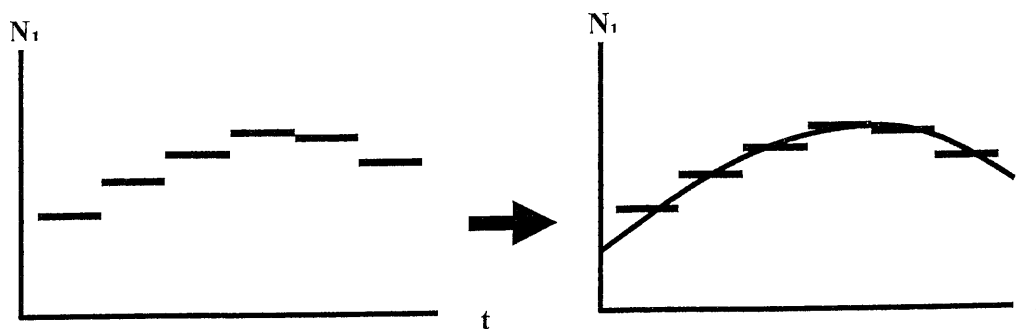


Figure 2.3.1 Smoothing a population curve.

Letting assume that in the span of time from t to $t + \Delta t$ the two populations change by amounts ΔN_1 and ΔN_2 , respectively. The quantities $\Delta N_1 / N_1$ and $\Delta N_2 / N_2$ are called the relative (or fractional) changes, while the nations,

$$\frac{\Delta N_1 / \Delta t}{N_1(t)} \quad \text{and} \quad \frac{\Delta N_2 / \Delta t}{N_2(t)} \quad (2.3.1)$$

are the average relative rates of change. Letting $\Delta t \rightarrow \infty$ in (2.3.1) obtaining the relative rate of change of the population of each species,

$$\frac{1}{N_1(t)} \frac{dN_1}{dt} \quad \text{and} \quad \frac{1}{N_2(t)} \frac{dN_2}{dt}$$

Considering the relative birth rates denoting by B , relative mortality rates by M one might expect each of these rates for each of two species to depend upon the populations themselves, i.e it might have $B_1(N_1, N_2)$ and $M_1(N_1, N_2)$ for the N_1 species and $B_2(N_1, N_2)$ and $M_2(N_1, N_2)$ for the N_2 species. If the community is closed, then no other forces play a significant role in affecting the relative rates of change, and it might have that.

$$\frac{1}{N_1(t)} \frac{dN_1}{dt} = B_1(N_1, N_2) - M_1(N_1, N_2) = r_1(N_1, N_2)$$

$$\frac{1}{N_2(t)} \frac{dN_2}{dt} = B_2(N_1, N_2) - M_2(N_1, N_2) = r_2(N_1, N_2)$$

Assuming that the relative rates r_1 and r_2 are continuously differentiable in N_1 and N_2 for $N_1 \geq 0, N_2 \geq 0$. Cross multiplying, and then it is obtained the fundamental equations for a closed community of two interacting species.

$$\frac{dN_1}{dt} = r_1(N_1, N_2)N_1(t)$$

$$\frac{dN_2}{dt} = r_2(N_1, N_2)N_2(t)$$

If r_1 is constant, $N_1(t)$ grows or decays exponentially, $N_1(t) = N_0 e^{rt}$ but there is no interaction with N_2 – species at all. Since it assumes that the two species do interact, the coefficient r_1 must be a function of N_2 . It may also depend on N_1 . Assuming that r_1 is a linear polynomial of N_1 and N_2

$$r_1 = a_0 + a_1N_1 + a_2N_2$$

Where a 's are constants. Treating the rate equation for the N_2 species in the same way and obtaining the quadratic population model.

$$\frac{dN_1}{dt} = (a_0 + a_1N_1 + a_2N_2)N_1 \quad (2.3.2)$$

$$\frac{dN_2}{dt} = (b_0 + b_1N_1 + b_2N_2)N_2$$

Where the a 's and b 's are constants. If $a_2 = b_1 = 0$, then (2.3.2) models a pair of non-interacting species, each of which follows a generalized logistic law. On the other hand, if $a_1 = a_2 = b_1 = b_2 = 0$, the exponential growth models occurs.

The derivation of the rate equation has been theoretical, but the terms have biological interpretation.

1. Natural growth coefficients: the constants a_0 and b_0 represent the natural growth of the respective species in the absence of any other interactions. The terms a_0x and b_0y in (2.3.2) are called the biotic potentials of the species because they are the natural growth rate.
2. Single – species Social coefficients: The constant a_1 measures the effect of the population $N_1(t)$ on the growth rate of species $N_1(t)$ itself. If $a_1 < 0$, a_1 is the overcrowding (or selflimiting) coefficient and measures the negative effects of over population, if $a_1 > 0$, then is called the mutualism coefficient and indicates an increase in productivity with an increase in population. The first case indicates competition among the members of species N_1 for limited resources while the second case implies cooperation among the members. A similar analysis applied to b_2
3. Two – species Social coefficients: the coefficients a_2 and b_1 measure the effect of each species on the growth rate of the other; they are called two – species social coefficients or interaction constants.

The following are the cases if $a_2 b_1 \neq 0$:

- I. If $a_2 > 0, b_1 > 0$, the case of interspecies mutualism
- II. If $a_2 < 0, b_1 > 0$ (or $a_2 > 0, b_1 < 0$) in which case N_1 is the prey of the predator N_2 (or N_2 is the prey of the predator N_1)
- III. If $a_2 < 0, b_1 < 0$, where mutual predation occurs or competition for common resources.

What ever the signs of the coefficients may be, rate terms such as $a_1 N_1^2, a_2 N_1 N_2$, or $b_2 N_2^2$ are called social or mass - action terms; involving as they do inter – or intraspecific effects of the total population on the individual growth rates from this point on the coefficients will be taken to be non negative and a minus sign will be introduced when negative rate is intended.

Solutions of $N_1(t)$ and $N_2(t)$ of quadratic equations for two interacting species are of interest only in the first quadrant (the population quadrant) $N_1 \geq 0, N_2 \geq 0$, since negative populations have no meaning, the curve in the population quadrant defined parametrically by $N_1 = N_1(t)$ and $N_2 = N_2(t)$ is a population orbit.

2.4 Equilibrium Populations (No cycles)

Considering the below system as a model for interacting of two species:

$$\frac{dx}{dt} = (a_0 + a_1x + a_2y)x \quad (2.4.1)$$

$$\frac{dy}{dt} = (b_0 + b_1x + b_2y)y$$

it is impossible without any information about the coefficients to solve for $x(t)$ and $y(t)$ as specific function t . instead, considering equilibrium state. If the growth rates of the x - species and the y - species both vanish identically, then the two populations are constant. These constant populations correspond to equilibrium points of (2.4.1) and can be determined by setting the right – hand sides of (2.4.1) equal to 0.

$$(a_0 + a_1x + a_2y)x = 0$$

$$(b_0 + b_1x + b_2y)y = 0$$

There are four equilibrium points (that is constant population points)

1	$x = 0$	$y = 0$
2	$x = 0$	$y = -b_0/b_2$
3	$x = -a_0/a_1$	$y = 0$
4	$x = \frac{a_2b_0 - a_0b_2}{a_1b_2 - a_2b_1}$	$y = \frac{a_0b_1 - a_1b_0}{a_1b_2 - a_2b_1}$

As long as $a_1 b_2 \neq a_2 b_1$. Observing that the equilibrium point given by (4) represents a true population state if $x > 0$ and $y > 0$ (i.e if (x, y) lies in the population quadrant)

Now, another kind of simple equilibrium state exists. It could happen that the population numbers of neither species remain constant in time but fluctuate periodically. Thus, it may $x(t)$ and $y(t)$ are non constant periodic functions of time with common period. The corresponding population orbit is called a cycle. To show when the system of the form (2.4.1) can posses cycles. Letting begin by imposing two conditions on the coefficients of system (2.4.1)

Condition (A): The number $A = a_1 b_2 - a_2 b_1$ does not vanish

Condition (B): The number $B = a_1 b_0 (a_2 - b_2) - a_0 b_2 (a_1 - b_1)$ does not vanish.

Condition (A) asserts that the two lines

$$a_0 + a_1 x + a_2 y = \text{const}$$

$$b_0 + b_1 x + b_2 y = \text{const}$$

are not parallel . Whereas condition (B), its violation under certain conditions has a simple consequence: if any cycle at all exists then a continuous band of cycles exists.

No cycles Theorem:

"If the coefficients of the quadratic model (2.4.1) satisfy conditions (A) and (B), then (2.4.1) has no cycles in the population quadrant"

Proof: For $x > 0$ and $y > 0$ define the function

$$K(x, y) = x^\alpha y^\beta$$

Where

$$\alpha = \frac{b_2(b_1 - a_1)}{A} - 1 \text{ and } \beta = \frac{a_1(a_2 - b_2)}{A} - 1$$

Now let f and g denote the respective right – hand sides of two rate equations (2.4.1) and considering the function.

$$\frac{\partial}{\partial x}(Kf) + \frac{\partial}{\partial y}(Kg)$$

It follows that

$$\frac{\partial}{\partial x}(Kf) + \frac{\partial}{\partial y}(Kg) = \frac{B}{A}K \quad (2.4.2)$$

whether or not $B = 0$ as long as $A \neq 0$

Now suppose that (2.4.1) does have a cycle Γ inside the population quadrant. It shall derive a contradiction, thus showing that there are no cycles. Let R denote the union of Γ and its interior as shown in Fig 2.4.1. Since $K(x, y) > 0$ when $x > 0$ and $y > 0$ and since A and B are nonvanishing constants by conditions (A) and (B), hence, $(B/A)K(x, y)$, has a fixed sign in the population quadrant and does not vanish. Thus according to (2.4.2) the following have

$$0 \neq \iint_R \frac{B}{A} K(x, y) dx dy = \iint_R \left[\frac{\partial}{\partial x} (Kf) + \frac{\partial}{\partial y} (Kg) \right] dx dy \quad (2.4.3)$$

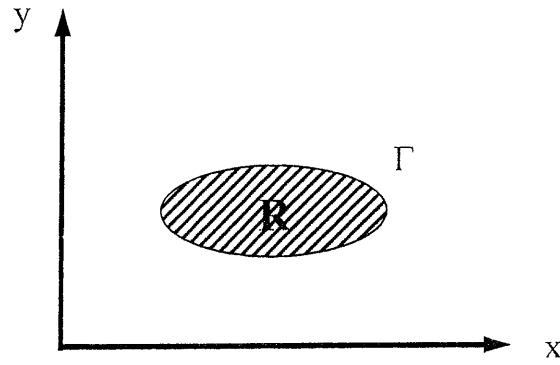


Figure 2.4.1 Cycle Γ and Region R

By Green's theorem in the plane, the last double integral can be replaced by a line integral around Γ :

$$\iint_R \left[\frac{\partial}{\partial x} (Kf) + \frac{\partial}{\partial y} (Kg) \right] dx dy = - \oint_{\Gamma} [Kg dx - Kf dy] \quad (2.4.4)$$

Since Γ is an orbit, so it has that along Γ , $dx/dt = f$ and $dy/dt = g$

Thus the line integral in (2.4.3) vanishes, since,

$$\begin{aligned}
 \oint_{\Gamma} [Kgdx - Kf dy] &= \int_0^T [Kg \frac{dx}{dt} - Kf \frac{dy}{dt}] dt \\
 &= \int_0^T [Kg f dt - Kf g dt] \\
 &= 0 \qquad (2.4.5)
 \end{aligned}$$

where the period of the cycle Γ is T . Form (2.4.3) & (2.4.5)

$$0 \neq \iint_R \left[\frac{\partial}{\partial x} (Kf) + \frac{\partial}{\partial y} (Kg) \right] dx dy = 0$$

The assumption that (2.4.1) has a cycle is untenable and No cycles theorem is proved.

Thus when the condition (A) and (B) are satisfied, the only possible equilibrium state for a pair of non vanishing species modeled by (2.4.1) is the constant population state given by (4) .

Example: considering the system

$$\begin{aligned}\frac{dx}{dt} &= x(a - \alpha x - by) \\ \frac{dy}{dt} &= y(-c + dx - \beta y)\end{aligned}\tag{2.4.6}$$

Where $a, \alpha, b, c, d, \beta$ are positive constant and the overcrowding coefficients α, β are small in comparison to a, b, c, d . The constant B no longer vanishes, nor does A , since:

$$B = \alpha c(-b + \beta) + a\beta(-\alpha - d) = -[\alpha bc + \alpha\beta a + \beta ad] + \alpha\beta c,$$

which is less than 0 if $\alpha\beta$ is sufficiently small.

$A = \alpha\beta + bd > 0$. The No Cycles theorem applies and (2.4.6) has no cycles.

References

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- 6) J. Mayhard Smith, Models in Ecology. Cambridge, 1974.
- 7) M.Kot, Elements of Mathematical Ecology, Cambridge University Press ,2007.
- 8) F. Arecht, H. Gatzka, A. Haddad and N.Wax, The Dynamics of two Interacting Populations, vol 46, pp.658 – 670, 1974.
- 9) H.I Freedman, Deterministic Mathematical Models in Population Ecology. New York : Marcel Dekker, 1980.
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Chapter Three

The Predator – Prey model

Chapter 3

The Predator – Prey Model

3.1 Introduction

In this chapter a model of population growth of two species in which one species is the primary food sources for the other is studied. One example of such a situation occurs in the upper Adriatic Sea, where the sharks eat the small fish, as their principle food source. Another example is wolves and rabbits in a closed forest, the wolves eat the rabbits in a closed principle food source and the rabbits eat vegetation in the forest. Still other examples includes sea otters as predators and a abalone as prey and the ladybird beetles, as predator and the cottony cushion insect as prey.

To keep the model simple, it will make some assumption that would be unrealistic in most of these predator – prey situations. Specifically, it will assume that

1. the predator species is totally dependent on a single prey species as its only food supply ,
2. the prey species has an unlimited food supply , and
3. there is no threat to the prey other than the specific predator

In later sections, it will construct a mathematical model of predator – prey community which was developed by Lotka and Volterra in 1920s.

This model is composed of a pair of differential equations that describe predator – prey dynamics (one predator population, one prey population). The solutions of this system is determined and compared with observations.

Then it will determine the effect of harvester or poison that kills both predator and prey. Harvesting of this type has a surprising consequence with important ecological implications (volterra's principle), and it will conclude with discussion of these implications.

Finally, Lotka – Volterra model has been both challenged and supported many times in the half- century since their formulation, Here with the attempt is to present and discuss its limitations.

3.2 Problem Identification

Very few such pure predator – prey interactions have been observation in nature, but there is a classical set of data on a pair of interacting populations that come close: the situation of sharks and the small fish consumed by the sharks. The sharks eat the small fish and the small fish live on the plankton in the sea. If the sharks eat too many fish, so that fish cease to be abundant, the food supply of the sharks is greatly reduced. Then the sharks will starve or leave the area in search of a new supply of fish. As the population of sharks dwindles, the fish population makes a comeback since not so many of them are being eaten.

As the fish population increases, the food supply for the sharks grows and consequently, so does the shark population. And more sharks are eating more and more fish a gain. In the pristine environment, does this cycle continue indefinitely or does one of the species eventually die out? It is possible that this process continues on indefinitely, in which case the ecosystem would consist of periodic population variations.

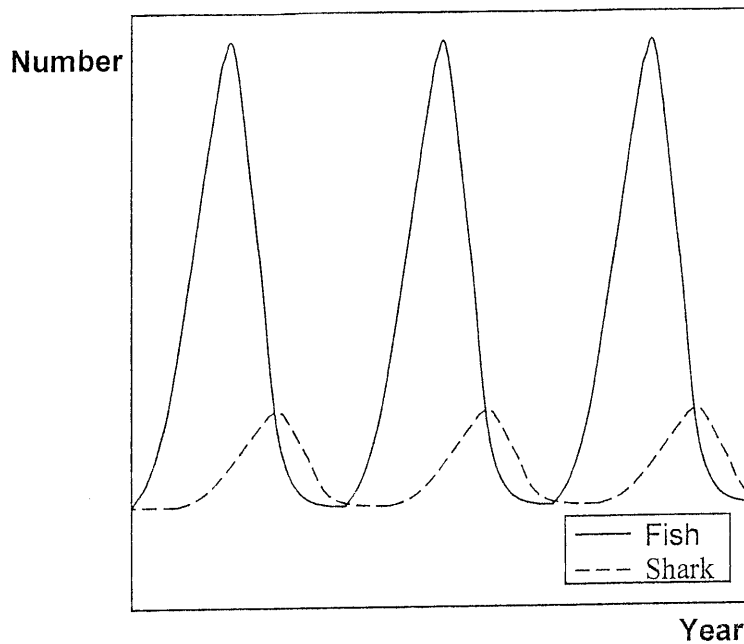


Figure 3.2.1 Periodic activity generated by the predator- prey model.

The sharks in the Adriatic Sea have been overexploited to the extent that their current population in the Adriatic Sea is around one- sixth its estimated pristine level. Thus there appear to be a surplus of the smaller fish. What effect does the limitation of the sharks have on the balance between the shark and fish populations? What are the implications that a small fish fishery may hold for the depleted stocks of sharks and for other species like seals, seabirds, penguins, and fish that depend on fish for their main sources of food? The ability to answer such questions is important to management of multispecies fisheries.

3.3 Derivation of the Lotka – Volterra Equations

A mathematical model for the population dynamics of competing species, one a predator and the other its prey, was developed independently by Lotka and Volterra in the early 1900.

Considering the interaction between sharks with population $S(t)$ and the small fish which are eaten by sharks with population $F(t)$. It assumes there is plenty of food available for the fish to eat, so the smaller fish do not compete very intensively among themselves for their food supply. Hence, in the absence of the sharks, the birth rate of the fish should follow the Malthusian or exponential law, that is, the birth rate of the fish is aF , where a is a positive proportionality constant. The death rate of the fish depends on the number of interactions between the sharks and the small fish. This is modeled by the expression cFS , where c is a positive proportionality constant. Therefore, the rate of change in the population of fish per unit time is:

$$\frac{dF}{dt} = aF - cFS$$

Assuming the sharks depend entirely on the smaller fish for their food, it is argued that the birth rate of the sharks depends on the number of interactions with the fish, that is, the birth rate of sharks is λFS , where λ is a positive proportionality constant. The death rate of the sharks is assumed to be kS , where k is positive proportionality constant, because without food the population would

die off at a rate proportional to the present population. Hence the rate of change in the population of sharks per unit time is:

$$\frac{dS}{dt} = -kS + \lambda FS$$

Combining these two equations, getting the Lotka – Volterra system for the population dynamics of two competing species:

$$\frac{dF}{dt} = F(a - cS)$$

$$\frac{dS}{dt} = S(-k + \lambda F)$$

Where a , c , k , λ described the different process are all positive. The Lotka – Volterra model consists of a system of linked differential equations that cannot be separated from each other and that cannot be solved in closed form. This is the simplest models of a predator and prey association includes only natural growth and decay and the predator- prey interaction itself.

3.4 Qualitative Solution of the Lotka- Volterra Equations.

Considering the system of differential equations for a predator - prey model.

$$\begin{aligned}\frac{dF}{dt} &= F(a - cS) \\ \frac{dS}{dt} &= S(-k + \lambda F)\end{aligned}\tag{3.4.1}$$

These equations imply that if there are very few sharks then the fish will grow in number. As the number of fish increases, the number of sharks must increase. Eventually the number of sharks will become so large that the growth rate of fish will become negative. At that time, the number of fish will cease to increase. It could continue the qualitative description of what should happen based on the differential equations.

In this section solution of differential equations (3.4.1) is calculated and compared to observations.

1. Graphical analysis of the model.

To determine whether the fish and the shark populations reach equilibrium levels. The equilibrium points correspond to the simultaneous solutions of the equations:

$$F(a - cS) = 0$$

$$S(-k + \lambda F) = 0$$

There are just two equilibrium points, the extinction point $(0, 0)$ and the points $(a/c, k/\lambda)$ which lie in first quadrant. Because the values for constants a, c, k and λ in the systems (3.4.1) will only be estimates, so it only needs to investigate the behavior of the solution trajectories near the two equilibrium points $(0, 0)$ and $(a/c, k/\lambda)$. Thus it only need to analyze the directions of dF/dt and dS/dt in the phase plane. Equations (3.4.1) have the particular solutions:

$$\begin{aligned} F(t) &= F_0 e^{at} & F(t) &= 0 \\ &\text{and} & \\ S(t) &= 0 & S(t) &= S_0 e^{-kt} \end{aligned}$$

Solutions that lie along the axis and isolate the first quadrant from the other quadrants. If $F=0$, then $dF/dS=0$ and if $S=0$, then $dF/dS=\infty$. Thus the lines $F=0$ and $S=0$ are both isoclines as well as solution curves. Consequently, a solution once positive can never become negative, since to do so it must cross either axis, which is an impossibility. Other, simple isoclines are:

$$S = \frac{a}{c} \quad \text{on which} \quad \frac{dF}{dS} = 0$$

and

$$F = \frac{k}{\lambda} \quad \text{on which} \quad \frac{dF}{dS} = \infty$$

These isoclines are not solution curves.

In the system (3.4.1), if $S = 0$ then $dF/dt = aF$. That is F always increase. (Ecologically if there are no sharks then the fish will grow.) Similarly, if $F = 0$ then $dS/dt = -kS$ and S decrease (the shark tend to wards extinction).

If the fish are at the number necessary to balance the growth of sharks, $F = \frac{k}{\lambda}$, then $\frac{dF}{dt} = \frac{k}{\lambda}(a - cS)$ this gives:

$$\text{If } S > \frac{a}{c} \quad \text{Then} \quad \frac{dF}{dt} < 0$$

and

$$\text{If } S < \frac{a}{c} \quad \text{Then} \quad \frac{dF}{dt} > 0$$

Similarly, If the sharks are at the number necessary to balance the growth of fish, $S = \frac{a}{c}$, then $\frac{dS}{dt} = \frac{a}{c}(-k + \lambda F)$, so it is obtained

$$\text{If } F > \frac{k}{\lambda} \quad \text{Then} \quad \frac{dS}{dt} > 0$$

and

$$\text{If } F < \frac{k}{\lambda} \quad \text{Then} \quad \frac{dS}{dt} < 0$$

Follow from equation (3.4.1). The directions of the associated trajectories are indicated in Fig (3.4.1).

To analyze the solution in the neighborhood of the equilibrium population $(0, 0)$. Linearizing the differential equations (3.4.1) in the vicinity of $S = 0, F = 0$ by using perturbation method. Thus, this has been accomplished by just neglecting the nonlinear terms in which case:

$$\frac{dF}{dt} = aF$$

$$\frac{dS}{dt} = -kS$$

The fish exponentially grow and the sharks exponentially decrease. The equilibrium point $(0, 0)$ is called a saddle point. The stability of this point is of important. 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 many cases of initial population levels. However, as the fixed point at the origin is a saddle point, and hence unstable, it finds that the extinction of both species is difficult in the model. In fact, this can only occur if the prey are artificially completely eradicated, causing the predators to die of starvation. If the predators are eradicated, the prey population grows without bound in this model. In the phase plane,

$$\frac{dF}{dS} = -\frac{aF}{kS} \quad \text{Or} \quad F = AS^{-a/k}$$

Thus, using information about population near this equilibrium population, it has been seen Fig. 3.4.1.

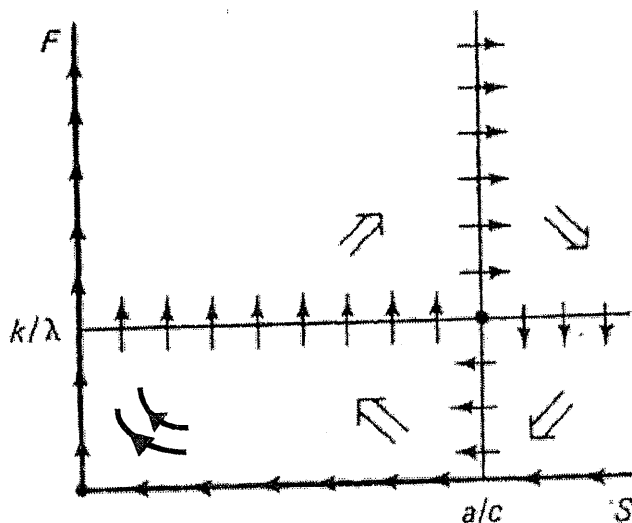


Figure 3.4.1 Qualitative behavior of predator – prey

On the other hand, the equilibrium point $(a/c, k/\lambda)$ is more complicated to analyze. The information given by Fig. 3.4.1 is insufficient to distinguish between the three possible orbits as shown in Fig. 3.4.2. It cannot tell whether the orbits are spiraling inwards, spiraling outwards or periodic.

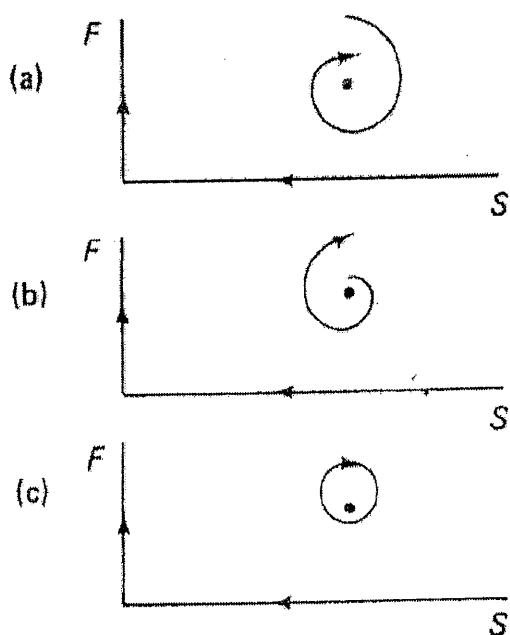


Figure 3.4.2 Possible orbits of the phase plane.

For example, supposing that the trajectories are shown in Fig. 3.4.3. As drawn, part of one solution curve is spiraling inwards and also part of another solution curve is spiraling outwards. If this is valid, then a little common sense would suggest that there exists a solution curve in between the two drawn, such that for that solution the population returns to the same value, yielding a periodic oscillation of population, called a limit cycle as sketched in Fig. 3.4.4.

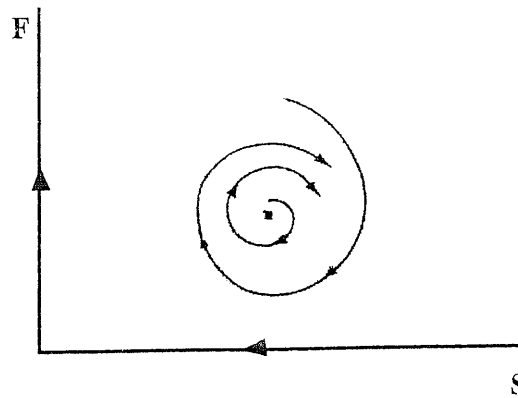


Figure 3.4.3 Solution curve between spiraling inward and spiraling outward

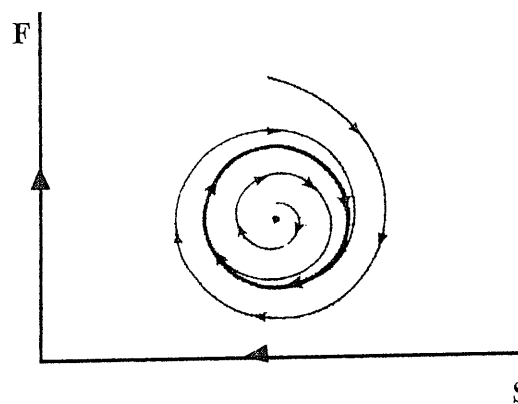


Figure 3.4.4 Limits cycle.

To develop an approximate solution to the Lotka - Volterra equations. The approximation is to be found for populations that are close to their equilibrium values. By using perturbation methods as follows:

$$F = \frac{k}{\lambda} + \varepsilon F_1 \quad (3.4.2)$$

$$S = \frac{a}{c} + \varepsilon S_1$$

Where $\varepsilon F_1, \varepsilon S_1$ represent population difference from the equilibrium population. Substituting this into the differential equation (3.4.1), yields

$$\varepsilon \frac{dF_1}{dt} = \left(\frac{k}{\lambda} + \varepsilon F_1 \right) (-c \varepsilon S_1)$$

$$\varepsilon \frac{dS_1}{dt} = \left(\frac{a}{c} + \varepsilon S_1 \right) (\lambda \varepsilon F_1)$$

Neglecting the nonlinear terms results in

$$\frac{dF_1}{dt} = -\frac{ck}{\lambda} S_1 \quad (3.4.3)$$

$$\frac{dS_1}{dt} = \frac{a\lambda}{c} F_1 \quad (3.4.4)$$

Eliminating F_1 from equation (3.3.4) yields

$$\frac{c}{a\lambda} \frac{d^2 S_1}{dt^2} = -\frac{ck}{\lambda} S_1,$$

or equivalently,

$$\frac{d^2 S_1}{dt^2} = -akS_1$$

Thus, the number of sharks oscillates around its equilibrium population,

$$S_1 = S_{10} \cos \omega t + Q \sin \omega t$$

Where $\omega = (ak)^{1/2}$ and S_{10} is the displacement from equilibrium population of sharks at $t = 0$. The fish also oscillate, since from equation (3.4.4)

$$F_1 = \frac{c}{a\lambda} (-\omega S_{10} \sin \omega t + \omega Q \cos \omega t)$$

If at $t = 0$, $F_1 = F_{10}$, then $F_{10} = (\frac{c}{a\lambda})\omega Q$. In other words,

$$S_1 = S_{10} \cos \omega t + \frac{a\lambda}{c\omega} F_{10} \sin \omega t$$

$$F_1 = F_{10} \cos \omega t - \frac{c\omega}{a\lambda} S_{10} \sin \omega t$$

The period of oscillation

$$T = \frac{2\pi}{\omega} = 2\pi(ak)^{-1/2},$$

Depends only on growth rates a and k . This period is only valid for small oscillations around the equilibrium population. An equivalent expression for the solution is:

$$S_1(t) = A \sin(\omega t + \Phi)$$

Where

$$A = (S_{10}^2 + \frac{a^2 \lambda^2}{c^2 \omega^2} F_{10}^2)^{1/2}$$

$$\Phi = \tan^{-1} \frac{c \omega S_{10}}{a \lambda F_{10}}$$

then

$$F_1(t) = \frac{cA}{a\lambda} \omega \cos(\omega t + Q)$$

In terms of original fish and sharks populations, it can write from equation 3.4.2.

$$F = \frac{k}{\lambda} (1 + \frac{\varepsilon c A \omega}{a k} \cos(\omega t + Q))$$

$$S = \frac{a}{c} (1 + \frac{\varepsilon c A}{a} \sin(\omega t + Q))$$

This representation of the solution makes explicit the oscillations of the two populations about their equilibrium values.

The result of linearized analyses predicts that populations oscillate with constant amplitude in the neighborhood of equilibrium population. The phase plane differential equation,

$$\frac{dF_1}{dS_1} = - \frac{c^2 k S_1}{a \lambda^2 F_1}$$

By separation and integration, yields

$$\frac{a^2 \lambda^2}{c^2} F_1^2 + a k S_1^2 = \text{constant} \quad (3.4.5)$$

Equation (3.4.5) is the equation for an ellipse in the coordinates F and S as shown in Fig. 3.4.5. Thus, it has proved that the smaller curves are closed on the $F - S$ diagram and very nearly elliptical.

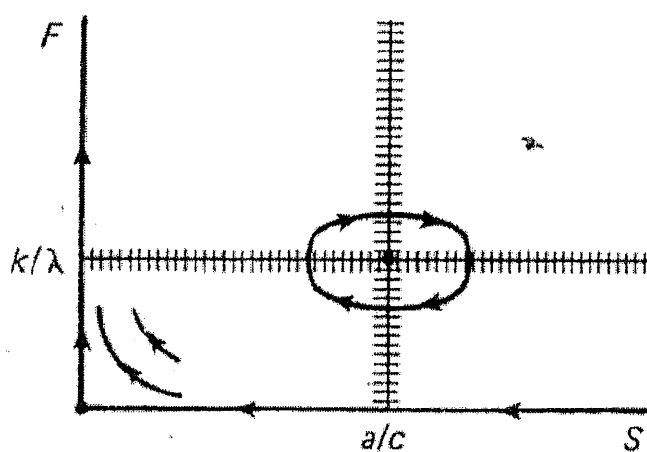


Figure 3.4.5

2. Stability

The stability of an equilibrium population is always determined by a linearizing stability analysis. Equations (3.4.3) and (3.4.4) are put into the form.

$$\frac{dx}{dt} = a_1 x + b_1 y$$

$$\frac{dy}{dt} = c_1 x + d_1 y$$

Where $x = F_1, y = S_1$ and

$$a_1 = 0$$

$$b_1 = -\frac{ck}{\lambda}$$

$$c_1 = \frac{a\lambda}{c}$$

$$d_1 = 0$$

Thus

$$P = a_1 + d_1 = 0$$

$$q = a_1 d_1 - b_1 c_1 = ak > 0$$

$$\Delta = p^2 - 4q = -4ak < 0$$

Since $p = 0$, the graph and table at the end of section 1.4 indicates that the equilibrium population is neutrally stable. A neutrally stable equilibrium population is called a center. This means that the levels of the predator and prey populations cycle, and oscillate around this fixed point.

3. An Analytic solution of the model

The phase plane equation of the system of equation (3.4.1) is:

$$\frac{dF}{dS} = \frac{F(a - cS)}{S(-k + \lambda F)} \quad (3.4.6)$$

Which is separable and may be rewritten

$$\begin{aligned} \frac{(\lambda F - k)}{F} dF &= \frac{(a - cS)}{S} dS \\ \left(\lambda - \frac{k}{F}\right) dF &= \left(\frac{a}{S} - c\right) dS \end{aligned}$$

Which integrate to

$$\lambda F - k \ln F = a \ln S - cS + E_0$$

For some constant E_0 . Upon exponentiating, it has that,

$$(F^k e^{-\lambda F})(S^a e^{-cS}) = e^{E_0} = E \quad (3.4.7)$$

where E is a positive constant determined from the initial population of the fish $F(t_0) = F_0$, and the initial population of sharks $S(t_0) = S_0$, for each value of E there corresponds one solution curve.

This is an implicit equation relating the population of fish and Sharks. Nevertheless it will show these equations represent close curves. A possible difference between closed and open curves is illustrated in Fig. 3.4.6.

For a curve which is somewhere spiral-like, there are values of S for which there are more than two values of F .

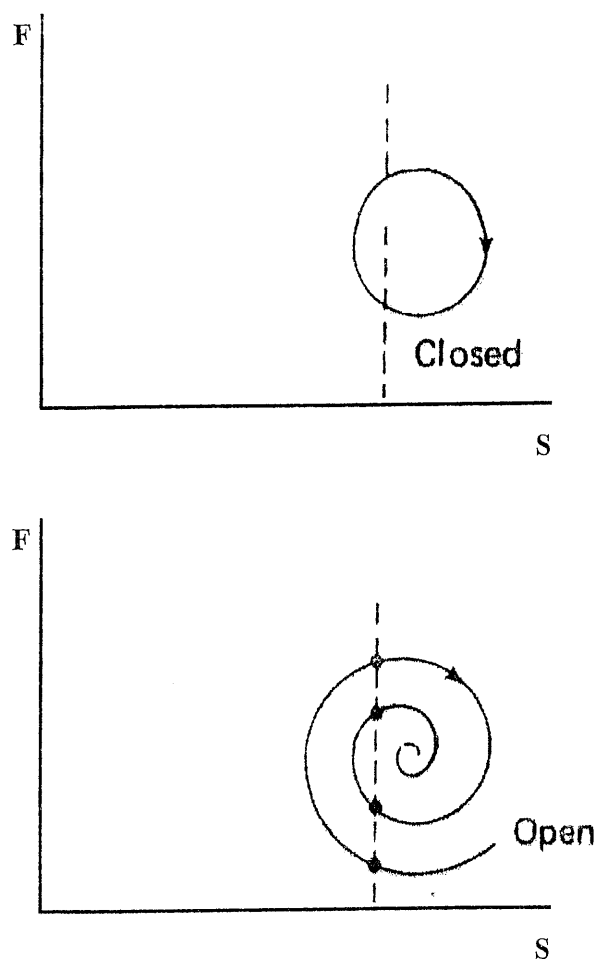


Figure 3.4.6 Difference between closed and open curves.

4. The predator – prey trajectories are periodic

Equation (3.4.7) defines the solution trajectories in the phase plane. The orbit define by (3.4.7) has the following properties.

1. It is simple closed curve surrounding $P=(a/c, k/\lambda)$ if

$$0 < E < E_1 = \left(\frac{k}{\lambda e}\right)^k \left(\frac{a}{ce}\right)^a$$

2. It is the single point P if $E = E_1$

3. It does not exist if $E > E_1$

The proof that the population or have properties (1) – (3) is as following:

Equation (3.3.7) can be written as:

$$\left(\frac{S^a}{e^{cS}}\right) = E \left(\frac{e^{\lambda F}}{F^k}\right) \quad (3.4.8)$$

The first step is to determine the behavior of the functions

$$f(S) = \frac{S^a}{e^{cS}} \quad \text{and} \quad g(F) = \left(\frac{F^k}{e^{\lambda F}}\right)$$

for S and F positive.

Observing that $f(0) = 0$ and $f(\infty) = 0$. $f(S)$ is positive for $S > 0$ Computing.

$$\begin{aligned}
 f'(S) &= \frac{aS^{a-1} - cS^a}{e^{cS}} \\
 &= S^{a-1} \frac{(a - cS)}{e^{cS}}
 \end{aligned}$$

$f(S)$ has a single critical point at $S = a/c$ so the maximum value $M_S = (a/ce)^a$ at $S = a/c$ and the graph of $f(S)$ has the form described in Fig. 3.4.7. Similarly, the maximum value of $g(F)$ is $M_F = (k/\lambda e)^k$ at $F = k/\lambda$ and the graph of $g(F)$ has the graph described in the same graph.

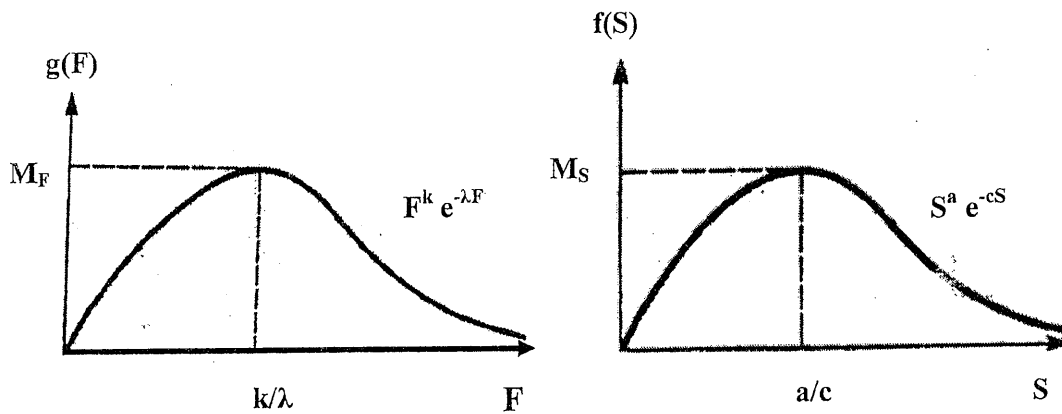


Figure 3.4.7 The graphs of the functions $f(S) = S^a e^{-cS}$ and $g(F) = F^k e^{-\lambda F}$

The Largest value for $F^k e^{-\lambda F} S^a e^{-cS}$ is $M_F M_S$. That is equation (3.4.7) has no solution if $E > M_F M_S$ and exactly one solution, $F = k/\lambda$ and $S = a/c$, when $E = M_F M_S$. By considering the case $E < M_F M_S$

Supposing $E = u M_S$ where $u < M_F$ is positive constant. Then the equation,

$$F^k e^{-\lambda F} = u$$

has exactly two solutions $F_m < k/\lambda$ and $F_M > k/\lambda$ as shown in Fig.

3.4.8. Now if $F < F_m$ then:

$$F^k e^{-\lambda F} < u \quad \text{so that} \quad F^{-k} e^{\lambda F} u > 1$$

And

$$f(S) = S^a e^{-cS} = EF^{-k} e^{\lambda F} = uM_S e^{\lambda F} F^{-k} > M_S$$

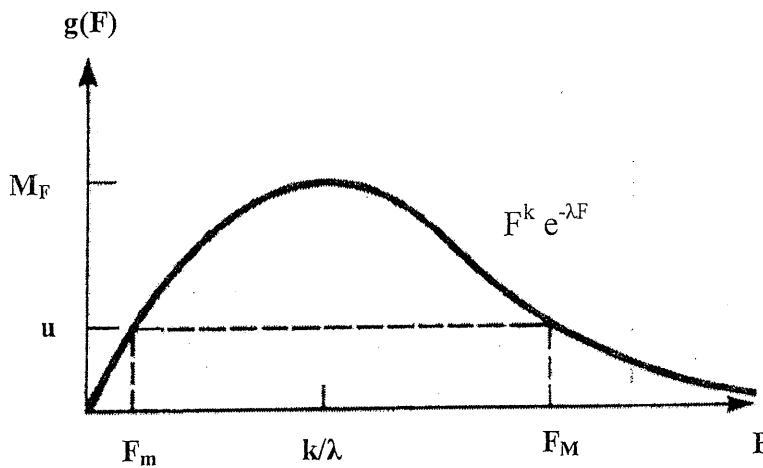


Figure 3.4.8 The equation $F^k e^{-\lambda F} = u$ has exactly two solutions for $u < M_F$

Therefore, there is no solution for S in equation (3.4.8) when $F < F_m$.

Likewise, there is no solution when $F > F_M$. If $F = F_m$ or

$F = F_M$ then equation (3.3.) has exactly the one solution $S = a/c$.

Finally, if F lies between F_m and F_M . Equation (3.4.8) has exactly two solutions. The smaller solution S_1 is less than a/c and the

largest solution S_2 is greater than a/c . This situation is shown in Fig. 3.4.9.

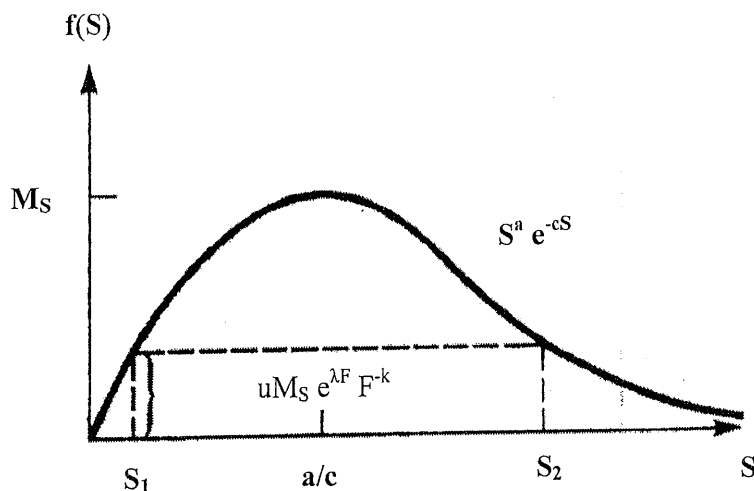


Figure 3.4.9 When $F_m < F < F_M$, there are exactly two solutions for S in equation 3.4.8

It follows that the trajectories defined by equation (3.3.7) represents a family of closed curves, so they are periodic and have the form as shown in Fig. 3.3.10. Each member of the family corresponds to different value of the constant E . for small value of the constant E , the closed curves are nearly elliptical, as the constant increases the resemblance to ellipses disappear. The periods are not constant from orbit to orbit, but increase monotonically with the distance of the orbit from point $(a/c, k/\lambda)$.

In fact as orbits shrink on to p the corresponding periods decrease to $2\pi(ak)^{-1/2}$, while as orbit expand without bound the periods tend to infinity.

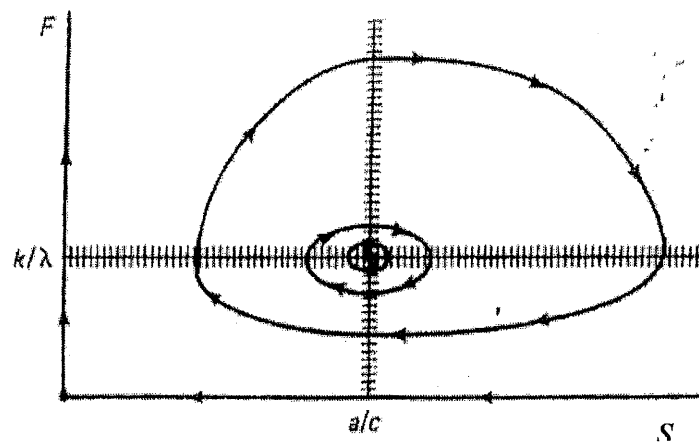


Figure 3.4.10 Trajectories of sharks (S) – fish (F) predator – prey ecosystem

5. Model interpretation

From the trajectories in Fig. 3.4.10, first it can be concluded that because the trajectories are closed curves, they predict that under the assumptions of the model (3.4.1), neither the sharks nor the small fish will become extinct. The second observation is that along a single trajectory the two populations fluctuate periodically around their equilibrium values. That is, starting with populations in the region where $F > k/\lambda$ and $S > a/c$, the fish population will decline and the shark population increase until the fish population reaches the level $F = k/\lambda$, at which point the shark population also begins to decline. Both populations continue to decline until the shark population reaches level $S = a/c$ and the fish population begins to increase and so on, around the trajectory. A sketch of the population curves is shown in Fig. 3.4.11.

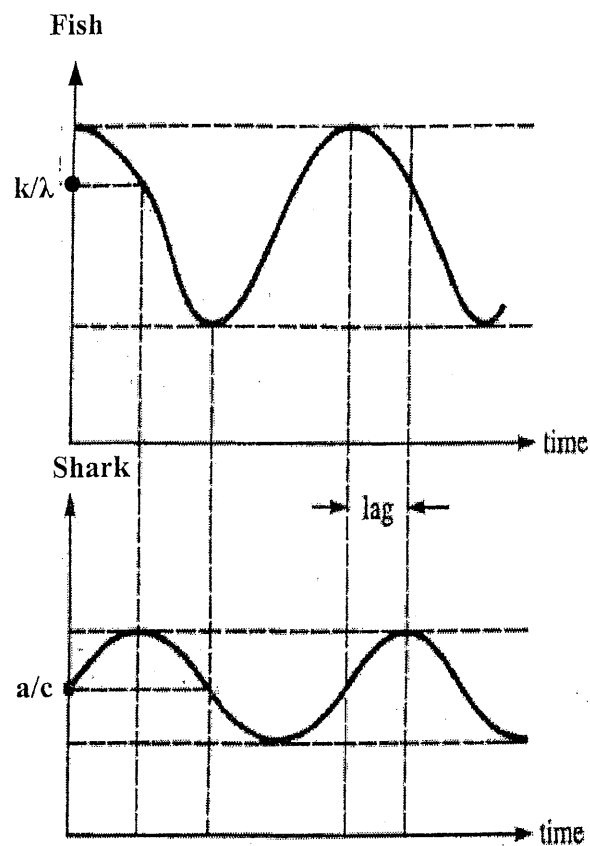


Figure 3.4.11 The shark population lags behind the fish population as both populations fluctuate periodically around their equilibrium values.

In this figure it can be shown that the predator lags behind the prey in a cyclic fashion. This model has no asymptotic stability; it does not converge to an attractor.

In closing this discussion it note that it has gained considerable information about the behavior of sharks – small fish population systems, yet it does not have an explicit solution for the two populations. It found that this coupled system behaves as an oscillator in the neighborhood of the equilibrium position.

6. The Lotka – Volterra Model: All cycles

On the other hand by using No Cycles theorem assert that there are cycles at all. No cycles exist if each of numbers A and B is nonzero, but $B = 0$ (although $A \neq 0$) in the Lotka – Volterra model. So the No Cycles theorem does not apply to (3.4.1) since one of its hypotheses does not hold.

3.5 Volterra's principles.

In 1926, Humberto D'Ancona, an Italian biologist, completed a statistical study of the changing populations of various species of fish in the upper Adriatic Sea over the time span 1910 to 1923. His estimates of the populations were based on the number of each species sold on the fish markets of three ports, Trieste, Fiume, and Venice, D'Ancona assumed, that the relative number of the various species in the markets reflected the relative abundance of those species in the marine community. Apart of the data is given in Table 3.4.1.

Port	1914	1915	1916	1917	1918	1919	1920	1921	1922
Fiume	12 %	21 %	22 %	21 %	36 %	27 %	16 %	16 %	15 %
Trieste	14 %	7 %	16 %	15 %	-	18%	15 %	13 %	11 %

Table 3.4.1 percentages of predator species (sharks, skates, rays Etc) out of the total fish catch.

D' Ancona observed that the percentage of predator species were higher during and immediately after world war 1 (1914- 1918) Fishing was reduced during the war years as the fishermen abandoned their nets to fight in the war, and D'Ancona concluded that the decline in fishing caused the change in the proportions of predator to prey. He formulated the hypothesis that during war the predator – prey community was close to its natural state of a high proportion of predator fish. While the more intensive fishing of the pre and postwar years disturbed that equilibrium to the advantage of

the prey species. Unable to give a biological or ecological reason for the phenomenon, D'Ancona asked his father in law Vito Volterra if there was a mathematical model that might cast some light on the matter. Volterra has outlined a series of models for the interactions of two or more species. The one of them which is analyzed in last section.

Volterra summarized his results for a predator –prey community of two species in the form of three principles the first one was verified in last section.

1. The Law of the Periodic Cycle.

“The fluctuations of the populations of the predator and its prey are periodic. “

2. The Law of the Conservation of Averages.

Considering the mathematical model of predators and preys analyzed in Sec. 3.4. For a given initial population level $F(0) = F_0$ and $S(0) = S_0$, the sharks and fish population will fluctuate with time around one of the closed trajectories depicted in Fig. 3.3.10. Let T denote the time it takes to complete one full cycle and return to the starting point.

The average values of the fish and shark populations over the time cycle are defined by the integrals:

$$\overline{F} = \frac{1}{T} \int_0^T F(t) dt$$

and

$$\overline{S} = \frac{1}{T} \int_0^T S(t) dt$$

respectively. Now, from the first rate equation of (3.4.1)

$$\frac{1}{F} \left(\frac{dF}{dt} \right) = a - cS$$

So that integration of both sides from $t = 0$ to $t = T$ leads to:

$$\int_0^T \frac{1}{F} \left(\frac{dF}{dt} \right) dt = \int_0^T (a - cS) dt$$

or

$$\ln F(T) - \ln F(0) = aT - c \int_0^T S(t) dt$$

Because of periodicity of the trajectory $F(T) = F(0)$ and this last equation gives the average value,

$$\overline{S} = \frac{a}{c}$$

A similar analysis of the second equation of (3.4.1) shows that average of the prey population $F(t)$ over a cycle is

$$\overline{F} = \frac{k}{\lambda}$$

This lead to the second principle.

Volterra's Law of the Conservation of Average:

"The averages of the numbers of the predator and the prey species over the period of a cycle have the constant values of the equilibrium levels as long as the parameters of growth, decay, and interaction remain constant"

Volterra's Law of the Conservation of the Average carriers us closer to real populations since averages are easy to calculate from numerical counts over time.

3. Volterra's principles on the Disturbances of the averages.

Finally, Volterra introduced the effect of fishing on the predator - prey community. The simplest model is that of constant – effort harvesting in which the amount caught per week is proportional to the number the of fish present.

Assuming that the effect of fishing for food fish it to decrease its population level at a rate $H_1 F(t)$. The constant H_1 is a positive and indicates the intensity of fishing and includes such factors as the number of fishing vessels at sea, the number of fisherman casting nets for fish, and so forth. Since less food is now available for the sharks, assuming the shark population also decreases at a rate $H_2 S(t)$, the constant H_2 is a positive. Consequently, Volterra's model of predator – prey community of fish subjected to constant effort harvesting in which the fisherman pull out of the sea whatever is trapped in the nets. The equations of model are:

$$\begin{aligned}\frac{dF}{dt} &= F(a - cS) - H_1 F \\ &= [(a - H_1) - cS]F\end{aligned}\tag{3.5.1}$$

$$\begin{aligned}\frac{dS}{dt} &= S(-k + \lambda F) - H_2 S \\ &= [-(k + H_2) + \lambda F]S\end{aligned}$$

where H_1, H_2 are positive constants. The autonomous system (3.5.1) is of the same form as (3.4.1), provided that $a - H_1 > 0$, with a replaced by $a - H_1$ and k replaced by $K + H_2$. The equilibrium point inside the population quadrant, first quadrant, is now shifted from its original location at $(a/c, k/\lambda)$ to the new point $((a + H_1)/c, (k - H_2)/\lambda)$. It is assumed that $a > H_1$, for other wise the average population size of the harvested predator is not a positive number. The analysis is the same as before, and the harvested populations

continue their periodic oscillations, but now about the new equilibrium as shown in Fig 3.5.1. Since $(k + H_2) / \lambda > K / \lambda$ and $(a - H_1) / c < a / c$, this leads to the third principle.

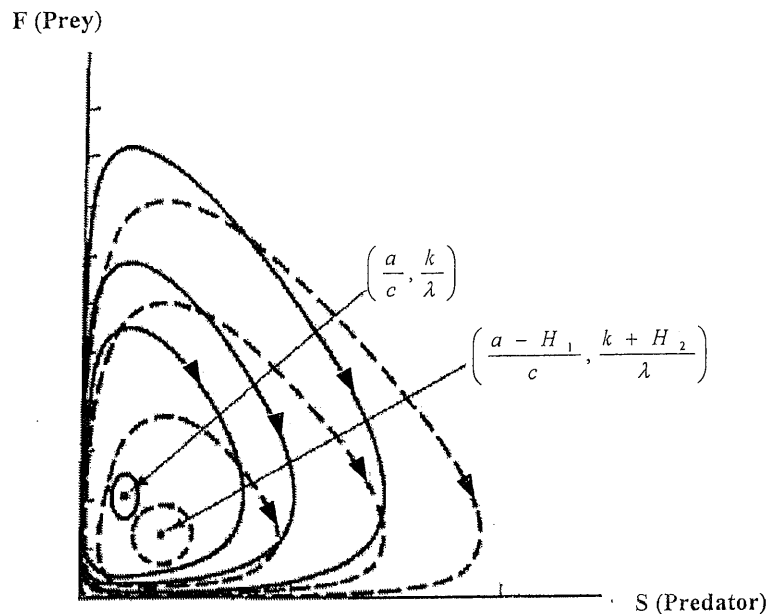


Figure 3.5.1 Effect of constant effort harvesting. The unharvested cycle are indicated by solid lines, the harvested cycles by dashed lines.

Volterra's principle on the disturbance of the averages

"Constant – effort harvesting produces an increase in the average number of the prey and a decrease in the average number of the predator"

The increase of fish population is beneficial to other species in the southern ocean (seals, seabirds, penguins and fish) that depend on the fish for their main food source.

The third principles must be reformulated in percentages rather than actual numbers as following. The predator fractions of the total average catch are given by:

$$\text{no harvesting} \quad \frac{a/c}{a/c + k/\lambda} = \frac{a\lambda}{a\lambda + ck}$$

harvesting

$$\frac{(a - H_1)/c}{(a - H_1)/c + (k + H_1)/\lambda} = \frac{a\lambda - \lambda H_1}{a\lambda + ck + H_1(c - \lambda)}$$

But if H_1 is treated as a variable and differentiate the predator fraction (in the harvesting case) with respect to H_1

$$\left[\frac{a\lambda - \lambda H_1}{a\lambda + ck + H_1(c - \lambda)} \right]' = \frac{-ck\lambda - ac\lambda}{[a\lambda + ck + H_1(c - \lambda)]^2} \quad (3.5.2)$$

Since the right hand side of (3.5.2) is negative, the fraction and hence the percentages of predators must decrease as H_1 increases. A similar analysis shows that the fraction of prey increases with an increase in the harvesting rate.

Volterra's third principle, restated in terms of percentages, answers D' Ancona's question. If Volterra's model represents conditions in the upper Adriatic during the war years, the predator population should increase with a drop in fishing and decline when fishing resumes and conversely with the prey population.

Volterra's model have been challenged since its formulation, but the model continuous to be the starting point for most serious attempts to understand just how predator- prey communities evolve.

One confirmation of the general validity of Volterra's third principle occurred when the insecticide DDT was applied to control the cottony cushion scale insect which infested American citrus orchards. Its numbers were controlled by subsequent importation from Australia of the scale insect's natural predator, a particular kind of lady birds beetle. When DDT was discovered to kill scale insects, DDT kills all insects it touches. The consequences of the using of DDT was that numbers of lady birds drastically dropped while the population of the scale insects, freed from extensive lady bird predation increased. Consequently, there is a more cautious approach to the use of pesticides such as DDT than there once was. So, it has been observed that the effect of insecticides such as DDT is even more drastic then Volterra's model suggest

3.6 Limitations of the Lotka – Volterra Equations

A number of biologists and ecologists refused to accept Volterra's model as accurate. There are some difficulties with it. One objection is based on the fact that the model predicts an oscillation whose amplitude depends on the initial conditions similar to a linear problem. Thus, this model predicts that an observed oscillation of many periods duration is due to some earlier event. Although this seems reasonable for the sharks and fish of the Adriatic, it is entirely unbelievable that lynx and hares should oscillate in a manner determined by events a hundred (or more) years ago. Thus a predator prey model is sought which perhaps indicates oscillation of a type inherent to the systems, rather than determined by initial conditions.

Some scientists argue that the Lotka – Volterra model is unrealistic because they pointed to the fact that the oscillatory behavior predicted by Volterra's model is not in most predator– prey systems. Rather, most such systems tend to equilibrium states as time evolves. Nevertheless, regular population cycles, as suggested by the trajectories in Fig. 3.4.10 do occur in nature. It does not consider any competition among prey or predator. As a result, prey population may grow infinitely without any resource limits. Predators have no saturation: their consumption rate is unlimited. The rate of prey consumption is proportional to prey population. Thus, it is not surprising that model behavior is unnatural showing no asymptotic stability.

A more general model of predator – prey interactions is the system of differential equations:

$$\frac{dF}{dt} = F(a - bF - cS) \quad (3.6.1)$$

$$\frac{dS}{dt} = S(-k + \lambda F - \sigma S)$$

In this autonomous system, the term $b F^2$ indicates the degree of internal competition of the prey for tier limited resource (such as food and space) and the term σS^2 indicates the degree of completion among the predators to the finite amount of available prey. The constants b and σ are positive and would determine by experimentation or historical data. The solution of (3.6.1) is not periodic since the No Cycles theorem applies and (3.6.1) has no cycles.

There are other objections to the predator – prey models as developed here. One of these objections appears in the laboratory small scale ecosystems. Sometimes ecologists attempt to model situations using laboratory species in way similar to which the mathematician models using mathematics. As a counter example, the experiments of the mathematical biologist Gause. In these experiments, the population was composed of two species of protozoa, *Didinium nasatum*, feeds on the other, *Paramecium caudatum*. In all Gause's experiments, the *Didinium* quickly destroyed the *Paramecium* and then died of starvation. The

deterministic predator – prey population growth models do not result in any probability that one or become extinct. During a wildly oscillatory predator – prey fluctuation as shown by the trajectory in the phase plane in Fig. 3.6.1, there is a finite probability that when the population of prey is low, it will become extinct.

Thus it is possible that the prey does not recover to dominate in numbers over the predator at some later time. On the other hand, the model has its flaws since the averaging over all categories of age, fertility and sex is dubious, the parameters of the model probably depend on time, and so on.

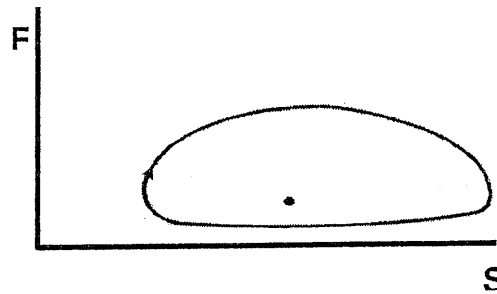


Figure 3.6.1 Wild predator – prey oscillation.

Finally, more realistic models incorporate random processes. These processes occur when the prey are provided with a refuge that is inaccessible to the predators. In these situations, it is impossible to make any definitive statements about the future number of predators and prey, since we cannot predict how many prey will be stupid enough to leave their refuge. This was verified directly in a famous experiment by Gauss. He placed five *Parameciums* and three *Didinium* in each of 30 identical test tubes, and provided the *Paramecium* with a refuge from the *Didinium*.

Two days later, he found the predators dead in four tubes, and a mixed population containing from two to 38 *Paramecium* in the remaining 26 tubes. Such predator – prey models will not be discussed. Neither will predator- prey models which exhibit delays be discussed. The process of mathematic modeling continues as more is learned about nature.

3.7 Conclusion

A good model must be simple enough to be mathematically tractable, but complex enough to represent a system realistically. Realism is often sacrificed for simplicity, and one of the shortcomings of the Lotka - Volterra model is its reliance on unrealistic assumptions.

For example, prey populations are limited by food resources and not just by predation, and no predator can consume infinite quantities of prey.

Many other examples of cyclical relationships between predator and prey populations have been demonstrated in the laboratory or observed in nature, but in general these are better fit by models incorporating terms that represent carrying capacity (the maximum population size that a given environment can support) for the prey population and for the predator population.

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ملخص

هذه الأطروحة هي عبارة عن عرض لنماذج رياضية تحاكي مظاهر حيوية موجودة في البيئة حيث يتم من خلالها دراسة العلاقة المشتركة بين كل من النباتات و الحيوانات و أثر بيئتها التي تعيش فيها. لغرض الدراسة تم إختيار و تصور وسط بيئي صغير من حياة بيئية مكونة من نوعين من الكائنات الحية و من ثم تم تسليط الضوء لدراسة التفاعل فيما بينها. إن العلاقة المتصورة بين النوعين قد تكون ذات طابع مشترك في التعايش كالتنافسها على مصادر الغذاء أو قد تكون إفتراس إحداها للأخرى للحصول على الغذاء. إن شكل النموذج الذي يمثل التفاعل بين نوعي الحيوانات المدروسة هو كالتالي:

$$\left. \begin{aligned} \frac{dx}{dt} &= x(a_0 + a_1x + a_2y) \\ \frac{dy}{dt} &= y(b_0 + b_1x + b_2y) \end{aligned} \right\} \quad (1)$$

حيث أن $x(t)$ و $y(t)$ ترمز الى عدد الحيوانات في الزمن t على التوالي، بينما حرفي a و b هما ثوابت و في حال كون $a_1 = a_2 = b_1 = b_2 = 0$ فإنه يسمى النموذج بـ **Malthusian model**، و الذي يمثل في حالته أبسط صورة لعملية تولد و وفاة نوعي الحيوانات المدروسة في النظام البيئي الطبيعي. من جهة أخرى، إذا كان في النموذج (1) $a_2 = b_1 = 0$ فإن الإفتراض أن النموذج المتولد لنوعي الحيوانات يعتبران غير متفاعلان في بيئتهما و بالتالي ينطبق عليهما قانون **Logistic law**.

في هذه الأطروحة، تم دراسة حالة السكون التي يعبر عنها بحلول الإتران (قيم ثابتة) للمعادلة (1) أو يعبر عنه بمنحنى مغلق والتي تدرس بواسطة نظرية **No cycles Theorem**.

تم دراسة نموذج "المفترس و الفريسة" ، حيث تم إنشاء بيئة بسيطة مكونة من فريسة و مفترس، وضع النموذج بواسطة Lotka – Volterra في سنة 1920s، والذي وضع بالصورة التالية:

$$\left. \begin{aligned} \frac{dx}{dt} &= x(a - cy) \\ \frac{dy}{dt} &= y(-k + \lambda x) \end{aligned} \right\} \quad (2)$$

حيث أن $x(t)$ و $y(t)$ ترمز الى عدد الفريسة و المفترس في الزمن t على التوالي، و الحروف a, c, k, λ هي ثوابت موجبة. خلال الدراسة تم التركيز على السلوك الوصفي ذو الحلول الصريحة والحلول النتائج تم تفسيرها بيئيا، حيث وجد أن شكل المسار المعبر عن الحلول بشكل منحنى مغلق و يمثل حركة متكررة.

تم دراسة أثر الإنسان من خلال عملية الحصاد أو أثر تسمم البيئة بالمواد الكيميائية لكلا النوعين، وقد وجد أن المتوسط الحسابي للفريسة هو $(k + H)/\lambda$ و $(a - H)/c$ للمفترس، حيث يرمز الحرف H لمعامل الحصاد. إن نتائج الحصاد وجدت ذات نتائج غير مألوفة و لها تطبيقات بيئية (**Volterra's Principle**) و من ثم تم عرض هذه التطبيقات. في الخاتمة، تم مناقشة بعض محدوديات النموذج.

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