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STATISTICAL INFERENCE FOR SOME PREDATOR-PREY MODELS

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RÉSUMÉ

On propose une méthode stochastique qui s'applique à des systèmes non linéaires d'équations différentielles qui modélisent l'interaction de deux espèces; le but est d'établir si un système déterministe particulier peut s'ajuster à des données qui présentent un comportement oscillatoire. L'existence d'un cycle limite est essentielle pour l'implantation de notre méthode. Cette procédure se base sur l'estimation des isoclines du système, en utilisant le fait que les isoclines traversent les solutions du système à des points maximum et minimum. Ensuite, nous proposons des tests qui permettent de comparer trois modèles: Holling (1959), Hanski *et al.* (1991), and Arditi *et al.* (2004). Finalement, on utilise des données simulées pour illustrer et étudier les propriétés de notre méthode, et nous appliquons la procédure à un ensemble de données bien connu.

Mots-clés: systèmes prédateur-proie, équations différentielles ordinaires, plan des phases, isoclines, modèle stochastique, régression linéaire, estimation par moindres carrés, test de t, test de Wilcoxon.

ABSTRACT

We propose a stochastic method applicable to two species nonlinear systems of differential equations; the purpose is to determine whether a particular deterministic model can be fitted to a given data set that exhibits oscillatory behavior. Existence of a limit cycle solution is crucial for implementing our method. This method is based on estimating the coefficients of the isoclines of the given system, based on the fact that the isoclines intercept the solutions of the system at their local minima and maxima. Next, we introduce several testing methods which allow to compare three models: Holling (1959), Hanski *et al.* (1991), and Arditi *et al.* (2004). Finally, we use simulated data to illustrate and study the properties of our method, and we apply the procedure to a well-known data set.

Key words: predator-prey systems, ordinary differential equations, phase plane, null-isoclines, stochastic model, linear regression, least squares estimation, t-test, Wilcoxon test.

INTRODUCTION

In the 1920s, Lotka (1925) and Volterra (1926) introduced a two dimensional nonlinear system of differential equations as a continuous-time model which could explain the behavior of a two-species population of predator and prey. Since then, the construction and study of deterministic models for general population dynamics of predator-prey systems has become a central subject in mathematical ecology. Besides Lotka-Volterra, other classical approaches use what is known as Holling type I, II and III functionals for modeling the interaction. For the classical references in this area we refer to Kot (2001).

Animal populations change by migration, birth and death. As seen in nature, either the predator or prey population, or both, can become extinct or coexist in a state of equilibrium. Moreover, extinction or equilibrium can be reached by oscillations. Furthermore, classical prey-predator models such as Lotka-Volterra, or Holling (1959) cannot express coexistence of the prey with its predator at a population level much lower than the maximum possible population size. This is known as the paradox of biological control. Indeed, the original models were mainly aiming to determine the effect of the prey population on the number of prey consumed by each predator over time. These models hardly discussed the effect of the predator population on the predator-prey interactions. Arditi *et al.* (2004) were those who first recognized that adding the effect of the predator population on the predator-prey interaction can solve the problem of coexistence at lower population levels. They proposed several such predator-dependent models.

In this thesis we introduce some of these models, namely those which had a major impact on the development of the mathematical theory of predator-prey interactions. We review the ecology of these models and we explain the interpretation of their parameters. We present some elements of the theory of dynamical systems in non-technical terms, as well as their links to mathematical ecology of predator-prey interactions. We point out how the qualitative analysis of dynamical systems helps us explain the behavior of the solutions to the predator-prey population systems of ordinary differential equations (ODEs).

Further, at the core of this work, we introduce a new stochastic model, which adds observational error to the solutions of the ODEs. An important part of the thesis deals specifically with statistical inference, namely estimating the parameters, as well as a comparison of models based on simple tests. In the end, we conduct simulation studies to illustrate our method, and check empirically the properties of our estimators and tests. We also apply the testing and estimation procedure to a real data set.

The thesis is organized as follows. In Chapter 1, we introduce the Lotka-Volterra, the Holling, the Hanski and the Arditi models, and explain their specific contribution to ecological modeling of predator-prey interactions. Chapter 2 is devoted to the deterministic analysis, where we study the four mentioned models separately. In Chapter 3, we propose and study our stochastic models. Moreover, we develop the estimation and testing procedures specific to our models. Finally, we devote Chapter 4 to simulation, in order to perform an empirical study of our inference methodology, as well as a short data analysis.

CHAPTER I

MOTIVATION FROM ECOLOGY

1.1 Mathematical Ecology

In ecology, there is a long tradition of modeling population sizes of interacting species by functions which are the solutions to a deterministic system of ordinary differential equations (ODE). Such functions are positive and often are either periodic or quasi-periodic; see Froda and Colavita (2005). Depending on the coefficients of a given ODE, the solution can carry on different behaviors such as admitting a limit cycle, stable node, etc. Due to the natural behavior of the predator and the prey, these systems often bear oscillatory behavior. Despite the abundance of such deterministic models, they are rarely used in quantitative studies, but appear mainly in the qualitative analysis. Time series models or stochastic differential equations, for discrete and continuous time models, respectively, are commonly used in order to assess the quantitative behavior. For more comments see Froda and Nkurunziza (2007).
As far as the historical background goes the story is as follows: During the First World War, there was an increase in the predatory fish population and a decrease in the prey fish population in the aftermath of a complete cease on fishery in the Adriatic sea, which led Volterra (1926) to formulate a mathematical model to describe the predator-prey population dynamics (Kot, 2001). In order to explain a mechanism by which predators regulate their prey, Volterra constructed a mathematical model that describes temporal changes in prey and predator abundances. He made several restrictive assumptions such as: (i) the predator-prey population levels are large enough to be considered as contin-

uous rather than discrete variables; (*ii*) the prey and the predator are both well-mixed in the environment; (*iii*) the populations are closed in the sense that there is no immigration or emigration; (*iv*) the population dynamics is completely deterministic, i.e. no random events are considered; (*v*) the prey population grows exponentially in the absence of predator; (*vi*) the predator rate consumption of prey is a linear function of prey and vice versa; (*vii*) the predator population declines exponentially in the absence of prey. Furthermore, Volterra (1926) introduced a two dimensional first order system of ordinary differential equations where solutions represent the prey and the predator population sizes, respectively.

Due to the simplicity of this model, some of the major basic facts in ecology were ignored in the system. For instance, the proposed parametrization supposes that the population of the prey will grow exponentially in the absence of predator. This model is also present in the Lotka (1925) work and therefore, is referred to the Lotka-Volterra model.

Later on, other researchers partially recovered this problem of the classical Lotka-Volterra model by introducing new terms to the system. One of the major contributions was made by Holling (1959). For our presentation we retain Holling's approach as well as the models proposed by Hanski *et al.* (1991) and Arditi *et al.* (2004).

In short, all these authors propose adding new parameters in order for avoiding exponential growth of the prey population in the absence of predator. In the new cases, the population of prey increases asymptotically instead of exponentially. They also proposed modified equations describing the growth of the predator population by including nonlinear terms in order to get around certain problems.

In this chapter, we describe each of these models in terms of their ecological interpretation.

1.2 Models

In this section, we introduce three systems of differential equations for the predator-prey interactions known as Holling (Holling, 1959), Hanski (Hanski *et al.*, 1991) and

Arditi (Arditi *et al.*, 2004), along with the classical Lotka-Volterra model as presented in Hirsch and Smale (1974). Our main emphasis is on the proposed parameterizations and their ecological meaning.

In what follows, let $x \equiv x_t$ denote the size of the prey population, and $y \equiv y_t$ denote the size of the predator population at time t. Some authors refer to x_t and y_t as the prey and predator density, respectively.

1.2.1 Lotka-Volterra System

As stated before, one of the original two-species biological models is called Lotka-Volterra (Hirsch and Smale, 1974). The model includes two equations, one which describes how the size of the prey population changes over time and the second one which describes how the predator population size changes over time. This model is often described by

$$\begin{cases} \frac{dx}{dt} = (\alpha - \beta y)x, \\ \frac{dy}{dt} = (\gamma x - \delta)y. \end{cases} \tag{1.1}$$

The parameters appearing in system (1.1) are defined as follows:

α : the natural growth (birth) rate of prey in the absence of the predator per capita,

β : the death rate per encounter of prey due to predation or predation rate coefficient,

γ : the reproduction rate of predators per one prey eaten,

δ : the natural death (decline) rate of the predator in the absence of prey.

Let us look more closely at each equation of system (1.1).

The prey equation is defined by

$$\frac{dx}{dt} = \alpha x - \beta xy. \tag{1.2}$$

Thus, by letting $\beta = 0$ *i.e.* when there is no predation, we can see that the prey is assumed to have an unlimited food supply to reproduce exponentially; this exponential growth is represented in equation (1.2) by the term αx. The rate of decrease due to predation is assumed to be proportional to the rate at which the predators and the prey meet; this is represented in equation (1.2) by $-\beta xy$. If either x or y is zero then there can be no predation. Finally, equation (1.2) can be interpreted as follows: the change in the prey population size is due to its own growth minus the rate at which it is preyed upon.

Further, the predator equation is given by

$$\frac{dy}{dt} = \gamma xy - \delta y. \tag{1.3}$$

By letting $\gamma = 0$ in equation (1.3), δy represents the natural death of the predators which is an exponential decay as opposed to the exponential growth of prey. On the other hand, in this equation, γxy represents the growth of the predator population and is due to predation. (Note the similarity to the predation rate in equation (1.2); however, a different constant is used as the rate at which the predator population grows is not necessarily equal to the rate at which the predator consumes the prey). Hence, equation (1.3) represents the change in the predator population size as the growth of the predator population due to predation, minus natural death.

The system of equations (1.1) admits periodic solutions which do not have a simple, analytic expression in terms of the usual trigonometric functions (Hirsch and Smale, 1974). However, later on we will see that an approximate linearized solution yields a simple harmonic motion with the population of predators following that of prey by 90°. In the Lotka-Volterra system, the predator population grows when there are plenty of prey but, ultimately surpass their food supply and decline. As the predator population reaches a lower level, the prey population can increase again. These dynamics continue in a growth-decline cycle (Kot, 2001).

The prey average population size over one period is δ/γ. Therefore, it depends only on the parameters which describe population growth and death of predator; at the same time, the predator average size over one period is α/β and therefore, depends only on the prey growth and death population parameters (Kot, 2001). Moreover, increasing the prey growth per capita rate α, which is sometimes called *enrichment* in the ecological literature, does not change the prey average size, but it increases the predator average size (Kot, 2001).

Can this model explain the question about the observed changes in predator and prey fish abundances during the First World War mentioned before?

Volterra (1926) hypothesized that fishery reduces the prey per capita growth rate α and increases the predator mortality rate δ, while the interaction rates β and γ do not change (Volterra, 1926). Thus, ceasing fishery should lead to an increase in α and decrease in δ and thus induce a decrease in the average prey fish population δ/γ and to an increase in the average predator fish population α/β, which is exactly what was observed during the First World War.

1.2.2 Holling System

Holling system was introduced in Holling (1959). Before presenting it, we explain a modification of the Lotka-Volterra model known as the competitive Lotka-Volterra system (Hirsch, 1990). The competitive Lotka-Volterra equations are a simple model of the population dynamics of species competing for some common resource. The form is similar to the classical Lotka-Volterra equations (1.1).

Before introducing this new type of model, let us introduce the logistic population model for one species which is common in ecology,

$$\frac{dx}{dt} = \alpha x(1 - \frac{x}{K}),$$

where x is the size of the population at a given time, α is inherent per-capita growth rate, and K is the carrying capacity (Kot, 2001).

Definition 1.2.1 *The equilibrium maximum of the population of an organism is known as the ecosystem's carrying capacity for that organism.*

In non technical terms, the carrying capacity is the asymptotic limit for the population size of an organism. Moreover, as population size increases, birth rates often decrease and death rates typically increase. The difference between the birth rate and the death rate is called natural increase. The carrying capacity could support a positive natural increase, or could require a negative natural increase. Carrying capacity is thus the number of individuals an environment can support without significant negative impacts to the given organism and its environment. A factor that keeps population size at an equilibrium is known as a regulating factor.

In the logistic model

$$\frac{dx}{dt} = \alpha x(1 - \frac{x}{K}),$$

below carrying capacity K, populations asymptotically increase until they reach their asymptote, which is the horizontal line at height K in this case. The carrying capacity of an environment may vary for different species and may change over time due to a variety of factors including food availability, water supply, environmental conditions, and living space (Kot, 2001).

Holling (1959) studied predation of small mammals on pine sawflies, and found that predation rates increased with increasing prey population size. This was resulted from two effects:

(*i*) each predator increased its consumption rate when exposed to a higher prey population, and

(*ii*) predator population increases with the increasing prey population. So he proposed what is known as the Holling system.

Holling system is very similar to the competitive Lotka-Volterra model. Given two populations, x and y, with logistic dynamics, the Lotka-Volterra formulation adds an additional term to account for the species' interactions. Thus the competitive Lotka-Volterra equations are

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \beta xy, \\ \frac{dy}{dt} = \gamma xy - \delta y - \delta y^2. \end{cases} \tag{1.4}$$

In the Lotka-Volterra model (1.1), the prey population can increase indefinitely in the absence of predator, *i.e.* if $\beta = 0$. Moreover, if the initial value slightly changes the trajectory (x_t, y_t) in the plane will dramatically change *i.e.* the amplitudes of x_t and y_t are very different. So this system is unstable in a certain sense (Hirsch and Smale, 1974). To correct these problems, introducing additional terms to the model (1.1) seems necessary. Holling (1959) proposed adding a nonlinear term to the original Lotka-Volterra prey equation and set logistic growth for prey in the absence of predator, as in system (1.4). His next major contribution to the theory of predator-prey interactions was to replace βxy by $f(x)y$, *i.e.* to add different predator functional responses $f(x)$ to the prey equation. There are three major types of functional responses proposed by Holling (Kot, 2001):

A type I functional response is a linear relationship between the number of prey eaten by the predator per unit time and the prey population size, *i.e.*

$$f(x) = \beta x,$$

as it appears in (1.4).

The resulting curve may increase up to some fixed maximum or it may increase indefinitely (Figure 1.1).

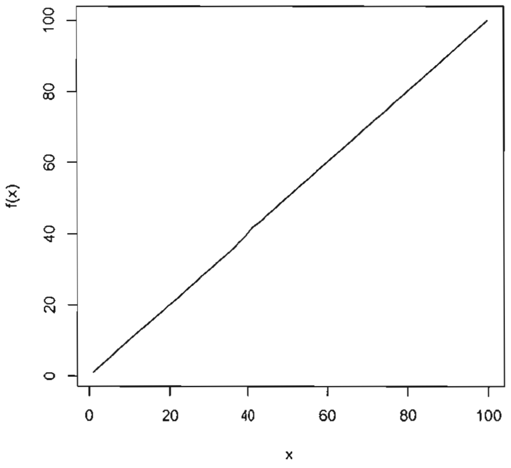


Figure 1.1 Type I functional response

A Type II functional response remains most popular among ecologists. A type II functional response is often called a disc equation because Holling used paper discs to simulate the area examined by predators. It assumes that a predator spends its time on two kinds of activities: (*i*) searching for prey and (*ii*) prey handling which includes: chasing, killing, eating and digesting. Consumption rate of a predator is limited in this model because even if prey are so abundant that no time is needed for search, a predator still needs to spend time on prey handling. The type II functional response is

$$f(x) = \frac{\beta x}{\omega + x}, \quad \omega > 0.$$

One can see that for x approaching to ∞, $f(x)$ tends to β. This means that a type II functional response remains bounded unlike a type I functional response, βx. Since $f(\omega) = \frac{\beta}{2}$, ω is referred to as half-capturing saturation constant.

This function indicates the number of prey killed by one predator at various prey population sizes and is a typical shape of functional response for many predator species. At low prey population sizes, predators spend most of their time on search, whereas at high prey population sizes, predators spend most of their time on prey handling (Figure 1.2).

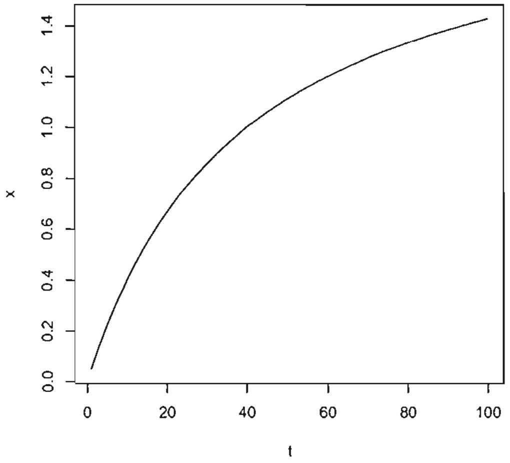


Figure 1.2 Type II functional response

A type III functional response occurs in predators which increase their search activity with increasing prey population size. For example, many predators respond to chemicals emitted by prey and increase their activity. Predator mortality increases first as prey population size increases, and then declines (Figure 1.3).

A type III functional response is the only type of functional response that allows prey mortality to increase with increasing prey population size. In this thesis, we only review

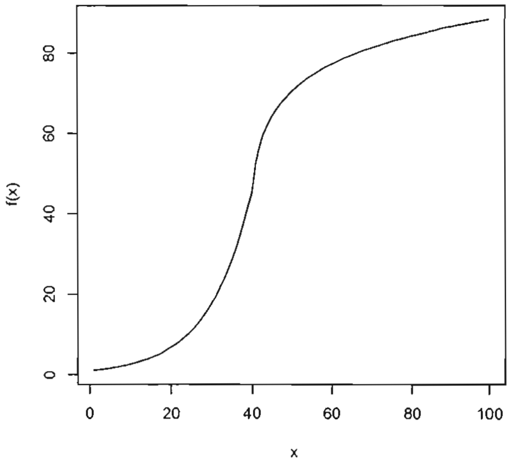


Figure 1.3 Type III functional response

a Holling model where the functional response is of type II. Holling (1959) explained the following disc equation for the functional response term,

$$f(x) = \frac{\beta x}{x + \omega},$$

where β is the maximum predator attack rate and ω is the prey population size where the attack is half-saturated. Therefore, Holling suggested the ODE system (1959)

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega}, \\ \frac{dy}{dt} = \frac{\gamma xy}{x + \omega} - \delta y, \end{cases} \tag{1.5}$$

where x and y are the prey and predator population sizes, respectively.

In the equations (1.5) the parameters are defined as follows:

K: carrying capacity of the prey population;

β: capturing rate, or search rate for predators, *i.e.* how effective the predators are;

ω: half-capturing saturation constant;

γ: conservation rate (predator birth rate);

δ: predators rate of death.

Further, we look at each equation separately. The prey equation is given by

$$\frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega}. \tag{1.6}$$

The prey is assumed to have an unlimited food supply, and to reproduce asymptotically unless subject to predation, *i.e.* in the absence of predation, $\beta = 0$. This asymptotic growth is represented by $\alpha x(1 - \frac{x}{K})$ in equation (1.6). The rate of predation upon prey is assumed to be proportional to the rate at which predator and prey meet. This is represented by $\frac{\beta xy}{x + \omega}$. If either x or y is zero then there can be no predation.

With these two terms, equation (1.6) can be interpreted as the change in the size of the prey population given by its own asymptotic growth minus the rate at which it is preyed upon. Finally, note that for very large carrying capacity, $K \to \infty$, the first term in equation (1.6) is identical to the first term in the classical Lotka-Volterra prey equation (1.1).

Further, consider the predator equation

$$\frac{dy}{dt} = \frac{\gamma xy}{x + \omega} - \delta y. \tag{1.7}$$

In this equation, $\frac{\gamma xy}{x + \omega}$ represents the growth of the predator population due to predation. (Note that the coefficient γ is not necessarily equal to the coefficient β.) In equation (1.7), δy represents the natural death of the predators which is an exponential decay as in the classical Lotka-Volterra system (1.1). Hence, equation (1.7) represents the change in the predator population as the growth of the predator population, minus natural death.

Depending on the domain of the parameters, the system of equations (1.5) admits periodic solutions in the limit, *i.e.* for $t \to \infty$, which do not have a simple, analytic expression (Kot, 2001). One such solution is given in figure 2.2.

1.2.3 Hanski System

There are several regional behavior and geographic variations which cannot be explained by the Holling system. Hanski *et al.* (1991) originally introduced a new model which tries to take into account these regional differences. In particular, Hanski model was meant to explain the interaction between microtine rodents and their predators in northern Europe (Hanski *et al.* 1991).

The system which is regarded as Hanski has several versions (Hanski *et al.* 1995). A class of models introduced in May (1973) by combining Leslie (1948) and Holling (1959) (see also Tanner 1975) was extensively studied by Hanski *et al.* (1991, 1995, 2001). In this thesis, we consider the following version

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x+\omega} \\ \frac{dy}{dt} = \gamma y(1 - \frac{\mu y}{x}) \end{cases} \tag{1.8}$$

In equations (1.8) the parameters are defined as follows:

K: carrying capacity of the prey population;

β: capturing rate, or search rate for predators, *i.e.* how effective the predators are;

ω: half-capturing saturation constant;

γ: conservation rate (predator birth rate);

δ: predators rate of death.

α: natural growth rate of prey in the absence of predator;

μ: reproduction rate per one prey eaten.

One can easily see that the prey equation given by

$$\frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x+\omega},$$

is identical to the one of the Holling model. Therefore, the same description presented for the Holling model is also valid here.

Further, the predator equation is described by

$$\frac{dy}{dt} = \gamma y - \gamma\mu\frac{y^2}{x}. \tag{1.9}$$

Mortality in the predator population is evidently related to the prey population size and is inversely proportional to it.

For specific types of predators, this model seems more appropriate than standard models such as Lotka-Volterra (Hanski 1999). However, this model holds a major shortcoming: the system is not well-defined when the environment does not contain any prey since the denominator of the predator equation (1.9) becomes zero, whereas in other models this problem does not occur. In other words, there is no way to quantify the behavior of the predator population in the absence of prey. One such solution is given in figure 2.3.

1.2.4 Arditi System

Although the inclusion of a more complex functional response $f(x)$ in the Holling and Hanski predator equation is intuitively appealing, there are some notable problems with this approach (Arditi and Ginzburg 1989). To overcome the problems, it was suggested that the functional response should be expressed in terms of the ratio of prey to predators (Jost and Arditi, 2001). Therefore, they defined the model as follows (Arditi *et al.* 2004)

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega y}, \\ \frac{dy}{dt} = \frac{\gamma xy}{x + \omega y} - \delta y. \end{cases} \tag{1.10}$$

or equivalently,

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta (x/y) y}{(x/y) + \omega}, \\ \frac{dy}{dt} = \frac{\gamma (x/y) y}{(x/y) + \omega} - \delta y. \end{cases}$$

We can note immediately the similarity with the Holling system where $f(x) = \frac{x}{x + \omega}$ is replaced by $f(x, y) = \frac{(x/y)}{(x/y) + \omega}$ and depends on the ratio x/y. Otherwise, the equations can be interpreted in a similar fashion.

Namely, the prey equation is defined as

$$\frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega y}, \tag{1.11}$$

where the production of prey in the absence of predators is described by $\alpha x(1 - \frac{x}{K})$, whereas $\frac{\beta x}{x + \omega y}$ is the functional response (number of prey eaten per predator unit per unit time.)

Besides, the predator equation becomes

$$\frac{dy}{dt} = \frac{\gamma xy}{x + wy} - \delta y. \tag{1.12}$$

Natural mortality of prey is considered to be negligible compared to mortality due to predation. The constant γ is the trophic efficiency, *i.e.* the ratio of predator population size level to the prey population size level, and predators are assumed to die with a constant death rate δ.

1.3 Concluding Remarks

In this chapter, four general predator-prey mathematical models, classical Lotka-Volterra, Holling, Hanski, and Arditi were briefly introduced. The Lotka-Volterra model assumes that the prey consumption rate of the predator is directly proportional to the prey abundance. This means that predator feeding is limited only by the amount of prey in the environment. While this may be realistic at low levels of prey population sizes, it is certainly an unrealistic assumption at high level of prey population sizes where predators are limited e.g. by time and digestive constraints. The need for a more realistic description of predator feeding came from an experimental work performed by Gause on predator-prey interactions (Kot, 2001). It was observed that to explain his experimental observations, the linear functional dependencies of the Lotka-Volterra model must be replaced by nonlinear functions.

Further, we introduced one of the original nonlinear models known as Holling. It incorporates the role of carrying capacity as an asymptote to the prey population size, which controls its maximum in the absence of predator. Moreover, a more complex functional response in the predator-prey interaction was introduced as a key step in improving the classical Lotka-Volterra model. Many questions in predator-prey theory revolve around the functional response. In the classical Lotka-Volterra model, the functional response is reduced to the form βx, while in the Holling model, the functional response becomes $\frac{\beta x}{x + \omega}$. Neither of these models explains searching for food efficiency since they do not actually depend on the predator population; they are of the form

$f = f(x)$. However, it was observed (Arditi *et al.* 2004) that changing the functional response to $f(x,y) = \dfrac{\beta(x/y)}{(x/y)+\omega}$ explains the searching efficiency more accurately. Moreover, a model by Hanski was introduced where the prey equation is identical to the one of Holling. Therefore, the same problem related to the functional response which appearing in the Holling model exists here as well. We also explained, another disadvantage in the Hanski predator equation regarding the situation where there is no prey in the environment.

In the next chapter, we proceed to performing an analysis of the dynamics on these four models.

CHAPTER II

DETERMINISTIC ANALYSIS

We start this chapter by studying the dynamical systems corresponding to equations (1.1), (1.5), (1.8), and (1.10). We introduce the concepts of equilibria and study their stability. This is motivated by the usual assumption that some equilibria indicate population extinction, while others correspond the averages of population sizes. Later in this chapter, we review the qualitative analysis of the aforementioned models with respect to their solution behavior. This includes identifying the equilibrium points and their stability.

We keep the technicalities to a minimum as we want to introduce only the elements of the qualitative analysis which are useful in the statistical development of Chapters 3 and 4. It should be mentioned that the concepts introduced in this chapter are presented mainly informally. We simply give the main ideas behind this type of analysis. For an extensive work on this issue one can refer to Hirsch and Smale (1974), Hirsch, Smale and Devaney (2004) and Kot (2001).

2.1 Dynamical systems

In this section, we introduce some key topics in dynamical systems, which are essential in the study of the behavior of the solutions of systems of ordinary differential equations (ODE) and, in particular, the predator-prey population models. We limit ourselves to planar systems only. (See figure 2.1 for the linear case.)

Let $F(x, y)$ and $G(x, y)$ be continuous real functions with continuous derivatives. An autonomous planar system is given by

$$\begin{cases} \frac{dx}{dt} = F(x,y), \\ \frac{dy}{dt} = G(x,y), \end{cases} \tag{2.1}$$

with the initial value (x_0, y_0). From now on, we limit ourselves to two dimensional systems of equations which represent a predator-prey system as a special case. A planar system can be either linear or nonlinear. An autonomous linear planar system is a system where F and G are linear functions, *i.e.*

$$\begin{cases} F(x,y) = ax + b, \\ G(x,y) = cx + d. \end{cases}$$

In this chapter, we look at the long term behavior of certain collection of solutions, *i.e.* namely for $t \to \infty$, and compare these behaviors via the qualitative analysis of the systems. This collection of representative solution curves (x_t, y_t) of the system (2.1) in $\mathbb{R}^2$ is called a phase plane (Hirsch, Smale and Devaney, 2004, p. 41).

Definition 2.1.1 Equlibrium *(Hirsch and Smale 1974, p. 22)*
Population equilibrium is an event when neither of the prey or predator population levels is changing. For the planar system (2.1) *this occurs when both* $F(x^*, y^*) = G(x^*, y^*) = 0$.

In this case, a solution reaching to (x^*, y^*) stays forever at (x^*, y^*).
The equilibrium point (x^*, y^*) is called non-trivial if $(x^*, y^*) \neq (0,0)$.
We are interested in studying the behavior of the solution around the equilibria of the planar system since equilibria play an important role in the theory of ODEs. There are different types of equilibria. However, we mention only those which play a role in our case. For an extensive study of equilibria, one can refer to Hirsch, Smale and Devaney (2004) p. 174.
An equilibrium is called stable if close by solutions stay close by for all future times. Stable focus is an example of a stable equilibrium where the solution stays near by the equilibrium if it is already near by (Figures 1.1 and 2.4). Moreover, a stable equilibrium

is asymptotically stable if the solution approaches the equilibrium in the long term. A classical example of an asymptotically stable equilibrium is a sink (or stable node), where the solution tends to the equilibrium in all directions and stays at the equilibrium for all times. An equilibrium that is not stable is called unstable. A common example of an unstable equilibrium is a source (or an unstable node) where the solution tends away from the equilibrium in all directions. A center is an unstable equilibrium where with a small perturbation it can either turn into a sink or a source. Another example of an unstable equilibrium is a saddle. Depending what direction the solution takes it could either converge to the saddle or diverge from it. Figure 2.1 indicates the six types of equilibrium points which occur in planar linear system.

Stability, limit sets and limit cycles (Kot, 2001 and Hirsch, Smale and Devaney, 2004 p. 227)

Consider the planar system of differential equations (2.1). A limit set is the set of points (x, y) where the solution curve (x_t, y_t) through some (x_0, y_0) accumulates on the point (x, y). If the solution (x_t, y_t) converges to a limit set and remains on that set, then we say that the solution of the system converges to a limit cycle (Figure 2.2). Note that limit cycles can be stable or unstable. For an unstable limit cycle, the periodic closed orbit can be lost if the initial value of the solution is perturbed even slightly. Therefore, it is essential to determine all possible limiting behaviors of solutions in the phase plane. Recall that we consider autonomous planar systems only. So, in this case, there is a classical result which settles the problem of the limiting behaviors.

Theorem 2.1.1 *Poincaré-Bendixon (Hirsch and Smale, 1974 p. 225)*
A nonempty, closed bounded limit set of the planar system of differential equations (2.1) that contains no equilibrium, is a closed orbit.

In other words, the Poincaré-Bendixon theorems states that the fate of any bounded solution of a differential equation is to converge to either an equilibrium point or to a

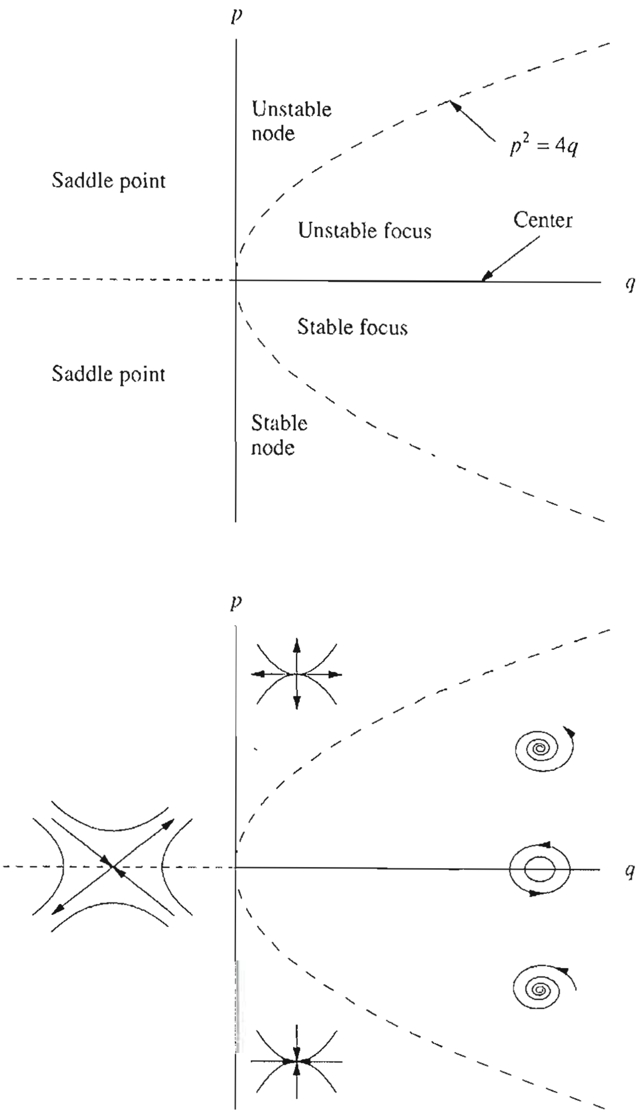


Figure 2.1 Classification of equilibria, linear systems - p: trace, q: determinant (figure courtesy of Kot, 2001)

limit cycle. Limit cycles can be interpreted as closed orbit attractors: there is an open set **O** of initial values (x_0, y_0) such that all solution starting in **O** will eventually lie on the limit cycle.

Consider the planar system of differential equations (2.1). As we said earlier, this sys-

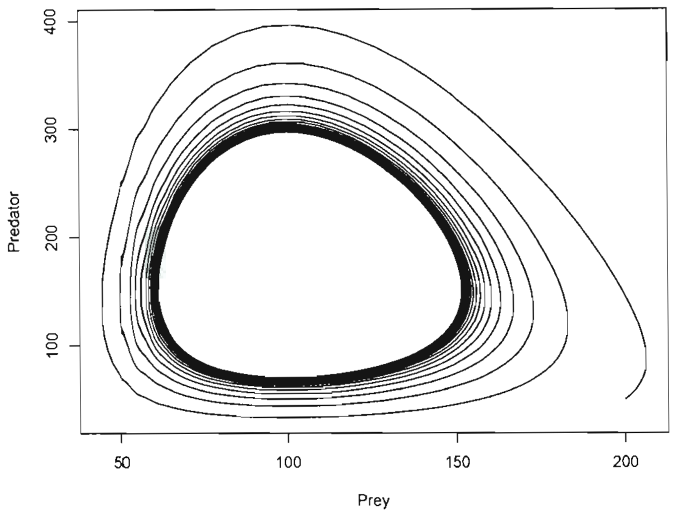


Figure 2.2 Example of limit cycle

tem can represent a predator-prey population dynamical system. Given the fact that in all discussed models the solutions stay in bounded regions, we can conclude that the solutions to Lotka-Volterra, Holling, Hanski, and Arditi systems all converge to either equilibrium points or to limit cycles.

Limit cycles may, in practice, lead to extinction due to environmental impacts (Hanski *et al.* 1995). A large limit cycle that periodically brings either population close to zero implies high probability of its extinction, if we consider possible external impacts that are not taken into account by the model (Berezovskaya *et al.* 2001). The importance of the existence of a limit cycle solution is in its periodic behavior.

Limit cycles can either consist of one or several periodic closed orbits (Figure 2.3). For example, in the Hanski Model, seasonal behaviors lead the population of prey and predators to converge to the summer and winter cycles. A more detailed description is given in Hanski and Kropimaki (1995).

Isocline (Hanski, 1999 and Hirsch, Smale and Devaney, 2004 p. 190)

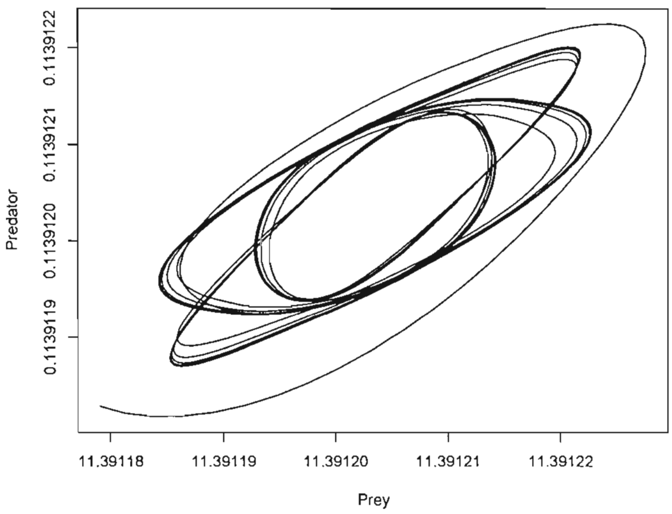


Figure 2.3 2-loop cycle

One of the most useful tools for analyzing nonlinear systems of differential equations (especially planar systems) are the isoclines. In population dynamics an isocline refers to the set of population sizes at which the rate of change, or derivative with respect to time, for one population in a pair of interacting populations is zero.

Isoclines can be used to find the equilibria of a system of differential equations. Since we are only discussing systems that include prey and predator interactions, *i.e.* two dimensional (two species) systems of differential equations, there are two isoclines for each model, which are called the prey isocline and the predator isocline. The prey isocline is defined where the rate of change for the prey population is zero. The predator isocline is instead satisfied when the rate of change for the predator population is zero.

The prey isocline is the non-trivial solution to the equation $dx/dt = 0$, whereas the predator isocline stands for the non-trivial solution to the equation $dy/dt = 0$.

It can be easily seen that the prey and predator isoclines for the Lotka-Volterra system are respectively the horizontal, the vertical lines, given by

$$y \equiv \frac{\alpha}{\beta}, \quad x \equiv \frac{\delta}{\gamma}.$$

The prey isoclines for the Holling and Hanski systems are identical to each other, since the prey equations for both models are identical. We can see that the prey isocline has the quadratic form

$$y = \frac{\alpha}{K\beta}(K - x)(x + \omega).$$

The Holling predator isocline is a vertical line

$$x = \frac{\omega\delta}{\gamma - \delta},$$

whereas the Hanski predator isocline is a line passing through the origin

$$y = \frac{1}{\mu}x.$$

The prey isocline for Arditi model is given by

$$y = \frac{\alpha x(1 - \frac{x}{K})}{\beta - \alpha\omega(1 - \frac{x}{K})},$$

while the Arditi predator isocline is a line passing through the origin given by

$$y = \frac{(\gamma - \delta)}{\omega\delta}x. \ .$$

In order to study the stability of equilibria and eventually find the limit cycles, we start by considering the linearized systems.

Linearization (Hirsch and Smale, 1974)

Linearization makes it possible to use tools for studying linear systems in order to analyze the behavior of a nonlinear function near a given point, which in our case is an equilibrium point. The stability of an equilibrium point can be determined by performing a linearization using partial derivatives about that equilibrium point.

Consider the system introduced in (2.1) and let (x_t, y_t) denote a solution. The linearization of a function is the first order term of its Taylor expansion around the point of interest e.g. the equilibrium point (x^*, y^*). The corresponding linearized system can be written as

$$\begin{cases} \frac{du}{dt} = \frac{\partial F}{\partial u}(x^*, y^*)u + \frac{\partial F}{\partial v}(x^*, y^*)v, \\ \frac{dv}{dt} = \frac{\partial G}{\partial u}(x^*, y^*)u + \frac{\partial G}{\partial v}(x^*, y^*)v, \end{cases}$$

where (u, v) is the new coordinate and $F(x^*, y^*) = G(x^*, y^*) = 0$. The above linear system of differential equations can be rewritten in the following matrix form

$$\begin{pmatrix} \frac{du}{dt} \\ \frac{dv}{dt} \end{pmatrix} = \begin{pmatrix} \frac{\partial F}{\partial u}(x^*) & \frac{\partial F}{\partial v}(y^*) \\ \frac{\partial G}{\partial u}(x^*) & \frac{\partial G}{\partial v}(y^*) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}.$$

Finding a detailed behavior of a nonlinear system is a case by case study. Still, the study of the linearization of a nonlinear system can give us ideas about the behavior of the nonlinear system.

In stability analysis, one can use the eigenvalues of the Jacobian matrix evaluated at an equilibrium point to determine the nature of that equilibrium. We can obtain the eigenvalues of the Jacobian matrix by solving the characteristic equation.

$$\det(J - \lambda I) = 0,$$

where J is 2×2 Jacobian matrix. Therefore, the characteristic equation is a polynomial equation of degree 2 which therefore has the roots λ_1 and λ_2 given by

$$\lambda_{1,2} = \frac{T \pm \sqrt{T^2 - 4D}}{2},$$

where D and T are the determinant and the trace of Jacobian matrix J evaluated at the equilibrium point (x^*, y^*).

We say that an equilibrium point (x^*, y^*) of a nonlinear system is hyperbolic if all of the eigenvalues of the Jacobian matrix J evaluated at (x^*, y^*) have nonzero real parts. Such equilibria are either stable or unstable (Hirsch and Smale, 1974 p. 187). Moreover, in a neighborhood of such equilibria, the nonlinear system has a similar behavior to the linearized one (Hirsch, Smale and Devaney, 2004 p. 168).

For non hyperbolic equilibria, not much can be derived from the linearized system, but there are other criteria for stability. For an extensive presentation of this issue, one can refer to Hirsch, Smale and Devaney (2004) p. 194.

Clearly, we are in the non-hyperbolic case if and only if one of the following conditions is s satisfied: (*i*) $T = 0$ and $D > 0$; (*ii*) $D = 0$. In case (*i*) the equilibrium is a center (for a linearized system) if $D > 0$. The nonlinear system may have or may not have a center in this case.

In what follows we check the signs of D and T in the hyperbolic case. Based on the Routh-Hurwitz stability criterion (Kot, 2001 p. 90 and Hirsch and Smale, 1974 p. 190), we have the following classification for the stability of hyperbolic equilibria:

(*i*) $D > 0$ and $T < 0$, *i.e.* both real parts of the eigenvalues of the characteristic equation are negative. We then have a sink which, as mentioned before, is an asymptotically stable equilibrium. Therefore, the solutions starting nearby the equilibrium tend towards it.

(*ii*) $D > 0$ and $T > 0$, *i.e.* both real parts of the eigenvalues of the characteristic equation are positive. In this case, the equilibrium is a source, which is an unstable equilibrium and the solutions tend away from it; therefore, this leaves open the possibility that there are solutions which spiral to a limit cycle; necessarily, as a corollary to the Poincaré-Bendixon theorem, this limit cycle must surround the equilibrium (Hirsch, Smale and Devaney, 2004 p. 229).

(*iii*) $D < 0$, *i.e.* the real part of one of the eigenvalues of the characteristic equation is positive and the other eigenvalue has a negative real part. We then have a saddle. In this case, the solutions tend toward the equilibrium along some curves of initial values, while along some other curves of initial values, the solutions tend away from the equilibrium, so a saddle is a highly unstable equilibrium.

In this thesis we are interested in systems of differential equations which admit limit cycles. However, there is no general criterion for the existence of a limit cycle for all cases. According to Hirsch, Smale and Devaney (2004) p. 217, one can summarize the behavior of planar systems as follows: a closed and bounded limit set other than a closed orbit is made up of equilibria and solutions joining them. A consequence of the Poincaré-Bendixon theorem is that if a closed and bounded limit set in the plane contains no equilibria, then it must be a closed orbit.

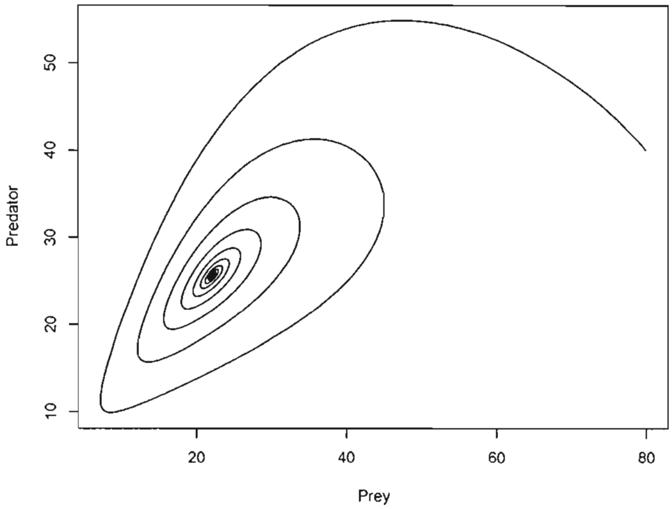


Figure 2.4 Stable equilibrium

2.2 Analysis of the Equilibria in Each Model

In this section, we use the dynamical systems and the theory stated in the previous section, to analyze the behavior of the equilibria of each predator-prey model introduced earlier. The goal is to identify sufficient conditions for the stability of the equilibria. Each model is discussed separately. It is important to note that any time we talk about stability, we mean stability of the equilibria, and therefore, the Routh-Hurwitz criterion is an appropriate tool to apply.

Let us note that our purpose is to give some elementary proofs. Otherwise, qualitative analyses exist in the literature, but they are very involved. Indeed, even for older models, full proofs were developed quite recently, with sophisticated mathematical tools. For example, the model of Lotka and Volterra was fully studied in Hirsch and Smale (1974), and a brief qualitative analysis of Holling's model can be found in Kot (2001). Hanski's model is studied numerically in Wollkind (1988) and Hanski *et al.* (1991), and a detailed phase portrait is done in Gasull *et al.* (1997) and Saez and Gonzales-Olivares (1999).

Qualitative analyses of Arditi's model are given in Jost *et al.* (1999) and Berezovskaya *et al.* (2001).

2.2.1 Lotka-Volterra Model

Recall that the classical Lotka-Volterra model is

$$\begin{cases} \frac{dx}{dt} = (\alpha - \beta y)x, \\ \frac{dy}{dt} = (\gamma x - \delta)y. \end{cases}$$

We now analyze the model starting with computing the equilibrium points. Lotka-Volterra predator-prey system of equations give

$$\begin{aligned} \frac{dx}{dt} &= 0 \Leftrightarrow (\alpha - \beta y)x = 0, \\ \frac{dy}{dt} &= 0 \Leftrightarrow (\gamma x - \delta)y = 0. \end{aligned}$$

The population level at this equilibrium depends on the values of the parameters α, β, δ, and γ.

It can be seen that $(x^*, y^*) = (0,0)$ is an equilibrium point. The other equilibrium can be determined by

$$(x^* = \frac{\delta}{\gamma}\ ;\ y^* = \frac{\alpha}{\beta}).$$

The Jacobian matrix of the predator-prey model can then be obtained by

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

Evaluated at the trivial equilibrium $(0,0)$ the Jacobian matrix becomes

$$J_{(0,0)} = \begin{pmatrix} \alpha & 0 \\ 0 & -\delta \end{pmatrix}.$$

We can see that the determinant of the Jacobian matrix evaluated at the trivial equilibrium is given by

$$\det(J_{(0,0)}) = -\alpha\delta,$$

which is always negative since, as mentioned before, all the coefficients are assumed to be positive.

Moreover, the trace of the Jacobian matrix evaluated at the equilibrium $(0,0)$ is

$$\mathrm{Tr}(J_{(0,0)}) = \alpha - \delta.$$

Note that according to the Routh-Hurwitz criterion, since $\det J_{(0,0)} < 0$, no matter what the sign of the trace of the Jacobian is, the trivial equilibrium is a saddle point. This means that if both population levels are at zero, then they will continue to be so, indefinitely. For more details refer to Kot (2001). However, the trivial equilibrium does not interest us. Therefore, we now study the stability of the non-trivial equilibrium point.

Evaluated at the non-trivial equilibrium (x^*, y^*), the Jacobian matrix J becomes

$$J_{(\frac{\delta}{\gamma},\frac{\alpha}{\beta})} = \begin{pmatrix} 0 & -\frac{\beta\delta}{\gamma} \\ \frac{\alpha\gamma}{\beta} & 0 \end{pmatrix}.$$

The determinant of the Jacobian matrix evaluated at the non-trivial equilibrium (x^*, y^*) is given by

$$\det(J_{(x^*,y^*)}) = \alpha\delta,$$

which is always positive.

Moreover, the trace of the Jacobian matrix evaluated at the non-trivial equilibrium (x^*, y^*) is

$$\mathrm{Tr}(J_{(x^*,y^*)}) = 0.$$

Therefore, according to the Routh-Hurwitz criterion, the non-trivial equilibrium is a center for the linearized system. Moreover, Hirsch and Smale (1974) show that it is also a center for the non-linear system. Thus, this second equilibrium point represents a fixed point at which both populations sustain their current behavior, indefinitely. In other words, the solutions are periodic and cycle around this equilibrium point.

The equilibrium point at the origin is a saddle point, and hence unstable, but we will find that the extinction of both species simultaneously is difficult to happen in the Lotka-Volterra model. In fact, this can only occur if the prey is artificially completely eradicated, causing the predator to die out of starvation. If the predator is eliminated, the prey population grows without bound in this simple model.

The Lotka-Volterra model shows that: (*i*) predators can control exponentially growing prey populations; (*ii*) both prey and predators can coexist indefinitely; (*iii*) the indefinite coexistence does not occur at equilibrium population, but along a population cycle.

2.2.2 Holling Model

Recall the Holling model

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x+\omega}, \\ \frac{dy}{dt} = \frac{\gamma xy}{x+\omega} - \delta y. \end{cases}$$

To perform its analysis, let us define

$$\begin{cases} f(x) = \frac{\beta x}{x+w}, \\ g(x) = \frac{\alpha}{K\beta}(K-x)(x+w), \end{cases} \tag{2.2}$$

and rewrite the Holling system as

$$\begin{cases} \frac{dx}{dt} = f(x)[g(x) - y], \\ \frac{dy}{dt} = \Lambda[f(x) - \Gamma]y, \end{cases}$$

where $\Lambda = \frac{\gamma}{\beta}$ and $\Gamma = \frac{\beta\delta}{\gamma}$.

The Jacobian matrix is given by

$$J_{(x,y)} = \begin{pmatrix} f'(x)[g(x) - y] + f(x)g'(x) & -f(x) \\ \Lambda y f'(x) & \Lambda[f(x) - \Gamma] \end{pmatrix}.$$

One can easily find the equilibrium points by solving the following equations

$$\begin{aligned} \frac{dx}{dt} = 0 &\Leftrightarrow \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x+\omega} = 0 \Leftrightarrow f(x)[g(x) - y] = 0, \\ \frac{dy}{dt} = 0 &\Leftrightarrow \frac{\gamma xy}{x+\omega} - \delta y = 0 \Leftrightarrow \Lambda[f(x) - \Gamma]y = 0. \end{aligned}$$

One of the equilibrium points is $(0,0)$, which implies $f(0) = 0$. Then, the Jacobian matrix evaluated at the equilibrium point $(0,0)$ is given by

$$J_{(0,0)} = \begin{pmatrix} \frac{\alpha}{\beta} & 0 \\ 0 & -\delta \end{pmatrix}.$$

Since $\det J_{(0,0)} < 0$, no matter what the sign of the trace would be, according to the Routh-Hurwitz criterion, this trivial equilibrium point is a saddle point.

Other equilibria can be determined by solving the system

$$\begin{aligned} &\alpha(1-\frac{x^*}{K}) - \frac{\beta y^*}{x^*+\omega} = 0, \\ &\frac{\gamma x^*}{x^*+\omega} - \delta = 0, \end{aligned} \tag{2.3}$$

which gives one point of coordinates

$$x^* = \frac{\delta\omega}{\gamma-\delta}; \quad y^* = \frac{\alpha\gamma\omega(K\gamma - K\delta - \delta\omega)}{K\beta(\gamma-\delta)^2}. \tag{2.4}$$

Moreover, it can be easily seen that

$$f(x^*) = \frac{\beta x^*}{x^*+\omega} = \frac{\delta\beta}{\gamma} = \Gamma. \tag{2.5}$$

Note that $f(x^*)$ and x^* cannot be 0. On the other hand, equations (2.2) and (2.3) imply that

$$f(x^*)(g(x^*) - y^*) = 0.$$

Therefore, we must have

$$g(x^*) = y^*. \tag{2.6}$$

The Jacobian matrix J evaluated at the equilibrium (2.4) is obtained by

$$J_{(x^*,y^*)} = \begin{pmatrix} f'(x^*)[g(x^*) - y^*] + f(x^*)g'(x^*) & -f(x^*) \\ \Lambda y^* f'(x^*) & \Lambda(f(x^*) - \Gamma) \end{pmatrix}. \tag{2.7}$$

Therefore, from (2.5), (2.6) and (2.7) it follows that the Jacobian matrix J evaluated at the second equilibrium point (x^*, y^*) is

$$J_{(x^*,y^*)} = \begin{pmatrix} f(x^*)g'(x^*) & -\Gamma \\ \Lambda y^* f'(x^*) & 0 \end{pmatrix} \tag{2.8}$$

Further, we apply the Routh-Hurwitz criterion, *i.e.* we study the signs of $\det(J_{(x^*,y^*)})$ and $\mathrm{Tr}(J_{(x^*,y^*)})$ to discuss the stability of this equilibrium, (x^*, y^*).

From (2.8) we see that

$$\mathrm{Tr}(J_{(x^*,y^*)}) = f(x^*)g'(x^*),$$

and

$$\det(J_{(x^*,y^*)}) = \Lambda\Gamma y^* f'(x^*).$$

In order to obtain the sign of the determinant of the Jacobian matrix evaluated at this equilibrium (x^*, y^*) we determine the derivative of f from (2.2) and we obtain

$$f'(x) = \frac{\beta w}{(x+w)^2} > 0.$$

Moreover, note that $\Gamma\Lambda > 0$. Therefore, $\det(J_{(x^*,y^*)}) > 0$ if and only if $g(x^*) = y^* > 0$. Let us assume that

$$\gamma - \delta > 0.$$

Therefore, equation (2.4) gives the following inequality as a sufficient condition for $y^* = g(x^*) > 0$,

$$K(\gamma - \delta) - \delta\omega > 0,$$

or equivalently,

$$\frac{K}{\omega} > \frac{\delta}{\gamma - \delta}, \tag{2.9}$$

which is, consequently, a necessary and sufficient condition for the determinant of the Jacobian matrix evaluated at the second equilibrium to be positive.

Moreover, from (2.2),

$$g(x) = \frac{\alpha}{K\beta}\big[-x^2 + (K-\omega)x + K\omega\big],$$

which implies that

$$g'(x) = -\frac{2\alpha}{K\beta}x + \Big(\frac{\alpha}{\beta} - \frac{\alpha\omega}{K\beta}\Big) = \frac{\alpha}{\beta}\Big[-\frac{2x}{K} - \frac{\omega}{K} + 1\Big].$$

Hence, it can be seen that at the equilibrium point (2.4)

$$g'(x^*) = \frac{\alpha}{\beta}\Big[\frac{-2\delta\omega}{K(\gamma-\delta)} - \frac{\omega}{K} + 1\Big].$$

Note that $\mathrm{Tr}(J_{(x^*,y^*)}) > 0$ if and only if $g'(x^*) > 0$, since $f(x^*) > 0$.

A simple calculation shows that $g'(x^*) > 0$ if and only if

$$K(\gamma - \delta) - \omega(\gamma + \delta) > 0.$$

Since we assume that

$$\gamma - \delta > 0.$$

We obtain

$$\frac{K}{\omega} > \frac{\gamma}{\gamma - \delta} + \frac{\delta}{\gamma - \delta}.$$

Hence, a sufficient condition for the existence of an unstable equilibrium is

$$\gamma - \delta > 0$$

and

$$\frac{K}{\omega} > \frac{\gamma}{\gamma - \delta} + \frac{\delta}{\gamma - \delta}.$$

Moreover, $\mathrm{Tr}(J_{(x^*,y^*)}) < 0$ if and only if $g'(x^*) < 0$ or equivalently,

$$\gamma - \delta > 0$$

and

$$\frac{K}{\omega} < \frac{\gamma}{\gamma - \delta} + \frac{\delta}{\gamma - \delta}.$$

This condition, along with inequality (2.9) determines the following sufficient condition for the stability of the solution.

$$\frac{\delta}{\gamma - \delta} < \frac{K}{\omega} < \frac{\gamma}{\gamma - \delta} + \frac{\delta}{\gamma - \delta},$$

when

$$\gamma - \delta > 0 \qquad .$$

Additionally, if

$$\frac{K}{\omega} < \frac{\delta}{\gamma - \delta}$$

then $J_{(x^*,y^*)} < 0$.

This indicates that (x^*, y^*) is a saddle point. Finally,

$$\frac{K}{\omega} = \frac{\delta}{\gamma - \delta} + \frac{\gamma}{\gamma - \delta}$$

given that $\gamma > \delta$ implies that $J_{(x^*,y^*)} > 0$ and $\mathrm{Tr}(J_{(x^*,y^*)}) = 0$, which indicates that the equilibrium (x^*, y^*) is a center for the linearized system. To conclude, we found a sufficient condition for existence of an unstable equilibrium, which is not a saddle. Therefore, by theorem 2.1.1, the limit sets could be limit cycles around the equilibrium (x^*, y^*) when the parameters satisfy the above condition.

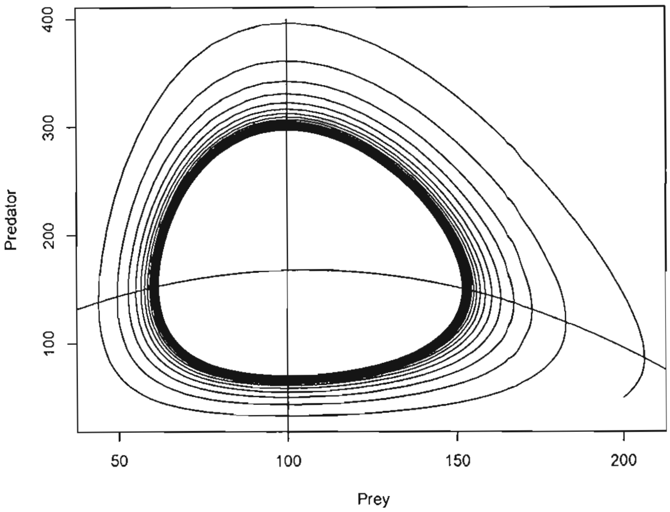


Figure 2.5 A stable solution for Holling Model: The model parameters are $\alpha = 0.1$; $K = 250$; $\beta = 0.05$; $\omega = 40$; $\gamma := 0.7$; $\delta = 0.5$.

2.2.3 Hanski Model

Recall that the Hanski model was defined by

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega}, \\ \frac{dy}{dt} = \gamma y(1 - \frac{\mu y}{x}). \end{cases}$$

The equilibrium points can be obtained by solving

$$\begin{aligned} \frac{dx}{dt} &= 0 \Leftrightarrow \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega} = 0, \\ \frac{dy}{dt} &= 0 \Leftrightarrow \gamma y(1 - \frac{\mu y}{x}) = 0. \end{aligned} \tag{2.10}$$

It can be seen that $(0, 0)$ is an equilibrium point for the Hanski model. However, like in the Holling case, we are only interested in the non-trivial equilibria. The equation corresponding to the prey in (2.10) implies that such an equilibrium satisfies

$$y^* = \frac{\alpha}{\beta}(1 - \frac{x^*}{K})(x^* + \omega), \tag{2.11}$$

whilst the predator equation in (2.10) can be reduced to

$$y^* = \frac{1}{\mu}x^*. \tag{2.12}$$

Therefore, one can determine the non-trivial equilibrium points by intersecting the two isoclines, and obtain

$$x^* = \frac{(K\alpha\mu - \alpha\mu\omega - K\beta) \pm \sqrt{(K\alpha\mu - \alpha\mu\omega - K\beta)^2 + 4\alpha^2\mu^2 K\omega}}{2\alpha\mu},$$

and

$$y^* = \frac{(K\alpha\mu - \alpha\mu\omega - K\beta) \pm \sqrt{(K\alpha\mu - \alpha\mu\omega - K\beta)^2 + 4\alpha^2\mu^2 K\omega}}{2\alpha\mu^2}.$$

Note that the term inside the square root is always non-negative. Hence, all the equilibrium points are real-valued. Moreover, we are only interested in the equilibrium in the first quadrant of the phase place, *i.e.* we look for $(x^*, y^*) > (0, 0)$. Therefore, the only admissible solution is

$$\begin{aligned} x^* &= \frac{(K\alpha\mu - \alpha\mu\omega - K\beta) + \sqrt{(K\alpha\mu - \alpha\mu\omega - K\beta)^2 + 4\alpha^2\mu^2 K\omega}}{2\alpha\mu}; \\ y^* &= \frac{(K\alpha\mu - \alpha\mu\omega - K\beta) + \sqrt{(K\alpha\mu - \alpha\mu\omega - K\beta)^2 + 4\alpha^2\mu^2 K\omega}}{2\alpha\mu^2}. \end{aligned} \tag{2.13}$$

Further, define the function

$$g(x) = \frac{\beta}{x + \omega}. \tag{2.14}$$

The derivative of g with respect to x is given by

$$g'(x) = -\frac{\beta}{(x + \omega)^2} = -\frac{1}{\beta}g^2(x). \tag{2.15}$$

Therefore, it can be seen that at the non-trivial equilibrium (x^*, y^*)

$$g'(x^*) = -\frac{\beta}{(x + \omega)^2} = -\frac{1}{\beta}g^2(x^*). \tag{2.16}$$

According to the Routh-Hurwitz criterion, an unstable equilibrium (x^*, y^*) occurs when both the determinant and the trace of the Jacobian matrix J evaluated at the equilibrium (x^*, y^*) are positive. Moreover, the equilibrium point is asymptotically stable if the Jacobian matrix J evaluated at the equilibrium (x^*, y^*) is positive and the trace of J evaluated at (x^*, y^*) is negative. The Jacobian matrix is given by

$$J_{(x,y)} = \begin{pmatrix} \alpha - 2\alpha x/K - yg(x) - xyg'(x) & -xg(x) \\ \mu\gamma y^2/x^2 & \gamma - 2\gamma\mu y/x \end{pmatrix}.$$

The Jacobian J evaluated at (x^*, y^*) using (2.11) is given by

$$J_{(x^*,y^*)} = \begin{pmatrix} \alpha - 2\alpha x^*/K - x^*g(x^*)/\mu - (x^*)^2g'(x^*)/\mu & -x^*g(x^*) \\ \gamma/\mu & -\gamma \end{pmatrix} \tag{2.17}$$

From(2.17), the determinant of J evaluated at (x^*, y^*), by using (2.17), is determined by

$$\det(J_{(x^*,y^*)}) = -\alpha\gamma + 2\frac{\alpha\gamma}{K}x^* + 2\frac{\gamma}{\mu}x^*g(x^*) - \frac{\gamma}{\beta\mu}(x^*)^2g^2(x^*). \tag{2.18}$$

On the other hand, by inserting y^* obtained from (2.12) into (2.11) we can write

$$x^*g(x^*) = \alpha\mu(1 - \frac{x^*}{K}). \tag{2.19}$$

Further, insert (2.19) into equation (2.18). We obtain

$$\det(J_{(x^*,y^*)}) = -\alpha\gamma + \frac{2\alpha\gamma}{K}x^* + 2\alpha\gamma(1 - \frac{x^*}{K}) - \frac{\alpha\gamma}{\beta}(\alpha\mu)(1 - \frac{x^*}{K}).$$

Finally, after reducing the terms we can see that

$$\det(J_{(x^*,y^*)}) = \alpha\gamma[1 - \frac{\alpha\mu}{\beta}(1 - \frac{x^*}{K})^2]. \tag{2.20}$$

It remains to check the sign of $\det(J_{(x^*,y^*)})$. First, we prove that $x^* < K$. Indeed we can see that

$$(\alpha\mu K - \alpha\mu\omega - \beta K)^2 + 4\alpha^2\mu^2\omega K < (\alpha\mu K + \alpha\mu\omega + \beta K)^2 \Leftrightarrow$$
$$(\alpha\mu K - \alpha\mu\omega - \beta K) + \sqrt{(\alpha\mu K - \alpha\mu\omega\beta K)^2 + 4\alpha^2\mu^2\omega K} < 2\alpha\mu K,$$

which is valid if and only if

$$x^* < K.$$

Therefore, we have

$$0 < (1 - \frac{x^*}{K})^2 < 1.$$

Now we return to signs of the determinant. The determinant of the Jacobian matrix evaluated at the non-trivial equilibrium (2.13) is positive if

$$1 - \frac{\alpha\mu}{\beta} > 0,$$

according to (2.20). Therefore, a sufficient condition for the determinant to be positive is given by

$$\beta > \alpha\mu. \tag{2.21}$$

We now evaluate the trace of the Jacobian (2.17).

$$\mathrm{Tr}(J_{x^*,y^*}) = \alpha - \frac{2\alpha}{K}x^* - \frac{1}{\mu}x^* g(x^*) - \frac{1}{\mu}(x^*)^2 g'(x^*) - \gamma. \tag{2.22}$$

We can simplify the above equation by using (2.16) and (2.19). It can be then seen that

$$\mathrm{Tr}(J_{x^*,y^*}) = \frac{\alpha^2\mu}{\beta}(1 - \frac{x^*}{K})^2 - \frac{\alpha}{K}x^* - \gamma.$$

We previously showed that

$$(1 - \frac{x^*}{K})^2 < 1.$$

Therefore, the following inequality satisfies

$$\mathrm{Tr}(J_{x^*,y^*}) < \frac{\alpha^2\mu}{\beta} - \frac{\alpha}{K}x^* - \gamma.$$

If we assume that equation (2.21) is satisfied, then not only, as shown before, is the determinant positive but also

$$\mathrm{Tr}(J_{x^*,y^*}) < \alpha - \frac{\alpha}{K}x^* - \gamma \Leftrightarrow \mathrm{Tr}(J_{x^*,y^*}) < \alpha(1 - \frac{x^*}{K}) - \gamma,$$

which implies that

$$\mathrm{Tr}(J_{x^*,y^*}) < \alpha - \gamma.$$

Therefore, the trace of the Jacobian matrix evaluated at the non-trivial equilibrium (2.13) is negative if

$$\alpha\mu < \beta \text{ and } \alpha < \gamma. \tag{2.23}$$

Condition (2.23) is sufficient for the asymptotic stability of the equilibrium point (2.13), since the first condition in (2.23) guarantees that the determinant is positive. In other cases, e.g. when either $\alpha\mu > \beta$ or $\alpha > \gamma$, and the equilibrium is unstable, limit cycles can occur.

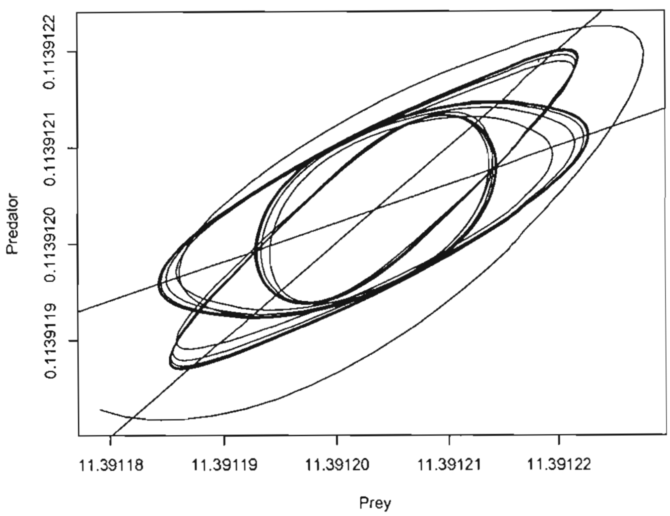


Figure 2.6 Limit cycle for the Hanski Model: the model parameters are $\alpha = 5.4$; $K = 50$; $\beta = 600$; $\omega = 5$; $\gamma = 2.8$; $\mu = 100$.

2.2.4 Arditi Model

Recall that the Arditi model was introduced as

$$\begin{cases} \frac{dx}{dt} = \alpha x(1-\frac{x}{k}) - \frac{\beta xy}{x+\omega y}, \\ \frac{dy}{dt} = \frac{\gamma xy}{x+\omega y} - \delta y. \end{cases}$$

In this model, the equilibrium points (x^*, y^*) can be obtained by

$$\begin{aligned} \frac{dx}{dt} &= 0 \Leftrightarrow \alpha x(1-\frac{x}{k}) - \frac{\beta xy}{x+\omega y} = 0, \\ \frac{dx}{dt} &= 0 \Leftrightarrow \frac{\gamma xy}{x+\omega y} - \delta y = 0. \end{aligned} \tag{2.24}$$

It can be seen that $(0,0)$ is an equilibrium point. However, just like in the Hanski model, Arditi predator-prey population system does not hold 0 as population size for either the prey or the predator since the denominator of both the prey and the predator equations become 0.

The non-trivial equilibrium points occur when

$$\alpha(1-\frac{x^*}{K}) - \frac{\beta y^*}{x^*+\omega y^*} = 0 \tag{2.25}$$

and

$$\frac{\gamma x^*}{x^* + \omega y^*} - \delta = 0.$$

The later equality implies that

$$y^* = (\frac{\gamma - \delta}{\omega\delta})x^*. \tag{2.26}$$

The non-trivial equilibrium points can be derived by solving (2.25) and(2.26). For example, we insert first y^* from (2.26) into (2.25) and solve for x^*. The values are given by

$$\begin{cases} x^* = K[1 - \frac{\beta}{\alpha\omega}(1 - \frac{\delta}{\gamma})], \\ y^* = \frac{K}{\omega}(\frac{\gamma}{\delta} - 1)[1 - \frac{\beta}{\alpha\omega}(1 - \frac{\delta}{\gamma})]. \end{cases} \tag{2.27}$$

Define the ratio

$$R = \frac{(\gamma - \delta)}{\gamma} = 1 - \frac{\delta}{\gamma}, \tag{2.28}$$

and note that

$$\frac{1}{1 - R} = \frac{\gamma}{\delta}.$$

Moreover, one can easily see that

$$\frac{R}{(1 - R)} = \frac{\gamma - \delta}{\delta} \times \frac{\gamma}{\delta} = \omega\frac{y^*}{x^*}.$$

Additionally, we define

$$g(x, y) = \frac{xy}{x + \omega y}, \tag{2.29}$$

and we rewrite (2.24) as

$$\begin{cases} \alpha x(1 - \frac{x}{K}) - \beta g(x, y) = 0, \\ \gamma g(x, y) - \delta y = 0. \end{cases}$$

The first partial derivatives of $g(x, y)$ with respect to x and y are

$$\begin{aligned} g_x(x, y) &= \frac{\omega}{(x/y + \omega)^2}, \\ g_y(x, y) &= \frac{1}{(1 + \omega y/x)^2}. \end{aligned}$$

Using equation (2.26) and (2.28) we can evaluate the above derivatives at the equilibrium point (2.27) and obtain

$$\begin{cases} g_x(x^*, y^*) = \frac{R^2}{\omega} \\ g_y(x^*, y^*) = (1 - R)^2. \end{cases} \tag{2.30}$$

Therefore, we can see that the Jacobian matrix of the system is

$$J = \begin{pmatrix} \alpha - 2\alpha x/K - \beta g_x(x,y) & -\beta g_y(x,y) \\ \gamma g_x(x,y) & \gamma g_y(x,y) - \delta \end{pmatrix}.$$

The determinant of the Jacobian matrix evaluated at the equilibrium point (x^*, y^*) is given by

$$\det(J_{(x^*,y^*)}) = -\alpha\delta + 2\alpha\delta\frac{x^*}{K} - 2\alpha\gamma\frac{x^*}{K}g_y(x^*,y^*) + \alpha\gamma g_y(x^*,y^*) + \beta\delta g_x(x^*,y^*).$$

Let now define

$$Z = \frac{1}{\delta}\det(J_{(x^*,y^*)}).$$

Then by using (2.27) and (2.28), we can see that

$$Z = -\alpha + 2\alpha\big[1 - \frac{\beta R}{\alpha\omega}\big] - 2\frac{\alpha\gamma}{\delta}\big[1 - \frac{\beta R}{\alpha\omega}\big]g_y^* + \beta g_x^* + \frac{\alpha\gamma}{\delta}g_y^*,$$

where $g_x^* = g(x^*, y^*)$ and $g_y^* = g(x^*, y^*)$. Finally, by substituting g_x^* and g_y^* from (2.30) we can write

$$Z = (\alpha - \frac{\beta}{\omega}R)R. \tag{2.31}$$

Note that $\text{sign}(\det(J_{(x^*,y^*)})) = \text{sign}(Z)$, since $\delta > 0$.

Moreover, the trace of the Jacobian matrix evaluated at the non-trivial equilibrium (2.28) is

$$\text{Tr}(J_{(x^*,y^*)}) = \alpha - \frac{2\alpha}{K}x^* - \beta g_x^* + \gamma g_y^* - \delta.$$

Then we can use (2.27) and (2.30) to obtain

$$\text{Tr}(J_{(x^*,y^*)}) = \alpha - 2\alpha(1 - \frac{\beta}{\alpha\omega}R) - \frac{\beta}{\omega}R^2 + \delta[\frac{\gamma}{\delta}(1-R)^2 - 1].$$

Therefore,

$$\text{Tr}(J_{(x^*,y^*)}) = -\alpha + \frac{2\beta}{\omega}R - \frac{\beta}{\omega}R^2 - \delta R. \tag{2.32}$$

We study the stability of the equilibrium (x^*, y^*) by discussing all possible cases for the signs of the determinant (2.31) and the trace (2.32).

Suppose first that $\gamma < \delta$, or equivalently, $R < 0$. Hence, equation (2.31) implies that

$\det(J_{(x^*,y^*)}) < 0$. Therefore, no matter what the sign of $\mathrm{Tr}(J_{(x^*,y^*)})$ would be, the equilibrium (x^*, y^*) is a saddle.

Alternatively, suppose that $\gamma > \delta$, or equivalently, $R > 0$. Then, there are two possibilities: the first case is

$$\alpha - \frac{\beta}{\omega}R < 0 \Leftrightarrow \alpha - \frac{\beta}{\omega}.\frac{(\gamma-\delta)}{\delta} < 0.$$

In this case, equation (2.31) implies that $\det(J_{(x^*,y^*)}) < 0$, which means that the equilibrium (x^*, y^*) is a saddle point.

We can therefore conclude that the equilibrium is a saddle point if

$$\text{either } \gamma < \delta \text{ or } 0 < \frac{\alpha}{1-(\delta/\gamma)} < \frac{\beta}{\omega}, \tag{2.33}$$

since $\alpha > 0$ and $1 - \frac{\delta}{\gamma} > 0$.

The other case is when

$$\alpha - \frac{\beta}{\omega}R > 0,$$

or equivalently,

$$0 < \frac{\beta}{\omega}R < \alpha, \tag{2.34}$$

which implies that $\det(J_{(x^*,y^*)}) > 0$.

Suppose (2.34) holds. From (2.32) we can obtain the inequality

$$\mathrm{Tr}(J_{(x^*,y^*)}) < \frac{\beta}{\omega}R(1 - R - \frac{\delta\omega}{\beta}) = \frac{\beta}{\omega}\delta R(\frac{1}{\gamma} - \frac{\omega}{\beta}).$$

Therefore, $\mathrm{Tr}(J_{(x^*,y^*)}) < 0$ if $(\frac{1}{\gamma} - \frac{\omega}{\beta}) < 0$ since we assumed that $R > 0$. Hence, a sufficient condition for the asymptotical stability of the equilibrium is

$$\delta < \gamma \text{ and } \frac{\beta}{\omega} < \gamma,$$

or equivalently, by (2.33)

$$\delta < \gamma \text{ and } \frac{\beta}{\omega} < \frac{\alpha}{1-(\delta/\gamma)}.$$

Finally, given that $\delta < \gamma$ and (2.34) are satisfied, we propose looking for a sufficient condition for the equilibrium to be unstable.

Since $R < 1$, we have

$$\mathrm{Tr}(J_{(x^*,y^*)}) > -\alpha + \frac{2\beta}{\omega}R - \frac{\beta}{\omega}R^2 - \delta R^2,$$

Then after reducing the terms, we have

$$\mathrm{Tr}(J_{(x^*,y^*)}) > -\alpha - \delta + \frac{\beta}{\omega}R(2-R),$$

In order to have an unstable equilibrium, according to the Routh-Hurwitz criterion, we must have $\mathrm{Tr}(J_{(x^*,y^*)}) > 0$ and $\det(J_{(x^*,y^*)}) > 0$. We have shown that for

$$0 < \frac{\beta R}{\omega} < \alpha,$$

and

$$\gamma - \delta > 0,$$

the determinant of the Jacobian matrix evaluated at the equilibrium (x^*, y^*) is positive. In order to have $\mathrm{Tr}(J_{(x^*,y^*)}) > 0$ it suffices to require that

$$-\alpha - \delta + \frac{\beta}{\omega}R(2-R) > 0,$$

or equivalently,

$$\frac{\beta}{\omega}R > \frac{\alpha+\delta}{2-R}.$$

Further, replace R from (2.28) and use (2.34) to reduce the above relations.

$$\frac{\alpha+\delta}{(1+\delta/\gamma)(1-\delta/\gamma)} < \frac{\beta}{\omega} < \frac{\alpha}{1-\delta/\gamma} \Leftrightarrow$$
$$\frac{\alpha+\delta}{2-T} < \frac{\beta}{\omega}T < \alpha.$$

In other words,

$$\frac{\alpha+\delta}{(1+\delta/\gamma)(1-\delta/\gamma)} < \frac{\beta}{\omega} < \frac{\alpha+\alpha\delta/\gamma}{(1-\delta/\gamma)(1+\delta/\gamma)},$$

is a sufficient condition for the equilibrium point (x^*, y^*) to be unstable. Note that this condition cannot be satisfied if $\alpha < \gamma$.

The complete analysis of this system is done in Berezovskaya *et al.* (2001). In fact, these authors find a domain in $(\alpha, \beta, \delta, \gamma, \omega, K)$ where the system admits a limit cycle.

2.3 Final Comments

In this chapter, the dynamical systems of four general predator-prey mathematical models known as classical Lotka-Volterra, Holling, Hanski, and Arditi were studied.

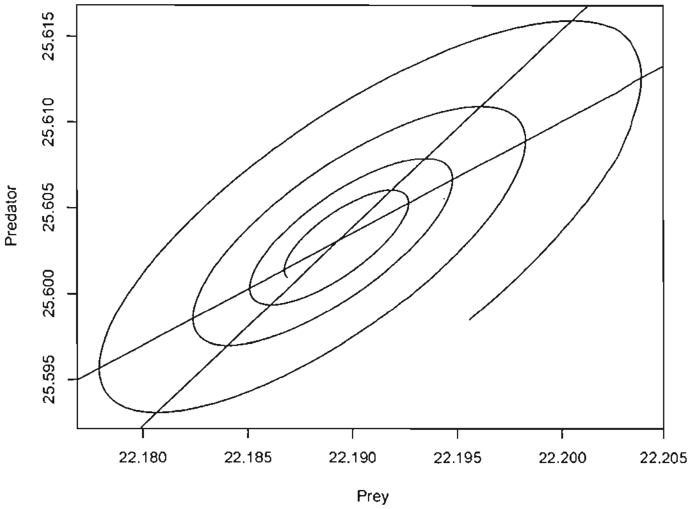


Figure 2.7 A stable solution for Arditi Model: The model parameters are $\alpha = 0.065$; $K = 150$; $\beta = 0.12$; $\omega = 1.3$; $\gamma = 0.060$; $\delta = 0.024$.

According to the Poincaré-Bendixon theorem we know that each system solution can possibly converge to a limit cycle or an equilibrium.

The complete analysis of these systems goes beyond the scope of this thesis. What we can provide here are the equations of the isoclines and of the non-trivial equilibria which are at the core of our inference method. Moreover, the linearized analysis allows us to point out subdomains of the parameters where limit cycles can occur. These are the subdomains that mainly interest us. A final issue concerns the following concept.

Definition 2.3.1 *Suppose* (x_t, y_t) *is a periodic solution to a dynamical system* (2.1).
The prey extremum is the set of all points $(\check{x}, \check{y})$ *where* $(\check{x}, \check{y}) \in \{(x_t, y_t)\}$ *and* $\check{x}$ *is the maximum or minimum value of* x_t *in some period.*
The predator extremum is the set of all points $(\check{x}, \check{y})$ *where* $(\check{x}, \check{y}) \in \{(x_t, y_t)\}$ *and* $\check{y}$ *is the maximum or minimum value of* y_t *in some period.*

Since the prey extremum takes place if $dx/dt = 0$, one can conclude that the prey isocline lies on the prey extremum. Moreover, since the predator extremum occurs if $dy/dt = 0$, it can be seen that the predator isocline lies on the predator extremum. Furthermore, for all four models discussed in this thesis, the prey and predator extremum sets exist and are non-empty. Furthermore, suppose that for a fixed s, $(\check{x}_s, \check{y}_s)$ belongs to the prey extremum set of the periodic solution (x_t, y_t) with period τ. Then $(\check{x}_{s+\tau}, \check{y}_{s+\tau})$ also belongs to the prey extremum. The same argument is also valid for any point belonging to the predator extremum set. Therefore, knowing only one point of the predator-prey extremum sets and the period of a given solution, one can obtain the predator-prey extremum sets. In the next chapter, we will show how to use the predator-prey extremum sets to estimate the predator-prey isoclines.

CHAPTER III

STOCHASTIC MODELS AND STATISTICAL INFERENCE

In the previous chapter we showed that the prey and the predator isoclines lie on the prey and the predator extremum sets, respectively. Therefore, if we consider to have a model with its respective extremum sets, we can use linear model techniques such as Ordinary Least Squares (OLS) to estimate the coefficients of the corresponding isoclines. On the other hand, by using different fitting tests such as the F-test, the t-test or the Wilcoxon test, one can compare the models through their isoclines. The key point in this comparison is that the prey and the predator isoclines of the four discussed models are different from each other: the predator-prey isoclines of the classical Lotka-Volterra model are a vertical line and a horizontal line, respectively; as for the Holling model, the predator-prey isoclines pair is a vertical line and a quadratic curve, respectively; whereas the Hanski predator-prey isolines are a straight line with a positive slope and a quadratic curve, respectively; and finally, the predator-prey isoclines of the Arditi model are different from the others. These differences could help us identify the model which can be fitted to a given pair of extremum sets, and further, predict a solution that corresponds to a given data set.

We start this chapter by proposing and studying the properties of four discussed stochastic models. Further on, we demonstrate how to estimate the coefficients of the isoclines. In the end, by using various types of testing techniques, we suggest a procedure for choosing a specific model.

3.1 Stochastic Models

Suppose $\mathfrak{A}$ is the set of pairs of the predator-prey population sizes observed at time t, $t > 0$. Furthermore, suppose that x_t and y_t represent the maximum and the minimum prey and predator population sizes at each period. It turns out that we can estimate the parameters fairly easily if we consider the model

$$\begin{cases} \log X_t = \log x_t + \epsilon_{X,t}, \\ \log Y_t = \log y_t + \epsilon_{Y,t}, \end{cases} \tag{3.1}$$

where X_t and Y_t are the observed prey and predator population sizes in $\mathfrak{A}$, respectively. The measurement errors $\epsilon_{X,t}$ and $\epsilon_{Y,t}$ are assumed to be independent standard normal random variables that are symmetrically distributed around zero, *i.e.* $\epsilon_{X,t} \sim \mathrm{N}(0, \sigma_X^2)$ and $\epsilon_{Y,t} \sim \mathrm{N}(0, \sigma_Y^2)$. The assumption that the errors with expectation zero act additively on the logarithm of the population sizes conceptually makes sense since x_t and y_t are both intrinsically positive. Therefore, $\log x_t$ and $\log y_t$ which appeared in (3.1) are in fact deterministic functions which correspond to the expectations of the observations $\log X_t$ and $\log Y_t$, respectively. Moreover, from (3.1) one obtains

$$\begin{cases} E[X_t] = x_t E[\exp(\epsilon_{X,t})], \\ E[Y_t] = y_t E[\exp(\epsilon_{Y,t})]. \end{cases} \tag{3.2}$$

Let $x_t \equiv x$, $y_t \equiv y$, $X_t \equiv X$ and $Y_t \equiv Y$. Note that $E[\exp(\epsilon_X)]$ and $E[\exp(\epsilon_Y)]$ are the respective moment generating functions of ϵ_X and ϵ_Y evaluated at $k = 1$. It is known that

$$\begin{aligned} E[\exp(\epsilon_{X,t})] &= \int_{-\infty}^{\infty} \frac{1}{\sigma_X \sqrt{2\pi}} \exp(-\frac{(x-\mu)^2}{2\sigma_X^2}) \exp(x) dx \\ &= \exp(\mu + \frac{\sigma_X^2}{2}). \end{aligned}$$

Given that $\mu = 0$ one can conclude that

$$E[\exp(\epsilon_{X,t})] = \exp(\sigma_X^2/2). \tag{3.3}$$

Similarly we have

$$E[\exp(\epsilon_{Y,t})] = \exp(\sigma_Y^2/2). \tag{3.4}$$

We also need to evaluate

$$E[\exp(2\epsilon_{X,t})] = \exp(2\sigma_X^2), \tag{3.5}$$

Therefore, the equations in (3.2) can be rewritten as

$$\begin{cases} E[X_t] = x_t \exp(\sigma_X^2/2), \\ E[Y_t] = y_t \exp(\sigma_Y^2/2). \end{cases} \tag{3.6}$$

We now use model (3.1) to study the four stochastic models we proposed earlier. In what follows, let

$$\begin{cases} I_X = \{t \mid dx/dt = 0\}, \\ I_Y = \{t \mid dy/dt = 0\}. \end{cases} \tag{3.7}$$

Therefore, the pairs (x_t, y_t), $t \in I_X$ correspond to the prey extremum set and (x_t, y_t), $t \in I_Y$ correspond to the predator extremum set.

3.1.1 Lotka-Volterra Model

Recall that the periodic two species classical Lotka-Volterra system is given by

$$\begin{cases} \frac{dx}{dt} = (\alpha - \beta y_t)x_t, \\ \frac{dy}{dt} = (\gamma x_t - \delta)y_t, \end{cases}$$

with the respective prey and predator isoclines as follows

$$y = \frac{\alpha}{\beta}; \quad x = \frac{\delta}{\gamma}.$$

or equivalently,

$$\log y = \log(\frac{\alpha}{\beta}); \quad \log x = \log(\frac{\delta}{\gamma}). \tag{3.8}$$

We propose using ordinary least squares (OLS) to fit the appropriate equations to the data set and estimate the parameters. Because OLS cannot fit a vertical line, we use a change of coordinates for the predator isoclines to transform it to a horizontal line. On the other hand, since we are ultimately going to compare all four models, we use this change of coordinates for the predator isoclines in all four models regardless of their slopes for consistency. Besides, since none of the prey isoclines is a vertical line, we limit this change of coordinates only to the predator isoclines and we leave the coordinates of the prey isoclines unchanged.

Let $(\tilde{x}, \tilde{y}) = (y, x)$. By rewriting the predator isocline in (3.8) in the new coordinates $(\tilde{x}, \tilde{y})$, we obtain

$$\log \tilde{y} = \log(\frac{\delta}{\gamma}).$$

Consider now the random counterparts of the linear functions in (3.8) and the above equation

$$\begin{aligned} &\log(\tfrac{\alpha}{\beta}) - \log Y_t, \quad t \in I_X, \\ &\log \tilde{Y}_t - \log(\tfrac{\delta}{\gamma}), \quad t \in I_Y, \end{aligned}$$

where I_X and I_Y were defined in (3.7).

The expected values of these variations can be obtained by

$$\begin{aligned} &\log(\tfrac{\alpha}{\beta}) - E[\log Y_t], \quad t \in I_X, \\ &E[\log \tilde{Y}_t] - \log(\tfrac{\delta}{\gamma}), \quad t \in I_Y. \end{aligned}$$

Then under model (3.1) we have

$$\begin{cases} E[\log Y_t] = \Omega_0, & t \in I_X, \\ E[\log \tilde{Y}_t] = \Lambda_0, & t \in I_Y, \end{cases} \tag{3.9}$$

where, by using equations (3.8), we obtain

$$\Omega_0 = \log(\frac{\alpha}{\beta}), \tag{3.10}$$

and

$$\Lambda_0 = \log(\frac{\delta}{\gamma}). \tag{3.11}$$

The above equations are satisfied since

$$\begin{cases} E[\log Y_t] = \log y_t, & t \in I_X, \\ E[\log \tilde{Y}_t] = \log \tilde{y}_t, & t \in I_Y. \end{cases} \tag{3.12}$$

3.1.2 Holling Model

Recall the periodic two species Holling system

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta x y}{x + \omega}, \\ \frac{dy}{dt} = \frac{\gamma x y}{x + \omega} - \delta y, \end{cases}$$

with the respective prey and predator isoclines as follows

$$\begin{cases} y + \frac{\alpha}{K\beta}x^2 - \frac{\alpha}{K\beta}(K-\omega)x - \frac{\alpha\omega}{\beta} = 0, \\ x - \frac{\delta\omega}{\gamma - \delta} = 0. \end{cases} \tag{3.13}$$

Let $(\tilde{x}, \tilde{y}) = (y, x)$. By rewriting the predator isocline in (3.13) in the new coordinates, we obtain

$$\log \tilde{y} - \log(\frac{\omega\delta}{\gamma - \delta}) = 0. \tag{3.14}$$

Therefore, consider the random counterparts of the functions in (3.13) and (3.14)

$$\begin{aligned} &Y_t + \frac{\alpha}{K\beta}X_t^2 - \frac{\alpha}{K\beta}(K-\omega)X_t - \frac{\alpha\omega}{\beta}, \quad t \in I_X, \\ &\log \tilde{Y}_t - \log \frac{\delta\omega}{\gamma-\delta}, \quad t \in I_Y, \end{aligned}$$

where I_X and I_Y are defined in (3.7). The expected values of these random perturbations are given by

$$\begin{aligned} &E[Y_t] + \frac{\alpha}{K\beta}E[X_t^2] - \frac{\alpha}{K\beta}(K-\omega)E[X_t] - \frac{\alpha\omega}{\beta}, \quad t \in I_X, \\ &E[\log \tilde{Y}_t] - \log \frac{\delta\omega}{\gamma-\delta}, \quad t \in I_Y. \end{aligned}$$

Then, under model (3.1), there exist new parameters Ω_0, Ω_1, Ω_2 and Λ_0 such that

$$\begin{cases} E[Y_t] = \Omega_2 E[X_t^2] + \Omega_1 E[X_t] + \Omega_0, \quad t \in I_X, \\ E[\log \tilde{Y}_t] = \Lambda_0, \quad t \in I_Y. \end{cases} \tag{3.15}$$

In fact, (3.3), (3.4) and (3.5) along with (3.13) and (3.14) imply that in order to obtain (3.15), one needs to set

$$\begin{cases} \Omega_2 = -\frac{\alpha}{K\beta}\exp((-4\sigma_X^2 + \sigma_Y^2)/2), \\ \Omega_1 = \frac{\alpha}{K\beta}(K-\omega)\exp((\sigma_Y^2 - \sigma_X^2)/2), \\ \Omega_0 = \frac{\alpha\omega}{\beta}\exp(\sigma_Y^2/2), \end{cases} \tag{3.16}$$

and

$$\Lambda_0 = \log(\frac{\delta\omega}{\gamma - \delta}). \tag{3.17}$$

3.1.3 Hanski Model

Recall the two species Hanski system

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + \omega}, \\ \frac{dy}{dt} = \gamma y(1 - \frac{\mu y}{x}), \end{cases}$$

with the respective prey and predator isoclines as follows

$$\begin{cases} y + \frac{\alpha}{K\beta}x^2 - \frac{\alpha}{K\beta}(K - \omega)x - \frac{\alpha\omega}{\beta} = 0, \\ y - \frac{1}{\mu}x = 0. \end{cases} \tag{3.18}$$

Let $(\tilde{x}, \tilde{y}) = (y, x)$. By rewriting the predator isocline in (3.18) in the new coordinate, we obtain

$$\log\tilde{y} - \log\tilde{x} + \log\mu = 0. \tag{3.19}$$

Now consider the random counterparts of the functions in the left hand side of (3.18) and (3.19)

$$\begin{aligned} & Y_t + \frac{\alpha}{K\beta}X_t^2 - \frac{\alpha}{K\beta}(K - \omega)X_t - \frac{\alpha\omega}{\beta}, \quad t \in I_X, \\ & \log\tilde{Y}_t - \log\tilde{X}_t - \log\mu, \quad t \in I_Y, \end{aligned}$$

where I_X and I_Y are defined in (3.7). The expected values of these random perturbations are

$$\begin{aligned} & E[Y_t] + \frac{\alpha}{K\beta}E[X_t^2] - \frac{\alpha}{K\beta}(K - \omega)E[X_t] - \frac{\alpha\omega}{\beta}, \quad t \in I_X, \\ & E[\log\tilde{Y}_t] - E[\log\tilde{X}_t] - \log\mu, \quad t \in I_Y. \end{aligned}$$

Then, under model (3.1), there exist new parameters Ω_0, Ω_1, Ω_2 and Λ_0 such that

$$\begin{cases} E[Y_t] = \Omega_2 E[X_t^2] + \Omega_1 E[X_t] + \Omega_0, \quad t \in I_X, \\ E[\log\tilde{Y}_t] = \Lambda_1 E[\log\tilde{X}_t] + \Lambda_0, \quad t \in I_Y. \end{cases} \tag{3.20}$$

By using (3.3), (3.4) and (3.5) along with (3.23), we see that (3.20) is satisfied when

$$\begin{cases} \Omega_2 = -\frac{\alpha}{K\beta}\exp((-4\sigma_X^2 + \sigma_Y^2)/2), \\ \Omega_1 = \frac{\alpha}{K\beta}(K - \omega)\exp((\sigma_Y^2 - \sigma_X^2)/2), \\ \Omega_0 = \frac{\alpha\omega}{\beta}\exp(\sigma_Y^2/2), \end{cases} \tag{3.21}$$

and

$$\begin{cases} \Lambda_1 = 1, \\ \Lambda_0 = \log\mu. \end{cases} \tag{3.22}$$

3.1.4 Arditi Model

Recall the two species Arditi system

$$\begin{cases} \frac{dx}{dt} = \alpha x(1 - \frac{x}{K}) - \frac{\beta xy}{x + wy}, \\ \frac{dy}{dt} = \frac{\gamma xy}{x + wy} - \delta y, \end{cases}$$

with the respective prey and predator isoclines as follows

$$\begin{cases} y - \dfrac{\alpha x(1 - \dfrac{x}{K})}{\beta - \alpha\omega(1 - \dfrac{x}{K})} = 0, \\ x - \frac{\gamma - \delta}{\omega\delta} y = 0. \end{cases} \tag{3.23}$$

Let $(\tilde{x}, \tilde{y}) = (y, x)$. By rewriting the predator isocline in (3.23) in the new coordinate we obtain

$$\log \tilde{y} - \log \tilde{x} + \log(\frac{\omega\delta}{\gamma - \delta}) = 0.$$

We rewrite the prey isocline obtained in (3.23) as

$$y + \frac{\alpha}{K(\beta - \alpha\omega)} x^2 - \frac{\alpha}{\beta - \alpha\omega} x + \frac{\alpha\omega}{K(\beta - \alpha\omega)} xy = 0.$$

Now consider the random counterparts of the functions in the last two equations

$$\begin{aligned} &Y_t + \frac{\alpha}{K(\beta - \alpha\omega)} X_t^2 - \frac{\alpha}{\beta - \alpha\omega} X_t + \frac{\alpha\omega}{K(\beta - \alpha\omega)} X_t Y_t, \quad t \in I_X, \\ &\log \tilde{Y}_t - \log \tilde{X}_t - \log(\frac{\omega\delta}{\gamma - \delta}), \quad t \in I_Y. \end{aligned}$$

Since we assumed that X_t and Y_t are independent random variables, the expected values of the random perturbations appearing above are given by

$$\begin{aligned} &E[Y_t] + \frac{\alpha}{K(\beta - \alpha\omega)} E[X_t^2] - \frac{\alpha}{\beta - \alpha\omega} E[X_t] + \frac{\alpha\omega}{K(\beta - \alpha\omega)} E[X_t]E[Y_t], \quad t \in I_X, \\ &E[\log \tilde{Y}_t] - E[\log \tilde{X}_t] - \log(\frac{\omega\delta}{\gamma - \delta}), \quad t \in I_Y. \end{aligned}$$

Then, under model (3.1), there exist new parameters Ω_0, Ω_1, Ω_2 and Λ_0 such that

$$\begin{cases} E[Y_t] - \Omega_2 E[X_t^2] - \Omega_1 E[X_t] + \Omega_0 E[X_t]E[Y_t] = 0, \quad t \in I_X, \\ E[\log \tilde{Y}_t] - \Lambda_1 E[\log \tilde{X}_t] - \Lambda_0 = 0, \quad t \in I_Y, \end{cases}$$

or equivalently,

$$\begin{cases} E[Y_t] = \dfrac{\Omega_2 E[X_t^2] + \Omega_1 E[X_t]}{1 + \Omega_0 E[X_t]}, \quad t \in I_X, \\ E[\log \tilde{Y}_t] = \Lambda_1 E[\log \tilde{X}_t] + \Lambda_0, \quad t \in I_Y. \end{cases} \tag{3.24}$$

By using (3.3), (3.4) and (3.5) along with (3.18) and (3.19), we see that (3.24) is satisfied when

$$\begin{cases} \Omega_2 = -\dfrac{\alpha}{K(\beta - \alpha\omega)} \exp((-4\sigma_X^2 + \sigma_Y^2)/2), \\ \Omega_1 = \dfrac{\alpha}{\beta - \alpha\omega} \exp((\sigma_Y^2 - \sigma_X^2)/2), \\ \Omega_0 = \dfrac{\alpha\omega}{K(\beta - \alpha\omega)} \exp(\sigma_Y^2/2), \end{cases} \tag{3.25}$$

and

$$\begin{cases} \Lambda_1 = 1, \\ \Lambda_0 = \log(\dfrac{\omega\delta}{\gamma - \delta}). \end{cases} \tag{3.26}$$

3.2 Estimation and Testing

3.2.1 General Algorithm

As we mentioned previously, the prey and the predator extremum sets exist and are non-empty. Moreover, it is known that there exist periodic solutions in the limit to the Lotka-Volterra, Holling, Hanski, and Arditi models for some parameter domain. Therefore, approximately, the prey isocline intersects the solution to the ordinary differential equations (ODE) at the maximum and the minimum prey population sizes in each period. Similarly, the predator isocline intersects the ODE solution at the points where the predator population obtains its maximum and minimum values. This property is fundamental in our proposal for estimating the parameters of the models, and consequently, for predicting the population sizes of the prey and the predator at future times.

In all four discussed models, we propose the following step-wise algorithm:

Step 1: Estimate $\sigma^2 = \sigma_X^2 = \sigma_Y^2$.

Step 2: Estimate the coefficients of equations (3.9), (3.15) and (3.24).

Step 3: Estimate separate ratios $\frac{\alpha}{\beta}$, $\frac{\gamma}{\delta}$ as well as K and ω.

The idea behind the proposal is the following: let $y = u(x)$ and $y = v(x)$ be the prey and the predator isoclines for a given system of differential equations, respectively. We denote the prey and the predator extremum sets by P and Q, respectively. Note that $y = u(x)$ and $y = v(x)$ intersect at an equilibrium point (x^*, y^*). Therefore, the first two equations which could be used to estimate the parameters are

$$y^* = u(x^*); \quad y^* = v(x^*).$$

Moreover by fitting the prey isocline equation to the set of the prey extremum, P, one can derive the third equation to estimate the parameters. The fourth parameter estimate equation can be obtained by fitting the predator isocline equation to the set of the predator extremum, Q. In this chapter, we apply this method to each of the models, separately.

3.2.2 Estimation of σ^2

Before we proceed with the model inferences, we show how to use the periodic property of the predator-prey solution in order to estimate the variance and the coefficients of the predator and the prey isoclines.

Let assume that the observed data is close to a limit cycle solution. Therefore, the solution is periodic. Now consider

$$P_{\text{min}} = \{\log x_t \mid x_t \in P \text{ and } x_t \text{ is the local minimum in each period}\},$$
$$P_{\text{max}} = \{\log x_t \mid x_t \in P \text{ and } x_t \text{ is the local maximum in each period}\}.$$

and

$$Q_{\text{min}} = \{\log y_t \mid y_t \in Q \text{ and } y_t \text{ is the local minimum in each period}\},$$
$$Q_{\text{max}} = \{\log y_t \mid y_t \in Q \text{ and } x_t \text{ is the local maximum in each period}\}.$$

Therefore, we have

$$E[\log X_t] = \log x_t \equiv \log x_{t,\text{min}}, \text{ where } x_{t,\text{min}} \in P_{\text{min}},$$
$$E[\log X_t] = \log x_t \equiv \log x_{t,\text{max}}, \text{ where } x_{t,\text{max}} \in P_{\text{max}}.$$

and

$$E[\log Y_t] = \log y_t \equiv \log y_{t,\text{min}}, \text{ where } y_{t,\text{min}} \in Q_{\text{min}},$$
$$E[\log Y_t] = \log y_t \equiv \log y_{t,\text{max}}, \text{ where } y_{t,\text{max}} \in Q_{\text{max}}.$$

Moreover, the variables $\log X_t$, where $\log x_t \in P_{\text{min}}$ or $\log x_t \in P_{\text{max}}$ and $\log Y_t$, where $y_t \in Q_{\text{min}}$ or $y_t \in Q_{\text{max}}$ are i.i.d and of the same variance σ^2.

We now define $\hat{P}$ and $\hat{Q}$ as the sets of the estimated prey and predator extremum for a given set of observations $\mathfrak{A}$. The estimated variance can obtained by

$$\begin{aligned} \hat{\sigma}^2 &= \frac{1}{4}\{\sum_{i=1}^{|\hat{P}_{\text{max}}|} \frac{(\log X_i - \overline{\log X}_i)^2}{|\hat{P}_{\text{max}}| - 1} + \sum_{i=1}^{|\hat{P}_{\text{min}}|} \frac{(\log X_i - \overline{\log X}_i)^2}{|\hat{P}_{\text{min}}| - 1} \\ &+ \sum_{i=1}^{|\hat{Q}_{\text{max}}|} \frac{(\log Y_i - \overline{\log Y}_i)^2}{|\hat{Q}_{\text{max}}| - 1} + \sum_{i=1}^{|\hat{Q}_{\text{min}}|} \frac{(\log Y_i - \overline{\log Y}_i)^2}{|\hat{Q}_{\text{min}}| - 1}\}, \end{aligned} \tag{3.27}$$

where $|\hat{P}_{\text{max}}|$ and $|\hat{P}_{\text{min}}|$ denote the cardinality of $\hat{P}_{\text{max}}$ and $\hat{P}_{\text{min}}$, respectively obtained from the data set $\mathfrak{A}$. We assume that $|\hat{P}_{\text{max}}| > 1$ and $|\hat{P}_{\text{min}}| > 1$. Additionally, $\log \bar{X}_i$ and $\log \bar{Y}_i$ are the average of the prey and the predator population sizes on the set of observed extrema $\mathfrak{A}$. Another possibility is to use a pooled estimator of variance.
We now return to the model estimates using the estimated variance obtained in this section.

3.2.3 Estimates for each model

Lotka-Volterra

In order to estimate the parameters of the Lotka-Volterra model, we consider the prey and the predator extremum sets $\hat{P}$ and $\hat{Q}$ obtained from the data set $\mathfrak{A}$ which admits the Lotka-Volterra system. Then, according to the previous arguments, the Lotka-Volterra prey isocline must be fitted in $\hat{P}$. Suppose the first equation in (3.9), which corresponds to the prey isocline, is fitted to the set $\hat{P}$. We have the relation

$$E[\log Y_t] = \Omega_0, \quad t \in I_X. \tag{3.28}$$

Then equation (3.10) implies the following relation among the estimates

$$\hat{\Omega}_0 = \log \widehat{(\frac{\alpha}{\beta})}. \tag{3.29}$$

Additionally, the Lotka-Volterra predator isocline must be fitted in set $\hat{Q}$. Therefore, the second relation among the estimates can be obtained by (3.11).

$$\hat{\Lambda}_0 = \log \widehat{(\frac{\delta}{\gamma})}, \tag{3.30}$$

assuming that the second equation (3.9), which corresponds to the predator isocline, is given by

$$E[\tilde{Y}_t] = \Lambda_0, \quad t \in I_Y. \tag{3.31}$$

Therefore one can estimate the parameters $\frac{\alpha}{\beta}$ and $\frac{\delta}{\gamma}$ by

$$\begin{cases} \widehat{(\frac{\alpha}{\beta})} = \exp(\hat{\Omega}_0), \\ \widehat{(\frac{\delta}{\gamma})} = \exp(\hat{\Lambda}_0). \end{cases} \tag{3.32}$$

A complete solution to estimating α, β, γ and δ cannot be obtained at this stage, but a different perspective is given in Froda and Colavita (2005) and Froda and Nkurunziza (2007) where all the parameters are estimated.

Holling Model

To estimate the parameters of the Holling model, we consider the prey and the predator extremum sets $\hat{P}$ and $\hat{Q}$ obtained from a data set $\mathfrak{A}$ which admits the Holling system. Then, according to arguments similar to the ones of the previous case, the prey isocline of the Holling system must be fitted in $\hat{P}$. Suppose the first equation in (3.15), which corresponds to the prey isocline, is fitted to the set $\hat{P}$. We have a relation among the parameters.

$$E[Y_t] = \Omega_2 E[X_t^2] + \Omega_1 E[X_t] + \Omega_0, t \in I_X. \tag{3.33}$$

Then by (3.16) the following relations must be satisfied for the parameter estimates.

$$\begin{cases} \hat{\Omega}_2 = \widehat{(-\frac{\alpha}{K\beta})} \exp((-4\hat{\sigma}_X^2 + \hat{\sigma}_Y^2)/2), \\ \hat{\Omega}_1 = (\widehat{\frac{\alpha}{K\beta}(K-\omega)}) \exp((\hat{\sigma}_Y^2 - \hat{\sigma}_X^2)/2), \\ \hat{\Omega}_0 = \widehat{(\frac{\alpha\omega}{\beta})} \exp(\hat{\sigma}_Y^2/2), \end{cases} \tag{3.34}$$

where $\hat{\Omega}_0$, $\hat{\Omega}_1$ and $\hat{\Omega}_2$ are obtained by minimizing in Ω_0, Ω_1 and Ω_2 the distance

$$\sum_{\hat{P}} (Y_t - \Omega_2 X_t^2 - \Omega_1 X_t - \Omega_0)^2.$$

Additionally, the Holling predator isocline must be fitted in Q. Therefore, the second set of relations among the estimates can be determined from

$$\hat{\Lambda}_0 = \log(\widehat{\frac{\omega\delta}{\gamma-\delta}}) \Leftrightarrow \widehat{(\frac{\gamma}{\delta})} = 1 + \frac{\hat{\omega}}{\exp(\hat{\Lambda}_0)}, \tag{3.35}$$

given that the second equation in (3.15), which corresponds to the predator isocline, is given by

$$E[\log \tilde{Y}_t] = \Lambda_0, t \in I_Y. \tag{3.36}$$

Equations (3.34) suggest the following relations among the parameter estimates.

$$\begin{aligned}\hat{\omega} &= \frac{\hat{\Omega}_1 \pm \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2}\exp(-3\hat{\sigma}_X^2/2),\\ \hat{K} &= \frac{-\hat{\Omega}_1 \pm \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2}\exp(-3\hat{\sigma}_X^2/2).\end{aligned}$$

However, only those are admissible where both $\hat{K}$ and $\hat{\omega}$ are positive, simultaneously. Since $\hat{\Omega}_2 < 0$, $\hat{\Omega}_1 > 0$ and $\hat{\Omega}_0 > 0$, we set

$$\begin{aligned}\hat{\omega} &= \frac{\hat{\Omega}_1 - \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2}\exp(-3\hat{\sigma}_X^2/2),\\ \hat{K} &= \frac{-\hat{\Omega}_1 - \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2}\exp(-3\hat{\sigma}_X^2/2),\\ \widehat{(\frac{\alpha}{\beta})} &= \frac{\hat{\Omega}_1 + \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2}\exp((\hat{\sigma}_X^2 - \hat{\sigma}_Y^2)/2),\\ \widehat{(\frac{\gamma}{\delta})} &= 1 + \frac{\hat{\Omega}_1 - \sqrt{\hat{\Omega}_1 - 4\hat{\Omega}_0\hat{\Omega}_2\exp(\hat{\sigma}_X^2)}}{2\exp(\hat{\Lambda}_0)\hat{\Omega}_2}\exp(-3\hat{\sigma}_X^2/2).\end{aligned} \tag{3.37}$$

Such estimates are biased. Moreover, to find the values of $\hat{\alpha}$, $\hat{\beta}$, $\hat{\gamma}$, and $\hat{\delta}$ more information is required. Therefore, the parameters are not identifiable individually and we may have to use other properties of the original system, but this work is still in progress.

Hanski Model

In order to estimate the parameters of the Hanski model, we consider the prey and the predator extremum sets $\hat{P}$ and $\hat{Q}$ obtained from the data set $\mathfrak{A}$ which admits the Hanski system. Then by similar arguments to the ones mentioned before, the prey isocline of the Hanski model must be fitted in $\hat{P}$. Suppose the first equation (3.20), which corresponds to the prey isocline, is fitted to the set $\hat{P}$. The equation among the parameters is given by

$$E[Y_t] = \Omega_2 E[X_t^2] + \Omega_1 E[X_t] + \Omega_0, \quad t \in I_X. \tag{3.38}$$

By using (3.21) the following set of relations must be satisfied by the parameter estimates.

$$\begin{cases} \hat{\Omega}_2 = \widehat{(-\frac{\alpha}{K\beta})} \exp((-4\hat{\sigma}_X^2 + \hat{\sigma}_Y^2)/2), \\ \hat{\Omega}_1 = (\widehat{\frac{\alpha}{K\beta}(K-}\omega)) \exp((\hat{\sigma}_Y^2 - \hat{\sigma}_X^2)/2), \\ \hat{\Omega}_0 = \widehat{(\frac{\alpha\omega}{\beta})} \exp(\hat{\sigma}_Y^2/2), \end{cases} \tag{3.39}$$

where $\hat{\Omega}_0$, $\hat{\Omega}_1$ and $\hat{\Omega}_2$ are obtained by minimizing in Ω_0, Ω_1 and Ω_2 the distance

$$\sum_{\hat{P}} (Y_t - \Omega_2 X_t^2 - \Omega_1 X_t - \Omega_0)^2.$$

Additionally, the Hanski predator isocline must be fitted in $\hat{Q}$. Therefore, the second set of relations among the original parameters (3.22) suggest to set

$$\begin{cases} \Lambda_1 = 1, \\ \hat{\Lambda}_0 = \log \hat{\mu}, \end{cases} \tag{3.40}$$

which corresponds to the predator isocline.

$$E[\tilde{Y}_t] = \Lambda_1 E[\tilde{X}_t] + \Lambda_0, \quad t \in I_X. \tag{3.41}$$

We get the estimate $\hat{\Lambda}_0$ by minimizing in Λ_0 the distance

$$\sum_{\hat{Q}} (\log \tilde{Y}_t - \log \tilde{X}_t - \Lambda_0)^2.$$

Therefore, one could estimate the original parameters by using (3.39) and (3.40).

$$\begin{aligned} \hat{\omega} &= \frac{\hat{\Omega}_1 - \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2 \exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2} \exp(-3\hat{\sigma}_X^2/2), \\ \hat{K} &= \frac{-\hat{\Omega}_1 - \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2 \exp(\hat{\sigma}_X^2)}}{2\hat{\Omega}_2} \exp(-3\hat{\sigma}_X^2/2), \\ \widehat{(\frac{\alpha}{\beta})} &= \frac{\hat{\Omega}_1 + \sqrt{\hat{\Omega}_1^2 - 4\hat{\Omega}_0\hat{\Omega}_2 \exp(\hat{\sigma}_X^2)}}{2} \exp((\hat{\sigma}_X^2 - \hat{\sigma}_Y^2)/2), \\ \hat{\mu} &= \exp(\hat{\Lambda}_0). \end{aligned} \tag{3.42}$$

Such estimates are biased. Moreover, to find the values of $\hat{\alpha}$ and $\hat{\beta}$ more information is required. Therefore, the parameters are not identifiable individually and we may have to use other properties of the original system, but this work is still in progress.

Arditi Model

To estimate the parameters of the Arditi model, we consider the prey and the predator extremum sets $\hat{P}$ and $\hat{Q}$ obtained from the data set $\mathfrak{A}$ which admits the Arditi system. Then, similar to the previous arguments, the prey isocline of the Arditi model must be fitted in $\hat{P}$. Suppose that the first equation (3.24), which corresponds to the prey isocline, is fitted to the set $\hat{P}$.

$$E[Y_t] = \frac{\Omega_2 E[X_t^2] + \Omega_1 E[X_t]}{1 + \Omega_0 E[X_t]}. \tag{3.43}$$

In view of (3.25), the following set of relations must be satisfied by the parameter estimates.

$$\begin{cases} \hat{\Omega}_2 = (-\widehat{\frac{\alpha}{K(\beta - \alpha\omega)}}) \exp((-4\hat{\sigma}_X^2 + \hat{\sigma}_Y^2)/2), \\ \hat{\Omega}_1 = (\widehat{\frac{\alpha}{\beta - \alpha\omega}}) \exp((\hat{\sigma}_Y^2 - \hat{\sigma}_X^2)/2), \\ \hat{\Omega}_0 = (\widehat{\frac{\alpha\omega}{K(\beta - \alpha\omega)}}) \exp(\hat{\sigma}_Y^2/2), \end{cases} \tag{3.44}$$

where $\hat{\Omega}_0$, $\hat{\Omega}_1$ and $\hat{\Omega}_2$ are obtained by minimizing in Ω_0, Ω_1 and Ω_2 the distance

$$\sum_{\hat{P}} (Y_t - \frac{\Omega_2 X_t^2 + \Omega_1}{1 + \Omega_0 X_t})^2.$$

Additionally, the Arditi predator isocline must be fitted in $\hat{Q}$. Therefore, the set of relations among the original parameters in (3.26) suggest the second set of relations among the estimates

$$\hat{\Lambda}_0 = \log((\widehat{\frac{\omega\delta}{\gamma - \delta}})), \tag{3.45}$$

given that the second equation in (3.24), which corresponds to the predator isocline, is given by

$$E[\log \tilde{Y}_t] = \Lambda_1 E[\log \tilde{X}_t] + \Lambda_0, \quad t \in I_Y. \tag{3.46}$$

To obtain $\hat{\Lambda}_0$ it suffices to minimize in Λ_0 the distance

$$\sum_{\hat{Q}} (\log \tilde{Y}_t - \log \tilde{X}_t - \Lambda_0)^2.$$

Finally, one could estimate the parameters by using (3.44) and (3.45) which gives

$$\begin{aligned}
\hat{\omega} &= -\frac{\hat{\Omega}_0}{\hat{\Omega}_2} \exp(-2\hat{\sigma}_X^2), \\
\hat{K} &= -\frac{\hat{\Omega}_1}{\hat{\Omega}_2} \exp(-3\hat{\sigma}_X^2/2), \\
\widehat{(\tfrac{\beta}{\alpha})} &= -\frac{\hat{\Omega}_0}{\hat{\Omega}_2} \exp(-2\hat{\sigma}_X^2) + \frac{1}{\hat{\Omega}_1} \exp((\hat{\sigma}_Y^2 - \hat{\sigma}_X^2)/2), \\
\widehat{(\tfrac{\gamma}{\delta})} &= 1 - \frac{\hat{\Omega}_0}{\hat{\Omega}_2 \exp(\hat{\Lambda}_0)} \exp(-2\hat{\sigma}_X^2),
\end{aligned} \tag{3.47}$$

Such estimates are biased. Moreover, to find the values of $\hat{\alpha}$, $\hat{\beta}$, $\hat{\gamma}$, and $\hat{\delta}$ more information is required. Therefore, the parameters are not identifiable individually and we may have to use other properties of the original system, but this work is still in progress.

3.2.4 Testing and Comparison of Models

Conversely, we would like to find out which model can be best fitted to a given data set $\mathfrak{A}$. We first construct the predator extremum $\hat{Q}$. After change of coordinates on the predator isoclines and applying the logarithmic transformations, the Lotka-Volterra, Holling, Hanski, and Arditi predator isoclines are respectively

$$\begin{aligned}
\log \tilde{y} &= \log \frac{\delta}{\gamma}, \\
\log \tilde{y} &= \log \frac{\delta\omega}{\gamma - \delta}, \\
\log \tilde{y} &= \log \mu + \log \tilde{x}, \\
\log \tilde{y} &= \log \frac{\delta\omega}{\gamma - \delta} + \log \tilde{x}.
\end{aligned} \tag{3.48}$$

Since the original variables are all positive, the above equations are well-defined. Considering the stochastic model (3.1) one obtains

$$\begin{cases}
\log X_t = \log \tilde{y}_t + \epsilon_{\tilde{Y},t}, \\
\log Y_t = \log \tilde{x}_t + \epsilon_{\tilde{X},t}.
\end{cases}$$

Therefore, if $t \in I_Y$ the following relations among the expected values of $(\log X_t, \log Y_t) \equiv (\log \tilde{Y}_t, \log \tilde{X}_t)$ are satisfied.

$$\begin{aligned} E[\log \tilde{Y}_t] &= \log \frac{\delta}{\gamma}, \\ E[\log \tilde{Y}_t] &= \log \frac{\delta\omega}{\gamma - \delta}, \\ E[\log \tilde{Y}_t] &= E[\log \tilde{X}_t] + \log \mu, \\ E[\log \tilde{Y}_t] &= E[\log \tilde{X}_t] + \log \frac{\delta\omega}{\gamma - \delta}. \end{aligned} \tag{3.49}$$

Note that all four isoclines are straight lines. The first two equations in (3.49) are horizontal lines while the last two ones have slopes equal to 1. Therefore, a straight line

$$y = \Lambda_1 x + \Lambda_0 \tag{3.50}$$

is fitted to the predator extremum $\hat{Q}$.

It must be noted that the usual linear models tests are conditional on the observed explanatory variables.

Further, we propose to apply a step-wise procedure to find out which model can be fitted.

Consider the following hypothesis testing problem:

$$H_0 : \Lambda_1 = 0 \text{ against } H_1 : \Lambda_1 \neq 0. \tag{3.51}$$

If the null hypothesis in (3.51) is not rejected, we can accept the Holling model as an appropriate model to fit the population sizes of the predator and prey. On the other hand, if the null hypothesis (3.51) is rejected, we could proceed to testing

$$H_0 : \Lambda_1 = 1 \text{ against } H_1 : \Lambda_1 \neq 1. \tag{3.52}$$

If the null hypothesis in (3.52) is not rejected, we could resort to the prey isoclines to discriminate between the Hanski and the Arditi models. Recall that the Hanski prey isocline is a quadratic curve. Therefore a quadratic curve

$$y = \Omega_2 x^2 + \Omega_1 x + \Omega_0 \tag{3.53}$$

is fitted to the prey extremum $\hat{P}$. We apply the hypothesis testing

$$H_0 : \Omega_2 = 0 \text{ against } H_1 : \Omega_2 \neq 0. \tag{3.54}$$

on the quadratic slope in (3.54). If the null hypothesis in (3.52) is rejected, we could accept the Hanski model. However, not rejecting the null hypothesis (3.54) does not imply that the Arditi model can be fitted and therefore, further analysis is required. Since the Holling model is one the most fundamental two species predator-prey system, the emphasize is on this model. Besides, other models are also tested against it. However, in this thesis, we only apply the testing method to find out wether or not the Holling model could explain the data set. This will be shown in the next chapter.

CHAPTER IV

APPLICATIONS: SIMULATIONS AND DATA ANALYSIS

In the previous chapter we showed how to estimate the coefficients of the predator and the prey isoclines in order to achieve parameter estimates for the four discussed models. We applied ordinary least squares (OLS) to estimate the variance and the coefficients of the isoclines by fitting them to the prey and the predator extremum sets. We then came up with a proposal for testing hypotheses to check whether a given data set can be fitted to the Holling or Hanski models. There are several ways to conduct the testing such as a test based on a regression model, a t-test, or a Wilcoxon test.
In this chapter we apply our method to simulated data and to a data set. In simulation experiments, we perform two analyses: parameter estimates, including estimating the variance, and further, the testing.

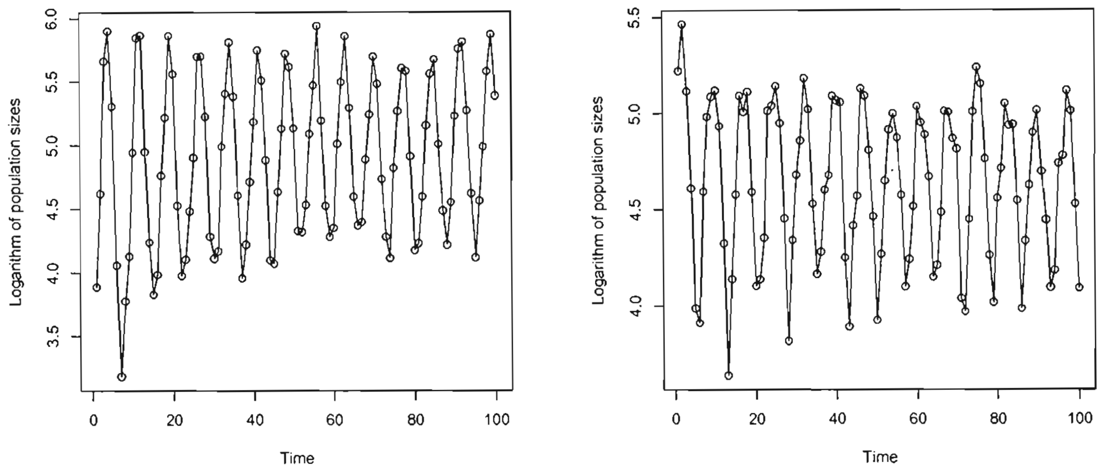
4.1 Description of the Simulation Study

We conducted the simulation only on the Holling model. We used Maple 9.5 and applied a Runge-Kutta type method to solve the ODE system (1.5) to retain equally spaced pairs (x_t, y_t), where t can indicate any time scale, such as years. We then created a set of numerical solutions with a prey and a predator initial population values equal to $(200, 50)$. Given the fact that we are interested in a limit cycle solution because of their periodicity property, we choose the parameters so that the solution asymptotically converges to a limit cycle. It can be seen empirically that the parameters $\alpha = 0.10$, $\beta = 0.05$, $\delta = 0.50$, $\gamma = 0.70$ and $K = 250$ provide a limit cycle solution. Also, they satisfy our sufficient condition for the existence an of unstable equilibrium and therefore, the solution does not tend to the non-trivial point which is

$$x^* = \frac{\delta\omega}{\gamma - \delta}; \quad y^* = \frac{\alpha\gamma\omega(K\gamma - K\delta - \delta\omega)}{K\beta(\gamma - \delta)^2}.$$

Unfortunately, a too small data set cannot provide us with good estimates and testing results; the larger the data set is the more precise the results are. However, since the data sets used for simulation should reflect real data sets, we have no choice but to create a data set with a reasonable size in order to conduct our simulation studies. Most real data sets collected in nature show an approximate 10-year cycle in the predator-prey population interactions (Froda and Colavita, 2005). This means that each prey and predator local minimum (maximum) observations appear after almost 10 yearly observations following the previous prey and predator local minimum (maximum) observations. In fact, our method for finding the local extrema is independent on the cycle length of the solutions. Therefore, we are not concerned if there are too many or too little observation pairs in each period. On the other hand, the number of cycles that the data set contains has to be realistic. For instance, in the Mink-Muskrat data set, which we will introduce in the next section, there are about 12 extrema points for each species since there are 64 couples of observations. Given that the period is about 10 years, the number of extrema for each species is roughly 12. This results in having about 24 observation pairs in both prey and predator extremum sets (Figure 4.2). We created a data set that contains approximately 25 observation pairs in each prey and predator extremum sets. The number of deterministic pairs created is 2000 (Figure 4.1). All 2000 deterministic pairs are perturbed by adding random errors, ϵ_X and ϵ_Y, and each simulation is repeated 5000 times. The extrema obtained from the first 1000 pairs are chosen to estimate the parameters, where the extrema obtained from the last 1000 pairs are chosen to estimate the variance and for the testing procedure. The reason we choose two separate sets of observation pairs will be explained shortly after this. Note that taking a large number of deterministic pairs, e.g. 1000 is useful only for getting more precise choice of extremum sets.

As we discussed in Chapter 3, ϵ_X and ϵ_Y are assumed to be independent. For simplic-



(a) (b)

Figure 4.1 Holling Model: Logarithm of (*a*) the predator and (*b*) the prey population sizes when $\sigma^2 = 0.01$. The model parameters are $\alpha = 0.1$; $K = 250$; $\beta = 0.05$; $\omega = 40$; $\gamma := 0.7$; $\delta = 0.5$.

ity, we took the variances of both random errors equal, *i.e.* we set $\epsilon_X \sim \mathrm{N}(0, \sigma^2)$ and $\epsilon_Y \sim \mathrm{N}(0, \sigma^2)$.

As mentioned in the previous chapter, the core tool to estimate the parameters of the model is to identify the predator and the prey isoclines through the predator and the prey extremum sets. Identifying the coefficients of the isoclines help us determine either the individual parameters of the original model or ratios of some of the parameters.

In order to evaluate the isoclines, one needs to obtain the predator and the prey extremum sets, which in fact consist of the predator local minimum-maximum values, and the prey local minimum-maximum values, respectively. Because of the perturbation due to the random error effect, it is not guaranteed to find the perturbation of the true minimum-maximum value at each period. In order to retain the local minimum-maximum observation pairs we proceed as follows. For illustration consider the prey: an observation is selected as prey local maximum if it is greater than: (*a*) the mean

value of all population sizes of observed preys and (*b*) the population sizes of the seven preceding and the seven succeeding prey observations. Moreover, an observation is selected as prey local minimum if it is smaller than: (*a*) the mean value of all population sizes of observed preys and (*b*) the population sizes of the seven preceding and the seven succeeding preys. Number seven is chosen because there is an approximate 20-year cycle (if t indicates years) in the prey and the predator populations. The same procedure applies to the perturbation of predators. Note that in practice, one could rely on visual interpretation or other empirical methods and does not necessarily need to use 'an algorithm' for choosing the elements of extremum sets. The algorithm was needed because we repeated the simulation a great number of times.
Figure 4.1 illustrates a numerical solution to the Holling model corresponding to the given parameters. We chose 1/10 of the points on the numerical solutions from each cycle in order to avoid having cluttered graphs.

4.1.1 Estimation

Suppose P and Q denote the prey and the predator extremum sets, respectively. Since the inference is done on a logarithmic scale, we use relatively small values for the variance of the random errors. The following four variances were chosen to run the simulations: $\sigma^2 = 0.01$, $\sigma^2 = 0.005$, $\sigma^2 = 0.001$ and $\sigma^2 = 0.0005$. As we mentioned earlier in this section, in order to estimate the variances, observations must be taken from a closed loop. That is because periodicity property of a closed loop is crucial to estimate the variance (see section 3.2.2). That is why we choose the extrema of the last 1000 observation pairs to estimate the variance. Since the chosen parameters create a numerical solution which asymptotically converges to a limit cycle, we can take the observations that are on the closed loop. We use equation (3.27) to estimate the variance from the extremum sets.
Unlike the variance, the parameters are better estimated if the observations are not on the closed loop part of the numerical solution. This is because the further the elements of the prey (and the predator) extremum sets are from each other in the phase plane the

less the random error affects the shape of the isocline curves. That is why the extrema of the first 1000 observations pairs are chosen to estimate the parameters. We apply ordinary least squares (OLS) to fit a vertical line to Q and a quadratic curve to P since according to equations (3.33) and (3.36), a vertical line and a quadratic curve must be fitted to the predator extremum and the prey extremum sets, respectively. Then, at each simulation, we estimate the coefficients Λ_0, Λ_1, Ω_0, Ω_1, Ω_2, and further, evaluate $\hat{\omega}$, $\hat{K}$, $\widehat{(\frac{\alpha}{\beta})}$ and $\widehat{(\frac{\gamma}{\delta})}$ by using (3.37). The results are given in tables 4.1 and 4.2 and are discussed in section 4.1.3.

4.1.2 Testing

Finally, the last part of the simulation is devoted to testing. We apply the 2-sided regression slope test, the 2-sided t-test and the 2-sided Wilcoxon test to find out whether or not a vertical line can be fitted to Q. Since Y_t is not normally distributed, these tests do not work on a quadratic equation. The regression slope test was described in Chapter 3. The t-test and the Wilcoxon test are applied when we compare 2-samples and further we explain why these tests could work in our case.

If we want to use the fact that both x_t and y_t are periodic with the same period τ, the observations must be taken from the closed loop. Therefore, the same pairs of observations used to estimate the variance can be used, *i.e.* the extrema of the last 1000 observation pairs.

For simplicity let $U_t = \log X_t$ and $V_t = \log Y_t$. We use the change of coordinate defined in Chapter 3 and we obtain $\tilde{U}_t = \log \tilde{X}_t$ and $\tilde{V}_t = \tilde{Y}_t$. We obtain

$$\begin{cases} \tilde{U}_t = \tilde{u}_t + \epsilon_{u,t}, \\ \tilde{V}_t = \tilde{v}_t + \epsilon_{v,t}, \end{cases}$$

where in our models, at times t where the deterministic $\tilde{u}_t$ has a maximum or minimum value. We have the relation

$$\tilde{V}_t = a + b\tilde{u}_t + \epsilon_{v,t}.$$

Since $\tilde{u}_t$ is periodic, the deterministic values $\tilde{u}_t$ take only two values at the times we consider (maximum and minimum); the values of the corresponding $\tilde{v}_t$ also repeat themselves. So we actually confront two hypotheses:

$b = 0$: $E[\tilde{V}_t]$ are the same for all $t > 0$ versus $b = 1$: $E[\tilde{V}_t]$ are different for maxima and minima of $\tilde{u}_t$. By using (4.1), we can write

$$\begin{cases} b = 0 \Rightarrow \tilde{V}_t = a + \epsilon_t, \\ b = 1 \Rightarrow \tilde{V}_t = a + \tilde{u}_t + \epsilon_{v,t}. \end{cases}$$

Since $E[\tilde{U}_t]$ lies on the extrema $\tilde{u}_{\max}$ and $\tilde{u}_{\min}$, under the $b = 1$ hypothesis, $\tilde{V}_t$ is from two populations of different means, $a + \tilde{u}_{\max}$ and $a + \tilde{u}_{\min}$. Then we can simply perform a 2-sample t-test which should accept the null-hypothesis of i.i.d data sets which give an almost 0 estimated slope.

Another case of 2-sample testing is the Wilcoxon-Mann-Whitney test which does not assume normality for the errors.

The results of the tests are shown in table 4.3.

4.1.3 Results

In this section we provide the results obtained from simulation. Tables 4.1 and 4.2 are devoted to parameter estimates; we can see how the parameter estimates change with an increase in $\hat{\sigma}^2$. The estimates of σ^2, Λ_0 and Λ_1 are excellent for the whole range of σ^2 values. The estimates of Ω_0, Ω_1 and Ω_2 are generally good but maybe less so for $\sigma^2 = 0.01$. On the other hand, the estimates of the individual parameters ω, K, $\frac{\alpha}{\beta}$ and $\frac{\gamma}{\delta}$ are greatly affected by the small bias in the coefficients Ω_0, Ω_1, Ω_2 and Λ_0. Therefore, even if the isoclines coefficient estimates have small relative bias, the estimates of the parameters of the system can have large relative bias.

It can be observed that the tests performed with the 2-sided regression slope test are excellent. However, we can see that the Wilcoxon test overestimates acceptance error, while the t-test underestimates. The somewhat surprising results on the t-test may be artifacts of the automatic procedure for choosing extrema in the simulation loops. Small experiments where the data were obtained by perturbing the numerical solution at exact times of maximum-minimum values gave very good results, i.e. very close to the nominal α values.

Table 4.1 Estimates of the parameters for $\sigma^2 = 0.0005$ and $\sigma^2 = 0.001$

Parameter	Real value	Mean	Q1	Median	Q3	Relative Bias
σ^2	0.0005	0.0004	0.0004	0.0004	0.0005	0.2
Ω_2	-0.008	-0.0066	-0.0084	-0.0062	-0.0044	0.175
Ω_1	1.68	1.4097	0.8961	1.3159	1.8228	0.1609
Ω_0	80.02	70.6486	45.9361	75.0602	100.1619	0.1171
Λ_1	0	0.0001	0	0	0	N.A.
Λ_0	4.6052	4.6059	4.5968	4.6062	4.6155	-0.0001
ω	40	68.5987	22.9157	46.7337	79.6355	-0.715
K	250	275.7349	239.3305	259.0887	285.2832	-0.1029
$\frac{\alpha}{\beta}$	2	1.654	1.246	1.6113	2.0189	0.173
$\frac{\gamma}{\delta}$	1.4	1.6851	1.2273	1.4664	1.7979	-0.2036
σ^2	0.001	0.0008	0.0007	0.0008	0.001	0.2
Ω_2	-0.008	-0.006	-0.0077	-0.0056	-0.0036	0.25
Ω_1	1.68	1.28	0.7342	1.1895	1.6995	0.2342
Ω_0	80.04	77.1728	52.3258	82.1294	109.0825	0.0358
Λ_1	0	0.0001	0	0	0	N.A.
Λ_0	4.6052	6.606	4.5951	4.6061	4.6171	0.0004
ω	40	169.3726	27.2548	54.9277	99.6829	-3.2343
K	250	295.0879	246.4028	269.112	304.0179	-0.1804
$\frac{\alpha}{\beta}$	2	1.5378	1.0918	1.4949	1.9084	0.2311
$\frac{\gamma}{\delta}$	1.4	2.688	1.271	1.5473	1.9991	-0.92

Table 4.2 Estimates of the parameters for $\sigma^2 = 0.005$ and $\sigma^2 = 0.01$

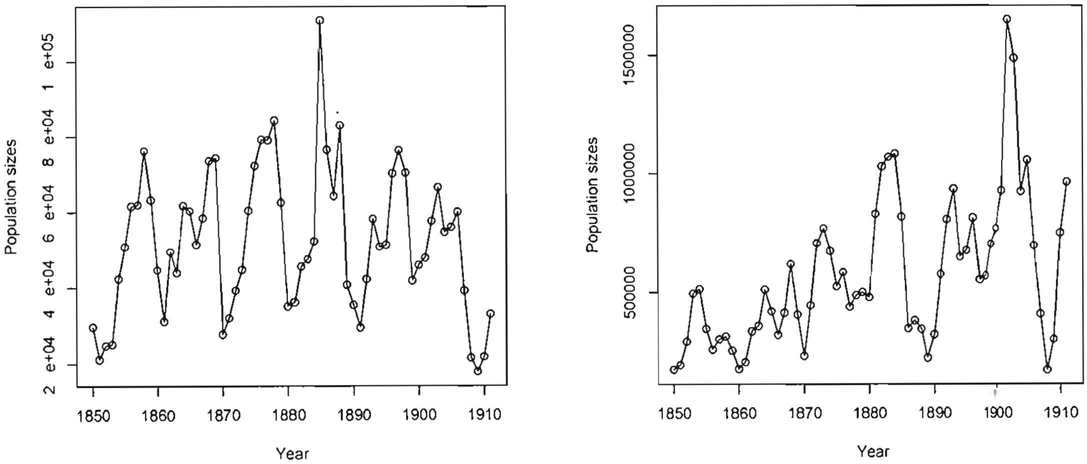
Parameter	Real value	Mean	Q1	Median	Q3	Relative Bias
σ^2	0.005	0.0041	0.0032	0.0039	0.0048	0.18
Ω_2	-0.0079	-0.0043	-0.0059	-0.0036	-0.0019	0.4557
Ω_1	1.68	0.9692	0.3731	0.797	1.363	0.4231
Ω_0	80.2003	94.3709	69.2848	103.9421	129.6153	-0.1767
Λ_1	0	-0.0003	0	0	0	N.A.
Λ_0	4.6052	4.6105	4.5928	4.6094	4.6262	0.0011
ω	40	164.0656	42.4329	91.1289	180.4262	-3.1016
K	250	354.7479	271.155	311.4028	382.1624	-0.419
$\frac{\alpha}{\beta}$	2	1.2281	0.7141	1.1285	1.6278	0.386
$\frac{\gamma}{\delta}$	1.4	2.638	1.4187	1.9073	2.7762	-0.8843
σ^2	0.01	0.0104	0.0074	0.0092	0.0115	-0.04
Ω_2	-0.0079	-0.0036	-0.0049	-0.0029	-0.0014	0.5443
Ω_1	1.68	0.8362	0.3023	0.6628	1.1806	0.5023
Ω_0	80.401	101.1914	78.8744	110.1739	132.0744	-0.2586
Λ_1	0	0	0	0	0	N.A.
Λ_0	4.6052	4.6139	4.5944	4.6138	4.6336	-0.0019
ω	40	169.0691	54.0566	110.9176	217.5539	-3.2267
K	250	412.8353	289.6489	341.5827	435.4674	-0.6513
$\frac{\alpha}{\beta}$	2	1.0934	0.5993	0.9969	1.4541	0.4533
$\frac{\gamma}{\delta}$	1.4	2.6656	1.5381	2.095	3.1609	-0.904

Table 4.3 Testing: How often the predator isocline is accepted as a vertical line

Type of Testing	Percentage of Acceptance
$\sigma^2 = 0.0005$	
2-sided Regression	0.9484
2-sided t-test	0.8209
2-sided Wilcoxon	1
$\sigma^2 = 0.001$	
2-sided Regression	0.9507
2-sided t-test	0.8588
2-sided Wilcoxon	1
$\sigma^2 = 0.005$	
2-sided Regression	0.9602
2-sided t-test	0.8914
2-sided Wilcoxon	1
$\sigma^2 = 0.01$	
2-sided Regression	0.9704
2-sided t-test	0.8884
2-sided Wilcoxon	1

4.2 Data Analysis

In this section we apply our method to the Canadian mink-muskrat data, the Hudson's Bay Company Records of fur-sales and trappings collected between 1850 and 1911 (Figure 4.2). The data set we are using here is reported in Brockwell and Davis (1991) pp. 557-558. There are several comments on the predator-prey relationship between the species listed in the Husdon-Bay data set (Bulmer, 1974). It appears that the muskrat cycle is due to predation by mink (Bulmer, 1974). As such, a mink-muskrat couple is a predator-prey pair which seems to satisfy the requirement that the prey muskrat is the main source of food for the predator mink. There exists an approximate 10-year cycle of the prey and the predator population (see Froda and Colavita, 2005). The results of testing on the mink-muskrat data set are given in table 4.4. The p-value corresponding to the predator isocline slope is greater that 0.873. Therefore, we do not reject the hypothesis test that the slope is 0. In other words, the Holling model could be fitted to the mink-muskrat data set. The result is also in agreement with a



(a) (b)

Figure 4.2 Observed population sizes: (a) Mink (b) Muskrat

Table 4.4 Results of testing on the mink-muskrat data set

Parameter	Estimate	Std. Error	t-value	$\Pr(>\lvert t\rvert)$
Λ_1	1.3303	8.0469	0.165	0.873
Λ_0	1.0932	0.7432	1.471	0.180

Lotka-Volterra model as used in Froda and Colavita (2005) and Froda and Nkurunziza (2007).

4.3 Discussion

In this chapter, we applied the method of isoclines, introduced in Chapter 3, to simulated data and to the Canadian mink-muskrat data set. In simulation, we considered various levels of stochastic error.

Our best results were in testing, especially when comparing regression slopes. In this case, even for the largest stochastic error taken, under H_0 we were very close to the nominal acceptance level for the slope. The other testing methods had a tendency to overestimate the acceptance level (Wilcoxon, not powerful enough) or underestimate it (t-test).

As far as estimation goes, the coefficients Ω_0, Ω_1 and Ω_2 were well estimated, even with relatively large error. But recovering the original parameters did not give good results, which is not so surprising because of the transformations we used to estimate them. Indeed, it appears that even a slight bias in the estimates of the coefficients of the isoclines has a noticeable impact on the parameter estimates of the model; as had to be expected, the larger the variance the larger the bias becomes.

Besides, we showed that it makes sense to base the variance estimates as well as the 2-group testing on observations coming from a closed loop, while the isoclines' coefficients seem to be better estimated if the observations are picked up from that part of a solution which has not yet reached the limiting closed loop. We could separate our simulated data in two subsets (closer to and further away from a closed loop) but in practice this may be a problem because of scarcity of available data; this is another question that should be addressed in the future.

Finally, as seen earlier, we are not yet able to estimate all the parameters of the model individually, and we limited ourselves to estimate the ratios $\widehat{(\frac{\alpha}{\beta})}$ and $\widehat{(\frac{\gamma}{\delta})}$. These ratios are important in themselves, since they express in a certain way how birth and death rates compare for each species. By emulating Froda and Colavita (2005) and Froda and Nkurunziza (2007), we expect that by relying on periodicity properties of the solution we should be able to develop a method which could estimate the four parameters α, β, δ and γ individually, and eventually make predictions based on these models.

CONCLUSION

In this thesis we describe some important deterministic models for predator-prey interactions, namely Lotka-Volterra, Holling (1959), Hanski (1991) and Arditi (2004). We explain the interpretation of their parameters, and present a brief analysis of their qualitative properties, from the dynamical systems point of view. Further, at the core of this work, we introduce a new stochastic model, which adds observational error to the solutions of the ODEs.

An important part of the thesis deals specifically with statistical inference, namely estimating the parameters, as well as a comparison of models based on simple tests. In the end, we conduct simulation studies to illustrate our method, and check empirically the properties of our estimators and tests (we compute relative bias and quartiles). We also apply the testing and estimation procedure to a real data set. These results are presented in Chapter 4.

The main idea behind our method is to estimate or to test the coefficients of the model isoclines. Further, the original parameters can be estimated from the estimated coefficients. For now, we proposed a simple method to achieve this final estimation, but we consider perfecting it in future. Indeed, while our results in testing seem good, especially when comparing regression slopes, the estimation needs more refinement.

Although the isoclines' coefficients Ω_0, Ω_1 and Ω_2 were well estimated, even with relatively large errors, transforming them to recover the original parameters did not give us good results. This is not so surprising, given that the transformations we used are not so-called invariant. Therefore, we may consider a maximum likelihood approach, or resorting to periodicity properties of the solution to be able to develop a method which could improve present estimates, and also allow us to estimate the four parameters α, β, δ, γ individually. Estimating the individual parameters is crucial in order to predict the population sizes of the species in future time. Other famous authors, like Froda and Colavita (2005) and Froda and Nkurunziza (2007), have relied on periodicity to estimate the Lotka-Volterra parameters from its Hamiltonian.

Another possibility is to try to make use of two more equations in order to find a unique set of solutions for the system of equations (3.37) and (3.47), corresponding to the Holling and the Arditi models, respectively. Note that we work in the phase plane. Therefore, one might be able to obtain an extra equation among the parameters of the model from a relation between the center of mass of the system and the equilibrium point of the solution. The mass center, as well as the asymptotically stable equilibrium of a limit cycle solution always lie inside the closed loop. We know that the location of an equilibrium point is where the isoclines intersect. But, detecting the location of the mass center without knowing the values of all the individual parameters is a challenge. Some nonparametric procedure may prove of help. On the other hand, when it comes to the Hanski model, only one extra equation is needed to enable us to find a unique solution for the equation (3.42). The periodicity property still seems a valid method to implement in this case.

To conclude: we feel that the proposed testing procedure is very promising, but the estimation method needs to be further developed.

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