

PREDATOR-PREY MODEL WITH TIME DELAY

**A THESIS SUBMITTED TO
THE GRADUATE SCHOOL OF APPLIED SCIENCES
OF
NEAR EAST UNIVERSITY**

by

SEÇKİN VAROL

**IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS
FOR
THE DEGREE OF MASTER OF SCIENCE
IN
MATHEMATICS**

NICOSIA 2010

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Seçkin Varol : PREDATOR-PREY MODEL WITH TIME DELAY

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

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ABSTRACT

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This work introduces a variety of mathematical models for biological systems, and presents the mathematical theory and techniques useful in analyzing those models. Material is organized according to the mathematical theory rather than the biological application. Undergraduate courses in calculus, linear algebra, and differential equations are assumed.

In this work, we are interested in predator-prey models. We first describe the predator-prey model and how differential equations relates to predator-prey. We consider Lotka-Volterra's model, aggregated model and May's model for predator-prey systems. Lotka-Volterra model as a classical application of mathematics in biology, models based on differential equations for interactions between species, thanks to analytical techniques and computerization, have become progressively more complex. Aggregated model, comprising a set of three ordinary differential equations governing the local dynamics present of prey and predator densities. These dynamics present two time scales, which enables us to use of aggregation of variables method. To evaluate the impact of density dependence in general, our model also uses a general predator density-dependent function for prey migration. We then study this model and its equilibrium points and a find a simple criterion of stability for positive equilibrium, depending on various parameters and on the density-dependent migration function. May presented limit cycle models of prey-predator interaction. He has shown that balancing a stabilising effect (limited prey population) against a destabilising effect (such as limited predator appetite) can lead to an unstable equilibrium point surrounded by a stable limit cycle. We discuss that a similar situation can be brought about when the destabilising effect is a time delay. Finally, we decide the May's model is appropriate model for our country.

Key words: Predator-prey model, Lotka-Volterra Model, Aggregated Model, May's Model, time delay, limit prey population, limit predator appetite.

ÖZET

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NEU Matematik Bölümü

Bu çalışma, biyolojik sistemler için çeşitli matematiksel modelleri tanıtır ve matematiksel teori ve teknikler bu modellerin analizinde yararlı sunulur. Materyal, biyolojik uygulamadan ziyade matematiksel teoriye göre düzenlenmiştir. Lisans dersleri calculus, doğrusal cebir ve diferansiyel denklemler varsayılr.

Bu çalışmada av-avcı modellerine ilgi duyacağız. İlk olarak av-avcı modelini ve diferansiyel denklemlerin av-avcı modeliyle nasıl ilgili olduğunu tanımlıyoruz. Av-avcı sistemleri için Lotka-Volterra modelini, Kümelenmiş modeli ve May's modelini göz önüne alıyoruz. Lotka-Volterra modeli, biyolojide klasik bir matematik uygulaması iken türler arasındaki etkileşimde diferansiyel denklemleri esas alır, analitik teknikler ve bilgisayara dayalı sistem olması sayesinde de giderek daha karmaşık bir hale gelmiştir. Kümelenmiş model, av ve avcı yoğunluklarının yerel dinamiğinde bulunan düzenlemeyi gösteren üç diferansiyel denklemi kapsayan modeldir. Bu dinamik bize değişkenlerin toplama yöntemini kullanmamıza olanak sağlayacağı mevcut iki zaman ölçeği gösterir. Genel yoğunluğa bağlı etkisini değerlendirmek için modelimizde av göçü için genel avcı yoğunluğuna bağımlı işlevi kullanır. Daha sonra bu modele ve bu modelin denge noktalarına ve çeşitli parametrelere ve göç yoğunluğu fonksiyonuna bağlı olarak pozitif denge için basit bir istikrar kriteri bulmak için çalışırız. May, av-avcı etkileşiminde sınırlı döngü modelleri sundu. O bir istikrar bozucu (dengeleme sınırlı yırtıcı iştah gibi) etkilerine karşı bir dengeleyici etkiye (sınırlı av nüfus), istikrarlı bir limit döngüsü tarafından çevrili kararsız bir denge noktasına yol göstermiştir. Benzer durumun istikrar bozucu etkiyi bir süre geciktirdiğimiz zaman ne gibi durum getirebileceğini tartışırız. Sonuç olarakda May's modeli ülkemiz şartları için en uygun modeldir.

Anahtar sözcükler: Av-avcı etkileşimi, Kümelenmiş model, May modeli, Lotka-Volterra modeli, zaman geciktirme olayı.

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CHAPTER 1

INTRODUCTION

In this chapter, we first learn some definitions dealing with the predator-prey models. Then we describe the what the predator-prey model is, how differential equations relates to predator-prey and a general predator-prey model.

1.1 SOME OF DEFINITIONS:

i) Exponential Growth

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

$$\frac{dN}{dt} = \frac{(b_0 - d_0)}{N_0} N \quad (1)$$

where:

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

d_0 = instantaneous death rate, deaths per individual per time period, and

dN_0 = current population size.

The difference between birth and death rates ($b_0 - d_0$) is also called r , the intrinsic rate of natural increase, or the Malthusian parameter. It is the theoretical maximum number of individuals added to the population per individual per time. By solving the differential equation (1) we get a formula to estimate a population size at any time:

$$N = N_0 e^{rt} \quad (2)$$

where $e = 2.718 \dots$ (base of natural logs).

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

$$\ln(N) = \ln(N_0) + \ln(e)rt \quad (3)$$

and

$$r = [\ln(N) - \ln(N_0)]/t \quad (4)$$

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

ii) Logistic Growth

We need to modify the basic equation (1) so that birth and death rates are no longer constant through time, but decrease and increase respectively as population size increases :

$$\frac{dN}{dt} = N[(b_0 - k_b N) - (d_0 + k_d N)] \quad (5)$$

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

$$b_0 - k_b N = d_0 + k_d N \quad (6)$$

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

$$N = \frac{(b_0 - d_0)}{(k_b + k_d)} \quad (7)$$

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

$$K = \frac{r}{(k_b + k_d)} \quad (8)$$

Since $b_0 - d_0 = r$. If we combine this new form of the carrying capacity equation with (5) we get the familiar form of the logistic growth equation:

$$\frac{dN}{dt} = rN \left[\frac{(K-N)}{K} \right]. \quad (9)$$

(Toronto, 1997)

iii) Stable and unstable:

Equilibrium is a state of a system which does not change. If the dynamics of a system is described by a differential equation (or a system of differential equations), then equilibria can be estimated by setting a derivative (all derivatives) to zero.

An equilibrium is considered **stable** (for simplicity we will consider asymptotic stability only) if the system always returns to it after small disturbances. If the system moves away from the equilibrium after small disturbances, then the equilibrium is **unstable**.

iv) Taylor Series:

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

$$f(x) = f(a) + (x - a)f'(a) + (x - a)^2 \frac{f''(a)}{2!} + (x - a)^3 \frac{f^{(3)}(a)}{3!} + \dots \\ + (x - a)^n \frac{f^{(n)}(a)}{n!} + \dots \quad (10)$$

v) Exponential Decay:

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

$$\frac{dN}{dt} = -\lambda N. \quad (11)$$

The solution to this equation is:

$$N(t) = N_0 e^{-\lambda t} \quad (12)$$

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

vi) Delay Model:

In general if we consider a population to be governed by

$$\frac{dN}{dt} = f(N) \quad (13)$$

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

One of the deficiencies of single population models like (13) is that the birth rate is considered to act instantaneously whereas there may be a time delay to take account of the time to reach maturity, the finited gestation period and so on. We can incorporate such delays by considering delay differential equation models of the form

$$\frac{dN}{dt} = f(N(t), N(t - T)), \quad (14)$$

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

1.2 What is the Predator-Prey Model ?

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

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

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

1.3 Differential Equations and how it Relates to Predator-Prey

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

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

1.4 A General Predator-Prey Model

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

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

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

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

CHAPTER 2

MODELS

In this section, we study the models of the predator-prey model which are Lotka-Volterra model and Aggregated model. Lotka-Volterra model looks at a predator-prey model where two species are involved. Thus, the differential equations describing the population dynamics must have two unknown variables, creating a system of differential equations. We then describe the predator-prey model which is Aggregated model, comprising a set of three ordinary differential equations governing the local dynamics of prey and predator population densities. These dynamics present two time scales, which enables us to use of aggregation of variables method. We then study this model and its equilibrium points and find a simple criterion of stability for positive equilibrium, depending on various parameters and on the density-dependent migration function.

2.1 Lotka Volterra Model

2.1.1 Lotka-Volterra Equation

The Lotka-Volterra equations, also known as the predator-prey equations, are a pair of first-order, non-linear, differential equations frequently used to describe the dynamics of biological systems in which two species interact, one predator and one its prey. They were proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926.

This model involves two equations

1. Describe how the prey population changes
2. Describe show the predator population changes.

They evolve in time according to the pair of equations:

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

(15)

$$\frac{dy}{dt} = y(-\gamma + \delta x)$$

where

y is the number of some predator (for example; sharks)

x is the number of its preys (for example; fishes)

$\frac{dy}{dt}$ and $\frac{dx}{dt}$ represents the growth of the two populations against time

t represents the time

and

α , β , γ and δ are parameters representing the interaction of the two species.

2.1.2 Physical Meanings of the Equations

When multiplied out, the equations take a form useful for physical interpretation. The origin should be considered from a more general framework,

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

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

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

These functions are too general, so a Taylor series approximation is performed to obtain linearized per capita rates,

$$f(x, y) = A_0 - A_1x - A_2y$$

$$g(x, y) = B_0 + B_1x - B_2y$$

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

Assumptions:

- 1) The prey population finds ample food at all times
- 2) The food supply of the predator population depends entirely on the prey populations
- 3) The rate of change of population is proportional to its size
- 4) During the process, the environment does not change in favor one species and the genetic adaptation is sufficiently slow.

2.1.2.1 Prey

The prey equation becomes

$$\frac{dx}{dt} = \alpha x - \beta xy \quad (16)$$

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

With these two terms the equation above (16), can be interpreted as: the change in the prey's numbers is given by its own growth minus the rate at which it is preyed upon.

2.1.2.2 Predators

The predator equation becomes

$$\frac{dy}{dt} = \delta xy - \gamma y \quad (17)$$

In this equation, δxy represents the growth of the predator population. (Note the similarity to the predation rate; however, a different constant is used as the rate at which the predator population grows is not necessarily equal to the rate at which it consumes the prey). γy represents the natural death of the predators: it is an exponential decay. Hence the equation represents the change in the predator population as the growth of the predator population, minus natural death.

2.1.3 Dynamics of the System

In the model system, the predators thrive when there are plentiful prey but, ultimately, outstrip their food supply and decline. As the predator population is low the prey population will increase again. These dynamics continue in a cycle of growth and decline.

2.1.3.1 Equilibrium Analysis

Population equilibrium occurs in the model when neither of the population levels is changing, i.e. when both of the derivatives are equal to 0. Thus, for the predator prey model above, we set

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

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

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

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

When solved for x and y the above system of equations yields

$$\{y = 0, x = 0\}$$

and

$$\left\{ y = \frac{\alpha}{\beta}, x = \frac{\gamma}{\delta} \right\}.$$

Hence, there are two equilibria. The first solution effectively represents the extinction of both species. If both populations are at 0, then they will continue to be so indefinitely. The second solution represents a fixed point at which both populations sustain their current, non-zero numbers, and, in the simplified model, do so indefinitely. The levels of population at which this equilibrium is achieved depend on the chosen values of the parameters α, β, γ and δ .

2.1.3.2 Stability of the Fixed Points

The stability of the fixed point at the origin can be determined by performing a linearization using partial derivatives, while the other fixed point requires a slightly more sophisticated method.

The Jacobian matrix of the predator-prey model is

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

First fixed point;

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

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

The eigenvalues of this matrix are $\lambda_1 = \alpha$ and $\lambda_2 = -\gamma$. In the model α and γ are always greater than zero, and as such the sign of the eigenvalues above will always differ. Hence the fixed point at the origin is a saddle point.

The stability of this fixed point is of importance. 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, we find 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 simple model).

Second fixed point;

Evaluating J at the second fixed point we get

$$J\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right) = \begin{bmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ \frac{\alpha\delta}{\beta} & 0 \end{bmatrix}$$

which yields the two complex conjugate eigenvalues $\lambda_1 = i\sqrt{\alpha\gamma}$ and $\lambda_2 = -i\sqrt{\alpha\gamma}$. The real parts of these two eigenvalues are both equal to 0. The linear stability analysis is thus inconclusive. It turns out that the equilibrium is neutral stable and this system of equations exhibits neutral oscillations (Wiens, 2010).

2.1.4 Nonlinear Systems of Differential Equations - Consumer-Resource Models

Nonlinear, autonomous systems of ordinary differential equations are of the form

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

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

⋮

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

where each of the functions f_i ($i=1,2,3,\dots,n$) on the right-hand side are real-valued functions in n variables. Most of the time, we will restrict the analysis to systems of two variables. We will focus on equilibria and stability.

2.1.4.1 Equilibria and Stability

Consider the system of two autonomous differential equations

$$\frac{dx}{dt} = f(x, y) \tag{18}$$

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

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

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

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

Each equation results in a curve in the x - y space. *Point equilibria* occur where the two isoclines intersect (Figure 2.1). A point equilibrium (\hat{x}, \hat{y}) of (18) therefore simultaneously satisfies the two equations

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

We will call the equilibria simply “equilibria”.

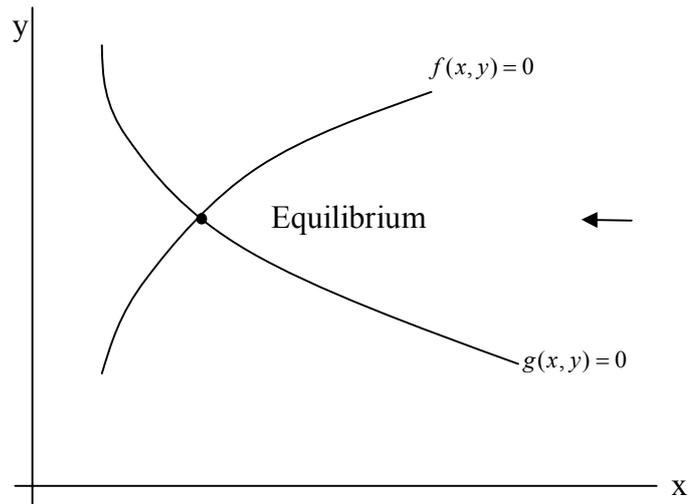


Figure 2.1: Zero isoclines correspond to the two differential equations. Equilibria occur where the isoclines intersect.

The *analytical approach to stability* relies on analyzing the effects of small perturbations. We say that the equilibrium (\hat{x}, \hat{y}) is locally stable if the system returns to (\hat{x}, \hat{y}) after a small perturbation, and unstable otherwise. Mathematically, this can be analyzed through linearizing the right-hand side of each of the two differential equations in (18) about the equilibrium.

The system (18) can be written in matrix form

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

where the right-hand side is a vector-valued function that maps a point in \mathbf{R}^2 (the two-dimensional real plane) into a point in \mathbf{R}^2 . To linearize a vector-valued function, we need to linearize each component separately. Linearizing a function of two variables about a specific point means to find the tangent plane at this point (this, of course, is not always possible). The equation of a tangent plane of $f(x, y)$ about (\hat{x}, \hat{y}) is given by

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

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

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

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

$$\begin{bmatrix} \frac{d\zeta}{dt} \\ \frac{d\eta}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial f(\hat{x}, \hat{y})}{\partial x} & \frac{\partial f(\hat{x}, \hat{y})}{\partial y} \\ \frac{\partial g(\hat{x}, \hat{y})}{\partial x} & \frac{\partial g(\hat{x}, \hat{y})}{\partial y} \end{bmatrix} \begin{bmatrix} \zeta \\ \eta \end{bmatrix} \quad (19)$$

The matrix

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

is called the *Jacobi matrix*.

The system (19) is a linear system of two equations, and we can use the results from linear systems of two differential equations to determine the stability of the equilibria. Namely,

- The equilibrium is a *node* if both eigenvalues of the Jacobian evaluated at the equilibrium are real, distinct, nonzero, and are of the same sign. The node is locally stable if the eigenvalues are negative, and unstable if the eigenvalues are positive.
- The equilibrium is a *saddle* if both eigenvalues of the Jacobian evaluated at the equilibrium are real and nonzero but have opposite signs. A saddle is unstable.
- The equilibrium is a *spiral* if both eigenvalues of the Jacobian evaluated at the equilibrium are complex conjugates with nonzero real parts. The spiral is locally stable if the real parts of the eigenvalues are negative, and unstable if the real parts of the eigenvalues are positive.

2.1.4.2 Consumer-Resource Models

Model 1: Lotka-Volterra Predator-Prey Model

There are a large number of models that deal with consumer and resource interactions. The oldest such model is the Lotka-Volterra model, which describes the interaction between a predator and its prey. If x denotes the abundance of the prey and y the abundance of the predator, then the model is given by the following set of differential equations:

$$\frac{dx}{dt} = bx - cxy \tag{20}$$

$$\frac{dy}{dt} = ecxy - dy$$

where the parameters b , c , d and e on the right-hand side are positive constants. The parameter b is the prey birth rate, c is the consumption rate, e is the conversion fraction of prey into new predators, and d is the predator death rate. The equilibria can be obtained algebraically by setting the right-hand sides equal to 0 and solving for x and y . We find the trivial equilibrium $(0,0)$ and a nontrivial equilibrium $(\hat{x}, \hat{y}) = \left(\frac{d}{ec}, \frac{b}{c}\right)$. The corresponding Jacobi matrix is given by

$$J(x, y) = \begin{bmatrix} b - cy & -cx \\ ecy & ecx - d \end{bmatrix}$$

If we evaluate this at the trivial equilibrium $(0,0)$ we find

$$J(0,0) = \begin{bmatrix} b & 0 \\ 0 & -d \end{bmatrix}$$

Therefore, the two eigenvalues are $\lambda_1 = b$ and $\lambda_2 = -d$. Both eigenvalues are real. Since one eigenvalue is positive and the other is negative, we conclude that the trivial equilibrium is a saddle and thus unstable.

If we evaluate the Jacobi matrix at the nontrivial equilibrium $(\hat{x}, \hat{y}) = \left(\frac{d}{ec}, \frac{b}{c}\right)$, we find

$$J\left(\frac{d}{ec}, \frac{b}{c}\right) = \begin{bmatrix} 0 & -c\frac{d}{ec} \\ ec\frac{b}{c} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{d}{e} \\ eb & 0 \end{bmatrix}$$

To compute the eigenvalues, we solve

$$\begin{aligned} \det\left[J\left(\frac{d}{ec}, \frac{b}{c}\right) - \lambda I\right] &= \det\begin{bmatrix} 0 - \lambda & -\frac{d}{e} \\ eb & 0 - \lambda \end{bmatrix} \\ &= (0 - \lambda)(0 - \lambda) - eb\left(-\frac{d}{e}\right) \\ &= \lambda^2 + bd = 0 \end{aligned}$$

which yields the two complex conjugate eigenvalues $\lambda_1 = i\sqrt{bd}$ and $\lambda_2 = -i\sqrt{bd}$. The real parts of these two eigenvalues are both equal to 0. The linear stability analysis is thus inconclusive.

It turns out that the equilibrium is neutral and this system of equations exhibits neutral oscillations.

Model 2: Density – Dependent Growth of the Prey

It is possible to stabilize the predator-prey model by including density-dependent growth of the prey in the form of logistic growth. This takes the form

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{K}\right) - cxy \tag{21}$$

$$\frac{dy}{dt} = ecxy - dy$$

where all parameters are positive. In the absence of the predator, the prey dynamics reduce to logistic growth in (21). Namely, if we set $y = 0$, then

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

The system of equations (21) has the nontrivial equilibrium $(0,0)$, which is always unstable. In addition, it has the prey only equilibrium $(K,0)$, which is locally stable provided $K < \frac{d}{ec}$. If $K > \frac{d}{ec}$, an additional nontrivial equilibrium in the first quadrant appears, which is locally stable. If $K > \frac{d}{ec}$, the prey only equilibrium is unstable.

Model 3: Saturating Functional Response

The functional response of a predator is defined as the per predator predation rate. In this case, the functional response is simply cx , a linear function of prey density. In nature, one often observes functional response curves that saturate with increasing prey density. This happens, for instance, if predators need to spend time handling prey.

A common form for a saturating functional response is

$$\frac{dx}{dt} = bx \left(1 - \frac{x}{K}\right) - \frac{cx}{a+x}y$$

(22)

$$\frac{dy}{dt} = e \frac{cx}{a+x}y - dy$$

This model is known as *Rosenzweig's model*. It has the trivial equilibrium $(0,0)$ and the prey only equilibrium $(K,0)$. If $0 < \frac{ad}{ec-d} < K$, there is an additional equilibrium in the first quadrant, which may be locally stable or unstable. The interesting property of this model is that when increasing the carrying capacity K , the equilibrium becomes unstable. This is known as Rosenzweig's paradox of enrichment (Neuhauser).

2.2 Aggregated Model

2.2.1 Use of Aggregation Method to Model a Prey-Predator System in a Heterogeneous Environment

The model can be thought for prey-predator systems in a two patches environment. On a first patch, preys can grow but are vulnerable because of an easy attack by the predators hunting on that patch; on the second patch, preys are safe from predation (or mostly safe). Hence, preys can go on the second patch considered as a refuge, but migrate also on the first patch where food and water are available.

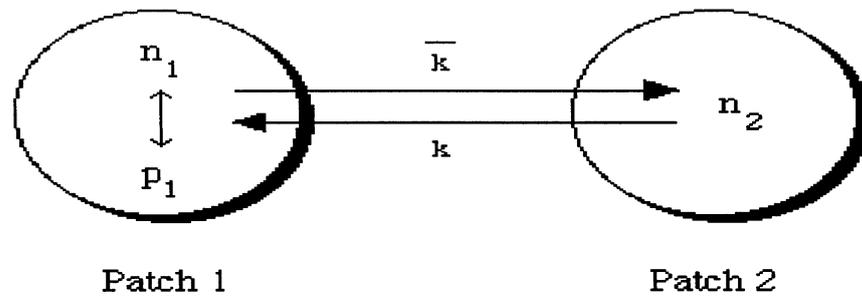


Figure 2.2: Flowchart of the model of prey's patch selection induced by predators.

2.2.2 Information of the Complete Model

Let us denote $n_i(t)$ as the density of the prey at time t on patch i ($i = 1, 2$) and $p_1(t)$ the density of the predator at time t on patch 1. Predators are present in patch 1 only, while preys can move and migrate from patch 1 to patch 2 and conversely. Preys are assumed to grow according to a logistic law on each patch characterised by a carrying capacity ' K_i ' and a growth rate ' r_i ' on patch i . We assume a Lotka-Volterra functional response for the predation relationship on patch 1, and we denote ' a ' the predation rate (/ predator/ prey/ time unit). We call ' c ' the conversion rate of prey biomass into predator biomass, and ' μ ' is the natural death rate of predators. The model also takes into account the migration of preys between the two patches, according to the rule shown in Figure 2.2. Finally, we make the hypothesis that migrations go faster than

growth and predation processed on each patch. Two time scales are thus involved in the model, a fast one for prey migration (each day for example) and a slow one for growth and predation.

The complete model, composed of a set of three ordinary differential equations, is described as follows:

$$\begin{aligned}\frac{dn_1}{dt} &= (kn_2 - \bar{k}n_1) + \varepsilon \left[r_1 n_1 \left(1 - \frac{n_1}{K_1} \right) - an_1 p_1 \right] \\ \frac{dn_2}{dt} &= (\bar{k}n_1 - kn_2) + \varepsilon r_2 n_2 \left(1 - \frac{n_2}{K_2} \right) \\ \frac{dp_1}{dt} &= \varepsilon (-\mu p_1 + can_1 p_1)\end{aligned}\tag{23}$$

where ε is a small parameter. The parameter ' k ' represents the prey migration rate from patch 2 to patch 1; and the another parameter ' \bar{k} ' represents the prey migration rate from patch 1 to patch 2. The analysis of the model showed that only two cases, might occur according to parameter values:

case 1: The predator population becomes extinct, while the prey population tends to a constant density;

case 2: The prey and the predator populations coexist at constant densities.

In a further contribution (Chiorino et al.,1999), was considered the case of a prey migration rate, \bar{k} from patch 1 to patch 2, which depends on the predator density on patch 1. Hence, it was assumed that $\bar{k} = \alpha p_1$ with α , a positive constant. Preys are then supposed to leave patch 1 at a rate increasing with the number of predators on that patch. Such an assumption is equivalent to a repulsive effect exerted by predators on preys. The mathematical analysis of the aggregated model has shown that the two previous cases may also occur, but that a new situation can arise:

case 3: Extinction of the predator population and coexistence of preys and predators can occur at the same time. There is a separatrix in the phase portrait, and according to the initial conditions on both sides of this separatrix, either the predator goes to extinction or both the prey and the predator coexist.

In the present work, we shall assume a reinforced repulsion effect of the predator on the prey, that is $\bar{k} = \alpha p_1^2$. Instead of leaving patch 1 with a rate simply proportional to the predator density as in Chiorino et al., the rate is now proportional to the square of the predator density. With this assumption, the complete model now reads:

$$\begin{aligned}\frac{dn_1}{dt} &= (kn_2 - \alpha p_1^2 n_1) + \varepsilon \left[r_1 n_1 \left(1 - \frac{n_1}{K_1} \right) - an_1 p_1 \right] \\ \frac{dn_2}{dt} &= (\alpha p_1^2 n_1 - kn_2) + \varepsilon r_2 n_2 \left(1 - \frac{n_2}{K_2} \right) \\ \frac{dp_1}{dt} &= \varepsilon (-\mu p_1 + can_1 p_1)\end{aligned}\tag{24}$$

2.2.3 The Aggregated Model

Let us define :

$$N = n_1 + n_2 \quad \text{and} \quad P = p_1$$

be the aggregated variables, which is the total prey and predator densities and added on both patches. The first step of aggregation consists of looking for the fast equilibrium of the model that is for the prey migrations. This fast equilibrium is obtained when the two migration flows are equal $kn_2 = \bar{k}n_1 = \alpha P^2 n_1$.

As migration is conservative (the total prey density N is a constant of motion for migrations), one can substitute $N - n_1$ for n_2 in the previous equation. After some algebra, we obtain the prey density at the fast equilibrium in terms of the total prey and predator densities:

$$n_1^* = \frac{kN}{k + \alpha P^2}\tag{25}$$

$$n_2^* = \frac{\alpha P^2 N}{k + \alpha P^2}$$

where n_1^* and n_2^* represent the fast equilibrium.

At high density of predators, preys avoid patch 1 and concentrate on patch 2. It can be easily shown that this fast equilibrium is asymptotically stable, that is, a condition needed in order to proceed to aggregation (Auger & Roussarie, 1994; Poggiale, 1994) holds.

The aggregated system is obtained by adding the two prey equations and by substituting the previous fast equilibrium (25) in the prey and predator equations:

$$\frac{dN}{dt} = \frac{N}{k + \alpha P^2} \left[r_1 k \left(1 - \frac{N}{K_1} \frac{k}{k + \alpha P^2} \right) + r_2 \alpha P^2 \left(1 - \frac{N}{K_2} \frac{k}{k + \alpha P^2} \right) - akP \right] \quad (26)$$

$$\frac{dP}{dt} = P \left(ca \frac{k}{k + \alpha P^2} N - \mu \right)$$

This aggregated system is an approximation of the complete system. It is valid when ε is small enough (typically 0.1 or less) and when the aggregated model is structurally stable. This model is very different from the local model on each patch, which assumes a logistic growth of the prey, a constant mortality of the predator and a Lotka-Volterra functional response. It shows how the density-dependent fast migrations, at the individual level, emerge at the population level.

2.2.4 Dynamics of the Aggregated Model

In this section, we shall consider the phase portrait in the (P, N) plane. Equilibrium points of the aggregated model can be obtained by looking to the nullclines of the system.

The N -nullclines are given by the next two functions:

$$N = 0 \quad \text{and} \quad N = \frac{K_1 K_2 (k + \alpha P^2)(r_2 \alpha P^2 - akP + r_1 k)}{K_1 r_2 \alpha^2 P^4 - K_2 r_1 k^2} \quad (27)$$

The P -nullclines are given by the next two functions:

$$P = 0 \quad \text{and} \quad N = \frac{\mu \alpha}{ca k} P^2 + \frac{\mu}{ca} \quad (28)$$

The positive quadrant is positively invariant, and the equilibrium points are found at the intersections between the N -nullclines and P -nullclines.

$(0,0)$ and $(0, K_1)$ are equilibrium points in the four cases, and if $K_1 < \frac{\mu}{ac}$, situations of Figure 2.3 can occur, while those of Figure 2.4 are possible when $K_1 > \frac{\mu}{ac}$.

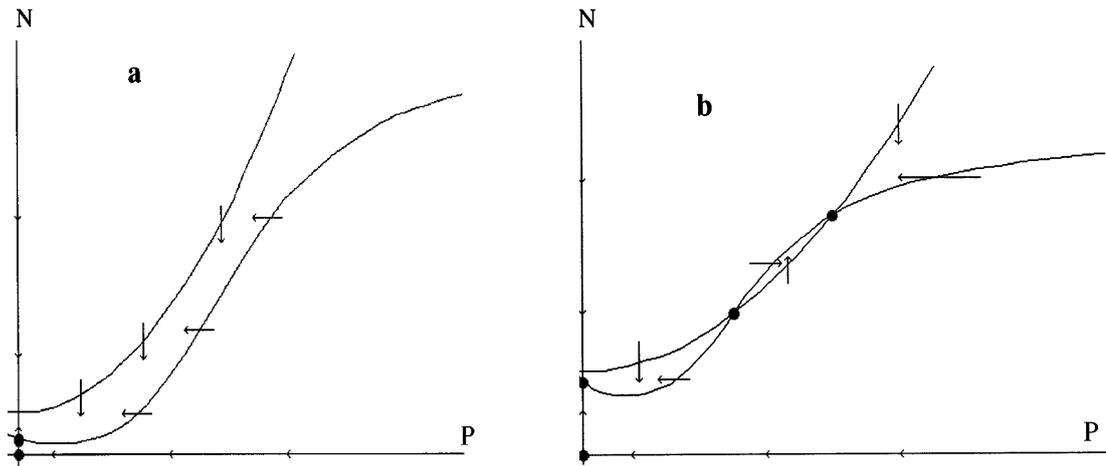


Figure 2.3: Nullclines and flow directions corresponding to model (26) in the case

$K_1 < \frac{\mu}{ac}$ in the plane (P, N) . (a) Two steady states; (b) Four steady states.

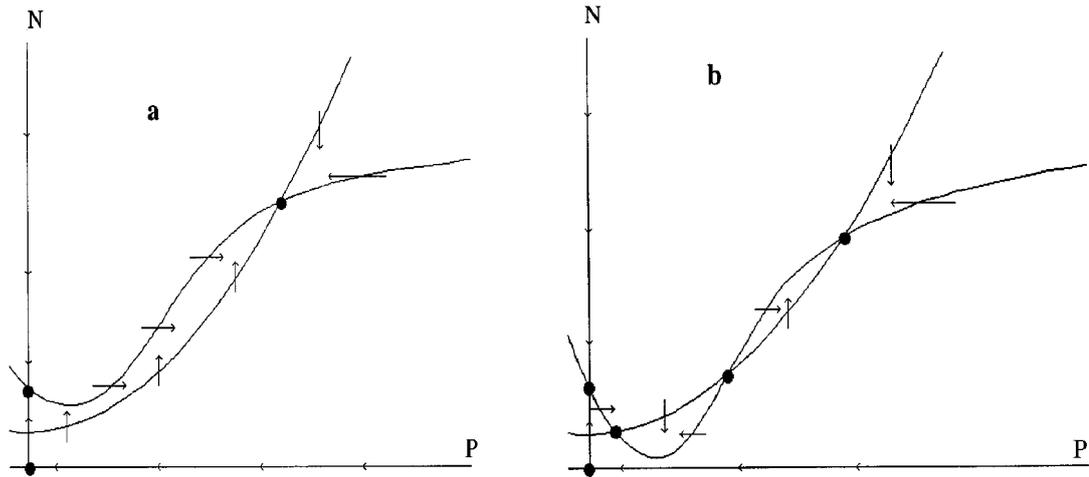


Figure 2.4: Nullclines and flow directions corresponding to model (26) in the case $K_1 > \frac{\mu}{ac}$ in the plane (P, N) . (a) Three steady states; (b) Five steady states.

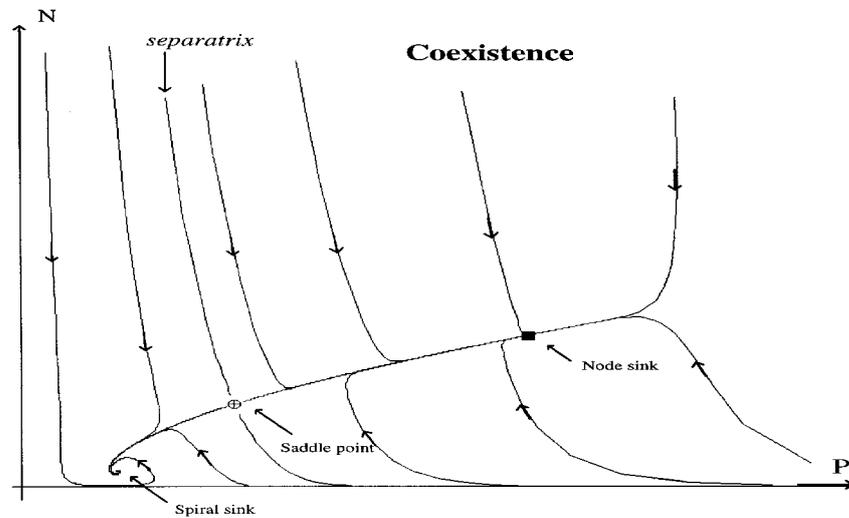


Figure 2.5: Phase portrait corresponding to the case of Figure 2.4b.

- When $K_1 < \frac{\mu}{ac}$, two or four equilibrium points can exist in the phase portrait:

- In the case of Fig.2.3a, $(0,0)$ and $(0, K_1)$ are the only equilibrium points. As indicated by the flow directions on the nullclines, the origin $(0,0)$ is unstable and the prey population tends to its carrying capacity of patch 1, while the predator is excluded.

- In the case of Fig.2.3b, two more equilibrium points exist in the positive quadrant. As indicated by the flow directions on the nullclines, $(0,0)$ is unstable and $(0, K_1)$

is stable. Among the two other equilibrium points, the one at high density is stable and the one at low density is a saddle point. Thus, there is a separatrix and according to the initial condition, either the predator population goes to extinction or the prey and predator population coexist.

- When $K_1 > \frac{\mu}{ac}$, three or five equilibrium points can exist in the phase portrait and $(0,0)$ and $(0, K_1)$ are always unstable (saddle points). Two types of situation can occur:
 - In the case of Fig.2.4a, there is only one stable equilibrium point in the positive quadrant, which corresponds to preys and predators coexisting at constant densities.
 - In the case of Fig.2.4b, there are three equilibrium points in the positive quadrant, two stable ones and a saddle point between them. According to the initial densities and with respect to the separatrix shown on Fig. 2.5, the prey and the predator coexist either at low densities or at high densities.

The dynamics is very interesting on a biological point of view:

- If the system is initially at the high-density equilibrium, capture of prey can push the population state through the separatrix and then to the low-density equilibrium.
- If the system is initially at the low-density equilibrium, a flow of migrants, coming from outside, can again push the population state through the separatrix and switch to the high-density equilibrium.

This situation of switching between two stable equilibrium points has interesting consequences in terms of management of the populations (Auger et al, 1999).

CHAPTER 3

MAY'S MODEL

This section model looks at a predator-prey model where two species are involved. May has shown that balancing a stabilising effect (limited prey population) against a destabilising effect (such as limited predator appetite) can lead to an unstable equilibrium point surrounded by a stable limit cycle. We discuss that a similar situation can be brought about when the destabilising effect is a time delay.

3.1 Analytical Results

The model proposed by May has limited prey population and limited predator appetite.

$$\frac{dN_1}{dt} = \varepsilon_1 N_1 \left\{ 1 - \frac{N_1}{k} \right\} - \frac{AN_1 N_2}{(N_1 + B)} \quad (29)$$

$$\frac{dN_2}{dt} = \varepsilon_2 N_2 \left\{ 1 - \frac{N_2}{CN_1} \right\}$$

In the appendix of May's book, he showed that the equilibrium point can be both stable and unstable.

The secular equation corresponding to (29) has the form

$$\lambda^2 - (A_{11} + A_{22})\lambda + (A_{11}A_{22} - A_{12}A_{21}) = 0 \quad (30)$$

where, as described in detail in May's reference.

$$A_{12} < 0, A_{21} > 0, A_{22} < 0$$

and

$$A_{11}A_{22} - A_{12}A_{21} > 0$$

So the equilibrium point is stable if and only if

$$A_{11} + A_{22} < 0$$

With exponential time delay the second equation of (29) is replaced by

$$\frac{dN_2}{dt} = \varepsilon_2 N_2 \left\{ 1 - N_2 \frac{N_3}{C} \right\}$$

(31)

$$\frac{dN_3}{dt} = a \left\{ \frac{1}{N_1} - N_3 \right\}$$

From (31) one finds the secular equation.

$$\lambda^3 - \lambda^2(A_{11} + A_{22} - a) + \lambda(A_{11}A_{22} - a(A_{11} + A_{22})) + a(A_{11}A_{22} - A_{12}A_{21}) = 0$$

(32)

As $a \rightarrow \infty$, (32) goes over to (30). As $a \rightarrow 0$, (32) goes over to (33)

$$\lambda^2 - \lambda(A_{11} + A_{22}) + A_{11}A_{22} = 0$$

(33)

This implies stability if

$$A_{11} + A_{22} < 0$$

and

$$A_{11} + A_{22} > 0$$

which in this model requires $A_{11} < 0$.

The Routh-Hurwitz conditions applied to (32) yields a quadratic equation in 'a', at the roots of which changes of stability occur. The following cases occur.

1. Unstable at $a = \infty$ implies unstable at $a = 0$. There are no real roots of the quadratic , so this case is unstable for all values of ‘ a ’.
2. Stable at $a = \infty$, with $A_{11} > 0$ implies unstable at $a = 0$. There is one real root. Hence, time delay induces instability.
3. Stable at $a = \infty$ with $A_{11} < 0$ implies stable at $a = 0$. If $|A_{11}|$ is small enough there are two real roots. So that as ‘ a ’ decreases instability appears and then vanishes. For larger (negative) A_{11} there are no real roots and the equilibrium point is stable for any value of ‘ a ’.

We may summarize as follows:

$A_{11} > A_{22} $	U
$0 < A_{11} < A_{22} $	$S \rightarrow U$
$A_{11} < 0$	$S \rightarrow U \rightarrow S$
	S

The possibility of two transitions is not merely a consequence of using the exponential delay. Even more complicated sequences occur with a peaked decay function (Hınçal, 1997).

CHAPTER 4

CONCLUSIONS

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

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

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

The aggregation method is a convenient tool to study complex systems composed of a larger number of elements and presenting a hierarchical structure. This method was applied to prey-predator models in a heterogeneous environment. In particular, the effect of density-dependent migration decisions of preys and predators on the structure of the global prey-predator model was studied. The method was also used to study the effects of different individual tactics hawk, and dove at the fast time scale, on the global growth of a cat population. And it is possible to implement aggregation methods in order to simplify community graphs. Finally, the method was developed in the case of discrete models.

Future developments are necessary to incorporate individual behaviour into population dynamics as well as the structure of the community. This could be carried out by considering three time scales or more. Stochastic processes should also be added in the models. Recent developments have been carried out along this line in stochastic discrete time models.

The May model the essential question is whether reasonable values of ' a ' lead to a limit cycle of reasonable dimensions. In our exact calculations this is the case. The effect of time delay is to increase the amplitude of the population oscillation. Where these exist in the instantaneous version, when the instantaneous version has stable equilibrium, time delay can lead to oscillations either for all ' a ' less than some critical ' a ' or for ' a ' between critical values a_1 and a_2 .

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