

An analysis of some models of prey-predator interaction

THIERRY BI BOUA LAGUI, MOUHAMADOU DOSSO, GOSSOUHON SITIONON

UFR Mathématiques et Informatique
University Université Félix Houphouët-Boigny
22 BP 582 Abidjan 22,
COTE D'IVOIRE

Abstract: Biological models of basic prey-predator interaction have been studied. This consisted, at first, in analyzing the basic models of population dynamics such as the Malthus model, the Verhulst model, the Gompertz model and the model with Allee effect ; then, in a second step, to analyze the Lotka-Volterra model and its models improved by taking into account certain important hypotheses such as competition and/or cooperation between species, existence of refuge for prey and migration of species. For each population evolution model presented, a numerical illustration was made for its verification.

Key- Words: Difference equations, Population dynamics, Malthus model, Verhulst model, Gompertz model, Allee Effect, Lotka-Volterra predator-prey model, Stability, competition and cooperation.

Received: April 16, 2023. Revised: December 2, 2023. Accepted: January 12, 2024. Published: March 11, 2024.

1 Introduction

Population dynamics is concerned with the fluctuation over time of the number of individuals within a population of living beings and also makes it possible to understand the environmental influences on the numbers. There are several criteria that determine the evolution of a given population. We have for example: Environmental constraints (i.e., abundance or scarcity of resources, quality of resources, ecological changes, etc.) Reproduction (fertility or not of individuals, etc.) which guarantees the survival of the species in the absence of constant interactions with other populations in the same environment and/or interactions with the environment.

The diversity of terrestrial or marine species, whether plants, animals, fungi and microorganisms, is generally subdivided into three levels:

- genetic diversity, which is the variability of genes within a same species or a given population. We also talk about intraspecific diversity, which is characterized by the difference between two individuals of the same species or subspecies;
- Ecosystem diversity which corresponds to the diversity of ecosystems present on earth, the interactions of natural populations and their physical environment.
- - Specific diversity, also called interspecific diversity, which corresponds to the diversity of species.

Throughout this article, we are interested in specific diversity. Thus, several problems on the preservation of the environment, fauna, flora and why not that of the survival of the human species, will result from it since humanity draws its resources there.

The modern foundations of population dynamics were laid in an early version of the book, *Essay on the Principle of Population*, [1]. This version opened the "ways" to the modern study of population dynamics. His idea was to assume that: "if a population is not checked, it grows geometrically". Later, in 1838, François Verhulst proposed an alternative model to that of Malthus by introducing a process of self-regulation or intra-specific competition, [2]. From 1926, Lotka and Volterra were to be the pioneers in the study of the dynamics of several interacting species, [3], [4]. Later, several contributions to the study of population growth rates and their interactions emerged.

Our work is organized as follows. In section 2, we present basic models of population dynamics. The models of Malthus and Verhulst which the first biological models were the subject of an analysis ; then we presented the Gompertz model and the model with Allee effect which take into account the possibility of an extinction of species. Then in sections 3 and 4, the Lotka-Volterra model and the models based on it are respectively the object of special attention.

2 A few basic models

We start with four basic models of population change over time. These are the Malthus', Verhulst's and Gompertz's models and the model with Allee effect.

2.1 Malthus's model

The Malthus model is one of the first models of population dynamics. In [1], the author dealt with the subject of the evolution of the human population by adopting a relatively simple approach using the following assumptions :

- $x(t)$ is the size of a population at time t ;
- the increase in this population is proportional to its size and the length of the time interval ;
- the size of the population is represented by its mean.

These hypotheses are therefore translated into the following linear differential equation, [5]

$$\frac{dx(t)}{dt} = rx(t) \quad (1)$$

where $\frac{dx(t)}{dt}$ denotes the population change for a time interval and r is a constant factor of proportionality which represents the coefficient of increase or growth rate. By integration of equation (1), we obtain as solution

$$\forall t \geq t_0, \quad x(t) = x_0 e^{r(t-t_0)} \quad (2)$$

with $x_0 = x(t_0) \in \mathbb{R}_+$ the size of the population at the initial time $t \in \mathbb{R}_+$, which implies the exponential growth of this population for a certain given initial size. The pace that this evolution will follow depends on the values taken by the intrinsic growth rate r of the population, also called the Malthusian rate. Thus, we have the following variations :

- When $r < 0$, the evolution of the population is negative, The size of the population decreases until the extinction of the species in question.
- When $r = 0$, no variation in population size can be observed. The population remains constant.
- When $r > 0$, the increase in the population will be exponential, leading to an infinite development of the species.

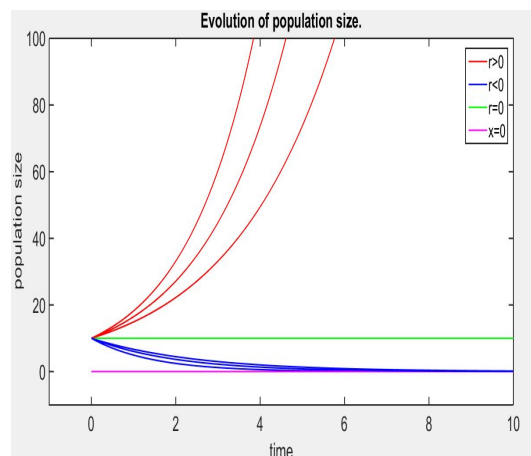


Figure 1: Malthus growth model

Figure 1 summarizes the different variations in population size as a function of the values of r .

We take as initial data in the Figure $x_0 = 10$ and different values of growth rate with $r \in \{-0.4; -0.5; -0.7\}$ in blue and $r \in \{0.4; 0.5; 0.6\}$ in red. This law applies well to microbial populations, it can be used to model the beginning of the growth of bacteria for example and it therefore remains valid as long as the host environment can contain the density of the population which occupies it. However, note that the Malthusian law has limitations. We present some of them :

- (i) The fact that the population increases infinitely is not biologically satisfying ;
- (ii) The prediction of the evolution over a long time by the model is problematic, since it does not take into account the fact that the host environment of the population could be saturated.
- (iii) The model also does not take into account the availability of resources vital to the survival of the population or at least assumes these resources to be infinite. Which, too, is not satisfactory.

Based on these limits, other models aimed at describing the evolution of populations over time will introduce the notion of carrying capacity, as we will see below.

2.2 Verhulst's Model

Verhulst's model is also called the logistic model, [2]. This model takes into account the environmental constraints and those related to the resources in the hypotheses (i) to (iii) missing in the evolution of the population of the biological

species. Hence the integration of the concept of reception capacity, which we note K . For Verhulst, a population cannot grow indefinitely without encountering obstacles. It will be assumed that the excessive density of individuals would lead to phenomena of competition, lack of food, unfavorable ecological conditions or simply the destruction of natural ecological balances. From where the differential equation below proposed in [6].

$$\frac{dx(t)}{dt} = rx(t) \left(1 - \frac{x(t)}{K} \right) \quad (3)$$

where

- $x(t)$ represents the size of the population at time t ;
- r is the intrinsic growth rate of the population ;
- K is the capacity of the environment to support population growth. Beyond this limit, the population will no longer be able to grow.
- $\left(1 - \frac{x(t)}{K} \right)$ represents the part of the biotic capacity still available at each instant t , that is to say the maximum value that a given population can reach in a given habitat.

With the following change of variable

$$z(t) = \frac{1}{y(t)}$$

equation (3) reduces to

$$\frac{dz}{dt} = -r \left(z - \frac{1}{K} \right). \quad (4)$$

the solution of which is

$$z(t) = z_0 e^{-r(t-t_0)} + \frac{1}{K}.$$

Which leads to the solution of the type below of equation (3) with the initial condition $x(0) = x_0$

$$x(t) = \frac{x_0 K}{x_0 + (K - x_0) e^{-r(t-t_0)}} \quad (5)$$

called logistic functions. There are different cases to describe the evolution of the population following this model.

- If $0 < x_0 < K$ then the environment can still accommodate individuals. We will observe a growth within this population which will approach over the years, the limit threshold K .

- If $x_0 = K$ then there will be no more evolution within this population.
- If $x_0 > K$ then intraspecific competition phenomena (fight for food, etc.) will occur. This will result in an increase in the mortality rate and therefore a decrease in the size of the population towards its limit K .

Figure 2 below summarizes this fact for different values of x_0

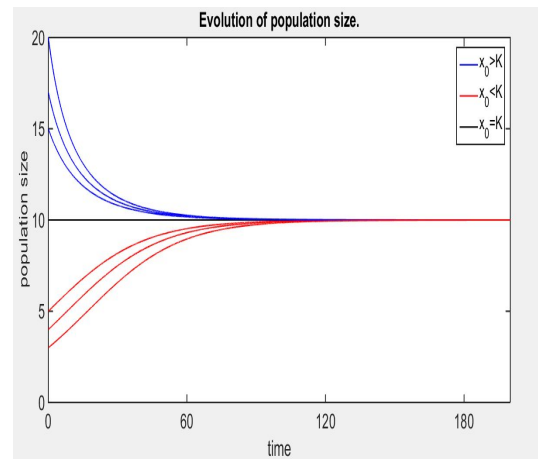


Figure 2: Verhulst's Growth Model

Here we have taken as carrying capacity $K = 10$, growth rate $r = 0.05$ and different values of population rate $x_0 \in \{15; 17; 20\}$ in blue and $x_0 \in \{3; 4; 5\}$ in red. Verhulst's model is suitable for several types of populations and has provided good results in some laboratory experiments. Practical examples of the use of the model to control certain populations exist. We have the example of the elephant population of Kruger Park.

However, Verhulst's model has a drawback. A drawback of the Verhulst model is that it does not deal with the possibility of species extinction. This reality will lead scientists to perfect the model. The examples of the models with Allee effect that we will see in subsection 2.4, take this parameter into account.

2.3 Gompertz's model

The Gompertz model is due to Benjamin Gompertz (1779-1865) a British mathematician, biologist, actuary and astronaut by self-taught training. In 1825, he tackled the subject of the aging population in a very long article, [7] in the review 'philosophical transactions of the Royal Society of London'. The function that he establishes makes it possible to model a situation where a population first grows exponentially and then ends up

stabilizing by approaching a certain ceiling value. His model defines the growth of the population according to the differential equation

$$\frac{dx(t)}{dt} = rx(t) \ln \left(\frac{K}{x(t)} \right) \quad (6)$$

with the parameters having the same as those of the model above. With the following change of variable

$$y(t) = \ln \left(\frac{x(t)}{K} \right),$$

equation (6) becomes

$$\frac{dy(t)}{dt} = -rKy(t) \quad (7)$$

which leads to the solution

$$y(t) = y(t_0)e^{-rK(t-t_0)}$$

Thus, with the change of variable (7), we obtain an explicit solution of equation (6) by, [7], [8],

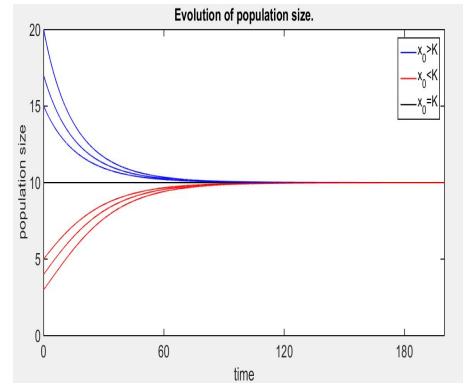
$$x(t) = Ke^{\ln \left(\frac{x_0}{K} \right) e^{-rK(t-t_0)}} \quad (8)$$

It should be noted that this model admits a single point of equilibrium which is $x = K$ which is stable. This model evolves similarly to the logistic model (both models have the same stable equilibrium, K). More precisely, we can see from the Figures that the model is equivalent to the logistic model in the neighborhood of the equilibrium K . However, when moving away from equilibrium K , the growth is much faster than in the logistic model.

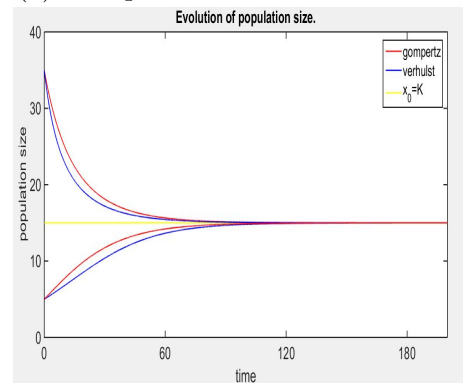
For this model, we take as carrying capacity $K = 10$, growth rate $r = 0.05$ and the different values of initial population rates are $x_0 \in \{15; 17; 20\}$ for the curves in blue and $x_0 \in \{3; 4; 5\}$ for those in red. Figure (3a) illustrates the evolution of the Gompertz model and Figure (3b) where $x_0 = \{5; 35\}$ and $k = 15$ gives the comparison of the Gompertz and logistic models.

The red curve, which grows according to the Gompertz model, reaches the threshold more quickly than the other blue curve of the logistic model curve.

As a domain of application of the Gompertz model, researchers have applied it to tumor growth. which led to the discussion of several dynamic functions of the growth rate. This Gompertz growth pattern showed cellular growth that slows with population density and is therefore suitable for observing the evolution of tumor



(a) Gompertz's Growth Model



(b) Comparison of Gompertz and logistic models

Figure 3: Evolution of Gompertz and Logistic models

size, [9]. The growth rate is obtained by the following equation

$$\dot{N}(t) = -\gamma N(t) \log \left(\frac{N(t)}{K} \right) \quad t > 0, \quad (9)$$

$$N(0) = n_0, \quad \gamma > 0 \text{ and } K > n_0$$

where $N(t)$ is the tumor cell concentration in the target organism, γ indicates the net rate of tumor replication and K is the tumor carrying capacity.

Other more general models have been proposed. We have, as an example, the famous Gompertz model below, which is a growth model for fitting real data, [10], [11].

$$\frac{dN_G(t)}{dt} = N_G(t) \left(\alpha - \beta \log \left(\frac{N_G(t)}{K} \right) \right), \quad \forall t \geq 0, \quad (10)$$

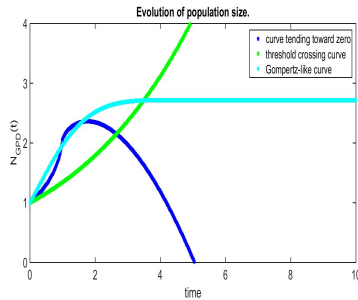
and $N_G(0) = K \geq 0$, with $\alpha, \beta \geq 0$. Note that reparametrizations of this model were done in [11] by Tjørve and Tjørve.

In the same continuity of research, it was proposed and studied in [10], the growth model

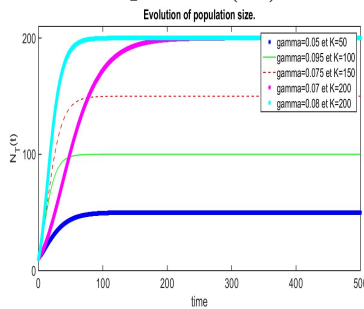
$N_{GPD}(t)$ solution of differential equation (11) which is an extension of the Gompertz model governed by equation (10).

$$\frac{dN_{GPD}(t)}{dt} = N_{GPD}(t)A \left(1 - \frac{1}{Ab} \log \left(\frac{N_{GPD}(t)}{K} \right) \right)^{1+a} \quad (11)$$

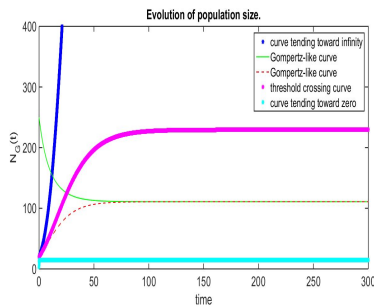
$\forall t \geq 0, N_{GPD}(0) = K, \text{ with } K > 0, A > 0, a \neq 0 \text{ and } b > 0.$



(a) The growth model $N_{GPD}(t)$, solution of differential equation (11)



(b) Tumor growth model $N(t)$, solution of differential equation (9)



(c) The growth model $N_G(t)$, solution of differential equation (10)

Figure 4: Gompertz's growth model extensions

According to the chronicles, we find the graph of the Gompertz model with the extensions (9), (10), (11). However, the models are more or less flexible compared to that of Gompertz. Curves

(4a) and (4b) of models (10) and (11) respectively, for example, present cases where the curve can tend towards infinity, or towards a finite limit (the carrying capacity), or even cross this limit threshold, or even tend towards zero. Curve (4c) of the model (9) does not cross the carrying capacity and depends largely on γ and K .

For the growth model $N_G(t)$, we take as carrying capacity $K = 100, \alpha = 0.05$ and the different values of $\beta = \{1; 1.5; 1.1; 1000\}$, for the growth model $N_{GPD}(t)$, we take as carrying capacity $A = 1, b = 1$ and the different values of $a = \{-0.2; -0.3; -0.5; \}$ and for tumor growth model $N(0) = 10,$

2.4 Model with Allee effect

This model is due to the American zoologist Warder Clyde Allee (1885-1955) who made modifications to the Verhulst model. Indeed, he noticed the fact that in the model of Verhulst, certain aspects that could significantly influence the evolution of a given population have not been taken into account. For a low density population, it can be observed the following, [12], [13], [14]:

- It can be difficult to find a mate in sexual species. This state of affairs induces a decrease in the rate of reproduction within the population. This would imply slow or even negative growth of the population in question.
- There is also weak intraspecific cooperation between individuals of a small population. In fact, the presence of many individuals promotes good survival within this population.
- Existence of less resistance to extreme climatic conditions.
- Genetic processes such as inbreeding depression and loss of genetic diversity can also influence the survival of small populations.

To materialize these hypotheses, Allee introduces a threshold effect into the equation of the logistic model. Below this threshold, the population is driven to extinction. Otherwise, it grows logistically until it reaches its carrying capacity limit. This model is expressed in the following form, [15]

:

$$\frac{dx(t)}{dt} = -rx(t) \left(1 - \frac{x(t)}{K_a} \right) \left(1 - \frac{x(t)}{K} \right) \quad (12)$$

where $x(t)$ represents the size of the population at time t and r is the rate intrinsic population

growth as defined in the models below with $r > 0$; K is the capacity of the environment that can support the growth of the population and K_a is the critical value below which the size of a population should not go down. We also say the threshold capacity of the Allee effect, or the critical population with $0 < K_a < K$.

A study of Equation (12) yields three equilibrium points

$$x_1^* = 0 \quad ; \quad x_2^* = K \quad ; \quad x_3^* = K_a$$

where x_1^* and x_2^* are stable and the equilibrium point $x_3^* = K_a$ is unstable. Thus, any small variation in the size of the population around the two stable equilibrium points is compensated by a variation in the growth rate, while a variation in the size of the population in the vicinity of the unstable equilibrium point is amplified by change in growth rate. Figures 5 gives an illustration of the evolution of a population subjected to an Allee effect.

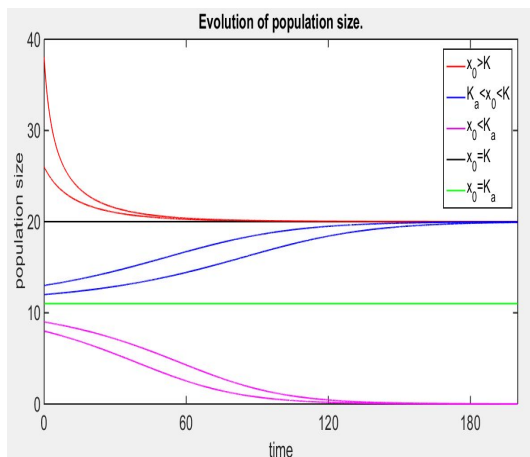


Figure 5: Growth model with "Allee effect"

To obtain Figure 5, we took as limit capacity $K = 20$, threshold capacity $K_a = 11$ and growth rate $r = 0.05$. Thus for different values of the initial population rate $x_0 \in \{8; 9.5; 12; 13; 26; 38\}$, we note that when the size of the population is above the limiting capacity K of the environment or between the threshold capacity K_a and the limiting capacity K , the evolution of the population follows the logistics law. On the other hand, when this number is below the threshold capacity K_a , the growth rate becomes negative leading to a decrease in numbers which itself induces a greater decrease in the growth rate and so on. Which leads to a very rapid extinction of the population. There are two types of Allee effect : The strong Allee effect and the weak Allee effect.

- We speak of a strong Allee effect when below the threshold capacity K_a , populations are threatened with extinction.
- The weak Allee effect is characterized by the fact that the populations suffer from a lower growth rate than if there were no Allee effect but are however not threatened with extinction.

However, to generate the correlation between per capita growth rate and population size, the authors of [15] use

$$\frac{dx(t)}{dt} = rx(t) \left(1 - \frac{x(t)}{K} \right) \left(\frac{x(t) - a}{K} \right) \quad (13)$$

with $x(t)$ the population size, a the critical point and K the force of competition which is known as the carrying.

Furthermore, to capture both effects (strong and weak) in a dynamic population model, we have equation (14) below which is analogous to that proposed by Nagumo in [16] in the context of active transmission of d 'an impulse along a nerve axon, [13].

$$\frac{dx(t)}{dt} = rx(x - a) \left(1 - \frac{x}{K} \right). \quad (14)$$

This model has three equilibria, $x = 0$, $x = K$ and $x = a$. When $0 < a < K$, $x = 0$ and $x = K$ are stable, while $x = a$ is unstable. This situation corresponds to the strong Allee effect.

3 Lotka-Volterra Model

The system of Lotka, [17], [18] and Volterra, [4], [19], also called prey-predator system, is one of the most famous systems of differential equations of its time. Its particularity is that it is the first mathematical model of two interacting populations. It is a non-linear autonomous dynamic system.

Lotka worked on the dynamics of autocatalytic chemical reactions, before extending his model to organic systems, then to the evolution of populations living in communities. As for Volterra, it wanted to explain qualitatively the fluctuations of fish stocks in the Adriatic Sea. Indeed, after the First World War, the zoologist Umberto d'Anconna, made a paradoxical observation, concerning the quantities of fish of different species that were caught in the Adriatic Sea; thus during the war the sardine fishery had decreased, the share of these in the catches, which should have increased, had however decreased in favor of their predators, the sharks as shown on Figure 6.

It makes the following assumptions :



Figure 6: Two fish populations interacting. (Image Futura-sciences)

- We consider two interacting fish species (preys and predators).
- The predator population is assumed to feed exclusively on the prey population.
- The population of prey has an unlimited food source.

Under these assumptions, the model describing the evolution over time of these two populations is as follows, [20], [21] :

$$\begin{cases} \frac{dx(t)}{dt} = x(t)(\alpha - \beta y(t)) \\ \frac{dy(t)}{dt} = -y(t)(\delta - \gamma x(t)) \end{cases} \quad \alpha, \beta, \gamma, \delta \in \mathbb{R}_+^* \quad (15)$$

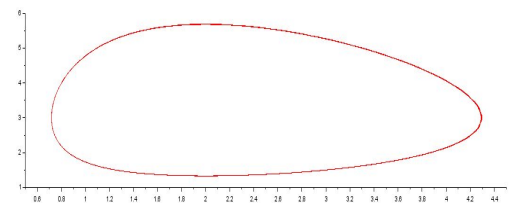
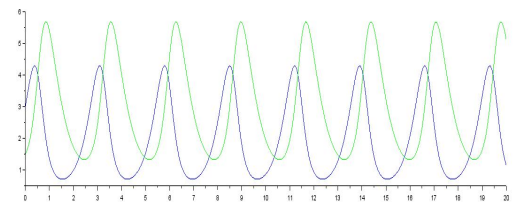
where $x(t)$ represents the population density of prey and $y(t)$ that of predators in the environment, $\frac{dx(t)}{dt}$ and $\frac{dy(t)}{dt}$ are respectively the variations of prey populations and predators, for a variation of time. By studying the system (15), we notice that:

- In the absence of predators the prey population follows the Malthusian law. It grows indefinitely. It is the same observation for predators in the absence of prey ; but this time, we are witnessing a rapid extinction of this population.
- The model admits two equilibrium points : $(x^*, y^*) = (0, 0)$ and $(x^*, y^*) = (\frac{\delta}{\gamma}, \frac{\alpha}{\beta})$ which are respectively unstable and stable.
- The average of the densities with respect to time remains constant and at equilibrium,

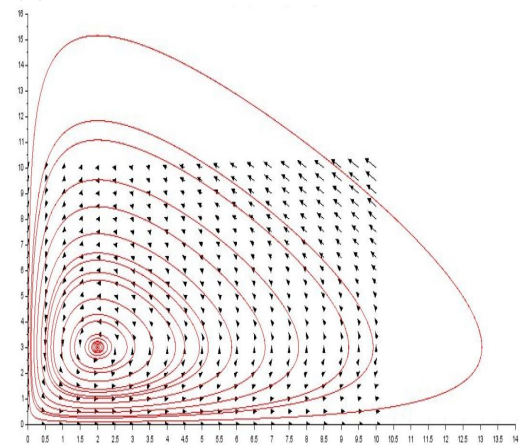
corresponds to $(\bar{x}, \bar{y}) = (\frac{\delta}{\gamma}, \frac{\alpha}{\beta})$ where \bar{x} and \bar{y} are the average density of prey and predators respectively.

- Trajectories are closed around equilibrium point.

These different points are illustrated by the evolution curves (7a) and the phase portrait (7b) by taking the initial population rates $x_0 = 3$ and $y_0 = 1.5$.



(a) Evolution of populations



(b) Field lines and phase portrait

Figure 7: Chronicles and phase portrait of Lotka-Volterra's model.

Indeed, Figure (7a) represents the evolution of prey populations (in green color) and predators (in blue color), as a function of time, as well as the phase portrait (bottom curve) of prey populations (on the abscissa) and predators (on the ordinate). The following remarks are made on the figures:

- The maximum amplitudes are constant for the two populations.
- The period is identical for the two populations.
- The phase difference between the amplitudes of the populations is constant.

As for Figure 7b, it represents the field lines and the phase portrait. The plot of this field gives a good idea of the dynamics of the system. We come to the conclusion that, for certain prey-predator interactions, the results obtained are actually observed in nature. The Lotka-Volterra model has specific characteristics and serves as a basis for other models.

However, the model does not take into account the capacities of the real environment, it assumes them to be unlimited. The phenomenon of intraspecific competition is not taken into account. Moreover, whatever the values of the parameters, we end up with limit cycles (see Figure 7b) while we expect the disappearance of prey when the reproduction rate is too low compared to the predation rate.

4 Models based on the Lotka-Volterra model

By considering the basic model of Lotka-Volterra, several other scientists will add certain hypotheses to try to describe observable phenomena in the sense of the evolution of populations in interaction. In fact, this evolution responds to laws that relate to the intrinsic organization of the different populations. As a result, remarkable behaviors are developed by populations in their own right to reach prey whenever necessary for predators or to find techniques of protection against their "executioners" for prey. Thus, the struggle for survival will lead animals of different species to associate with the aim of reaping mutual benefits from this union, without living at the expense of one another. We then speak of mutualism between populations where populations adopt simultaneous behaviors tending to monopolize the resources of an environment. In this case we speak of competition between living species. This competition can be intraspecific (between members of the same species) or interspecific (between populations of different species).

4.1 Model of competition

Competition between species induces a struggle for survival. Each species will negatively impact the other. This will cause the growth rate of

each species to decrease. We consider two species in competitive interaction, [22], [23]. The differential equation describing the interaction of competition between two species is given below.

$$\begin{cases} \frac{dx}{dt} = \alpha_1 x \left(1 - \frac{x}{K_1} - \beta_1 \frac{y}{K_1} \right) \\ \frac{dy}{dt} = \alpha_2 y \left(1 - \frac{y}{K_2} - \beta_2 \frac{x}{K_2} \right) \end{cases} \quad (16)$$

where the parameters $\alpha_1, \alpha_2, \beta_1, \beta_2, K_1$ and K_2 are all positive. The evolution of each population follows the logistic law. In this equation,

- x and y are the proportions of populations in interaction ;
- α_1 and α_2 are respectively the rates increase in populations x and y .
- β_1 and β_2 respectively characterize the competitive pressure exerted by the population x on the population y and that exerted by the population y on the population x .
- K_1 and K_2 respectively represent the carrying capacities of the environment of population x and population y .

A study of the model makes it possible to obtain four points of equilibrium. Indeed, by making the following time scale changes : $\tau = \alpha_1 t, u = \frac{x}{K_1}, v = \frac{y}{K_2}, \varphi_1 = \beta_1 \frac{K_2}{K_1}, \varphi_2 = \beta_2 \frac{K_1}{K_2}$ and $\rho = \frac{\alpha_2}{\alpha_1}$.

System (16) becomes

$$\begin{cases} \frac{du}{d\tau} = u(1 - u - \varphi_1 v) \\ \frac{dv}{d\tau} = \rho(1 - v - \varphi_2 u) \end{cases} \quad (17)$$

of the following points of equilibrium $(0, 0), (1, 0), (0, 1)$ and $(u^*, v^*) = \left(\frac{1 - \varphi_1}{1 - \varphi_1 \varphi_2}, \frac{1 - \varphi_2}{1 - \varphi_1 \varphi_2} \right)$.

The equilibrium point (u^*, v^*) has a biological sense when $\varphi_1 \varphi_2 \neq 1, u^* > 0$ and $v^* > 0$. Note also that the equilibrium point $(0, 0)$ is an unstable node, the second equilibrium point $(1, 0)$ is a saddle point, if $\varphi_2 < 1$ (respectively a stable node, if $\varphi_2 > 1$); as for the third equilibrium point $(0, 1)$, it is a saddle point, if $\varphi_1 < 1$ (respectively a stable node, if $\varphi_1 > 1$) and for the fourth equilibrium point (u^*, v^*) , it is a saddle point (respectively a stable node) if $\varphi_1 \varphi_2 < 1$ (respectively if $\varphi_1 \varphi_2 > 1$).

Let $x(0)$ and $y(0)$ be the initial densities of the populations assumed to be strictly positive. From a biological point of view, we have the following conclusions:

- If $\varphi_1 < 1$ and $\varphi_2 < 1$ then the densities converge to the equilibrium (u^*, v^*) ;
- If $\varphi_1 > 1$ and $\varphi_2 > 1$ then we have a bistability phenomenon. One of the populations dies out while the other tends towards its carrying capacity.
- If $\varphi_1 < 1$ and $\varphi_2 > 1$ then the densities converge towards the point of equilibrium $(1, 0)$ with the population x which dominates the other.
- If $\varphi_1 > 1$ and $\varphi_2 < 1$ then the reverse of the previous case occurs.

We illustrate the evolution of the populations in Figure 8 by assuming that the growth rates ($\alpha_1 = 0.9$ and $\alpha_2 = 0.7$), with the initial population rates ($u_0 = 40$ and $v_0 = 40$) . In addition, the carrying capacities ($k_1 = 8$ and $k_2 = 5.1$) are taken into account in the context of our example for all figures.

- 1) In Figure (8a), after a rapid reduction in the respective numbers due to the competitive pressure that each species exerts on the other, the two species maintain their numbers constant for a certain time. The considered parameters are ($\beta_1 = 0.02$; $\beta_2 = 0.05$), so that ($\varphi_1 < 1$; $\varphi_2 < 1$).
- 2) In Figure (8b), one of the species disappears to the benefit of the other as long as the other species resists the competition. We have considered the parameters ($\beta_1 = 1.6$; $\beta_2 = 0.7$), so that ($\varphi_1 < 1$; $\varphi_2 > 1$).
- 3) In Figure (8c), with the choice of parameters ($\beta_1 = 1.7$; $\beta_2 = 0.98$) such that ($\varphi_1 > 1$; $\varphi_2 > 1$) , the interspecific competition of species 1 on species 2 is higher than the intraspecific competition of species 1. Species 2 dies out while the other tends toward its carrying
- 4) The case of Figure (8d) is the opposite of the case of (8c). We take as parameters ($\beta_1 = 1, 8$; $\beta_2 = 1, 98$) which imply ($\varphi_1 > 1$; $\varphi_2 < 1$). In this case, species 1 is extinguished while the other tends towards its carrying capacity

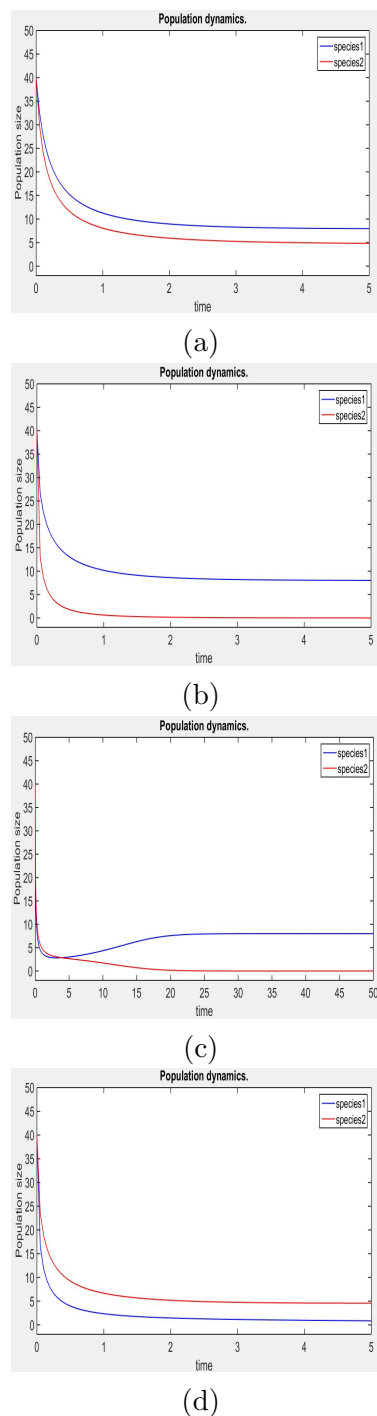


Figure 8: Chronicles of the competition model according to the values of $\varphi_{1,2}$

4.2 Model of cooperation

Cooperation (or mutualism) between populations can be intraspecific or interspecific. It occurs when the individuals of the different populations come together for their mutual survival. This interaction will allow mutualist populations to take advantage of each other immediately for some or

delayed in time for others.

The Lotka-Volterra model of cooperation, proposed in [24], is given by the system of differential equations below

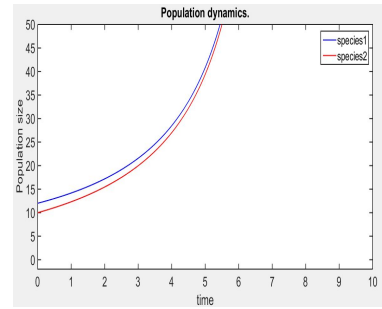
$$\begin{cases} \frac{dx}{dt} = \alpha_1 x \left(1 - \frac{x}{K_1} + \mu_1 \frac{y}{K_1} \right) \\ \frac{dy}{dt} = \alpha_2 y \left(1 - \frac{y}{K_2} + \mu_2 \frac{x}{K_2} \right) \end{cases} \quad (18)$$

where μ_1 and μ_2 represent the impact of cooperation on the size of the population x and on that y respectively. Note that the model of cooperation is opposed to the model of competition, [25]. The evolution of each population follows the logistic law. As in the competition model, we also have four points of equilibrium $(0, 0)$, $(1, 0)$, $(0, 1)$ and $(\bar{u}, \bar{v}) = \left(\frac{1 + \varphi_1}{1 - \varphi_1 \varphi_2}, \frac{1 + \varphi_2}{1 - \varphi_1 \varphi_2} \right)$ where $\varphi_1 \varphi_2 \neq 1$, $\varphi_1 > 0$ and $\varphi_2 > 0$. A study of equilibrium points shows that

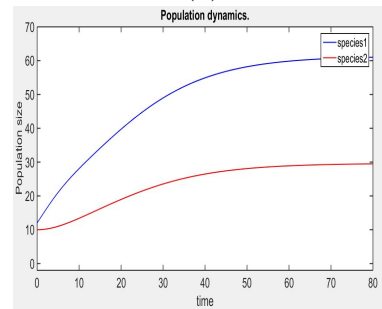
- the point of equilibrium $(0, 0)$ is an unstable node and the points of equilibrium $(1, 0)$, $(0, 1)$ are saddle points.
- When $\varphi_1 \varphi_2 < 1$, the equilibrium (\bar{u}, \bar{v}) is globally asymptotically stable. Cooperation is then weak and the two populations coexist with constant numbers at equilibrium.
- When $\varphi_1 \varphi_2 > 1$, the equilibrium point (\bar{u}, \bar{v}) is unstable. In this case, the cooperation is strong and the two populations grow without limit.

The equilibrium point (\bar{u}, \bar{v}) induces a problem of overcrowding of populations. But, what will happen when the capacity of the respective environment of each population is exceeded? Won't the populations enter into competition? Recent studies, in [26], have highlighted this phenomenon. We illustrate this in the following example by taking as growth rates $\alpha_1 = 0.09$ and $\alpha_2 = 0.07$; and the carrying capacities $k_1 = 8$ and $k_2 = 5.1$. We therefore obtain Figure 9 which shows the evolution of the populations in three different cases.

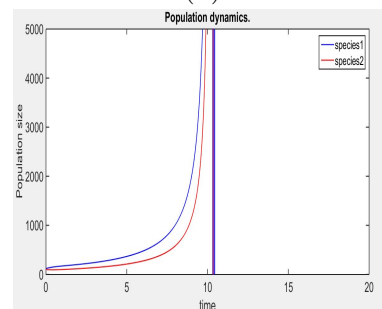
1) In Figure (9a), we consider the parameters $\beta_1 = 1.8$ and $\beta_2 = 1.63$ such that $\varphi_1 \varphi_2 > 1$, and the initial population rates $u_0 = 12$ and $v_0 = 10$. Cooperation is strong in this case and the two populations grow without limit.



(a)



(b)



(c)

Figure 9: Chronicles of the cooperation model

- 2) In Figure (9b), we take $\beta_1 = 1.8$ and $\beta_2 = 0.4$ so that $\varphi_1 \varphi_2 < 1$, and the initial population rates ($u_0 = 12$ and $v_0 = 10$). The cooperation is then weak and the two populations coexist with constant numbers in equilibrium.
- 3) Figure (9c) shows a phenomenon of overpopulation. The initial population rates are ($u_0 = 120$ and $v_0 = 100$). This phenomenon leads to the destruction of natural ecological equilibrium. We then witness the extinction of the species.

4.3 Model of competition and cooperation

In this section, we want to know if we can go from an interspecific cooperation phenomenon to an interspecific competition phenomenon, depending on the density of the species populations. Indeed, the possibility for a population to pass from

mutualism to competition according to the evolution of population density is inevitable. Too high a density of mutualist populations could therefore be the basis of a change in interaction for certain associations. Consequently, to rethink the terms cooperation or competition, the authors of [26] proposed the following coefficient for a certain population x_j .

$$\delta_{ij} = \frac{b_i x_j - c_i x_j^2}{1 + d_i x_j^2} \quad i, j = 1, 2 \text{ and } i \neq j. \quad (19)$$

where b_i , c_i and d_i are constants depending on the environment. Thus, for two interacting populations x , y , we have the following system of differential equations

$$\begin{cases} \frac{dx}{dt} = \alpha_1 x \left(1 - \frac{x}{K_1} + \delta_{12} \frac{y}{K_1} \right) \\ \frac{dy}{dt} = \alpha_2 y \left(1 - \frac{y}{K_2} + \delta_{21} \frac{x}{K_2} \right) \end{cases} \quad (20)$$

putting $(x, y) = (x_1, x_2)$. The other parameters are the same as those defined in subsection 4.2.

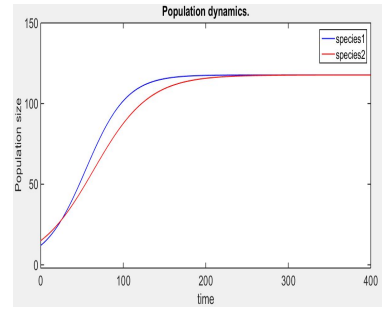
We get equilibrium points (x^*, y^*) which change in nature according to the variation of the different parameters. For example, we have the equilibrium point $(K_1, 0)$ which is an unstable saddle point when the interaction is mutualistic and becomes stable when the populations move towards competition, [26].

The ecologist Zhibin Zhang in "Chinese Academy of Sciences" worked on a model of species coexistence by associating competition and cooperation, [27]. The system of equations describing this interaction is

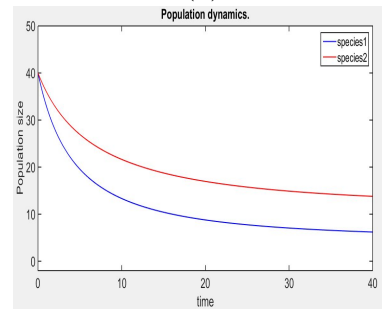
$$\begin{cases} \frac{dx}{dt} = \alpha_1 x [c_1 - x - a_1(y - b_1)^2] \\ \frac{dy}{dt} = \alpha_2 y [c_2 - y - a_2(x - b_2)^2] \end{cases} \quad (21)$$

where α_1 , α_2 , a_1 , a_2 , b_1 , b_2 , c_1 and c_2 are all positive. The coefficients α_1 and α_2 are respectively the rates increase in populations x and y .

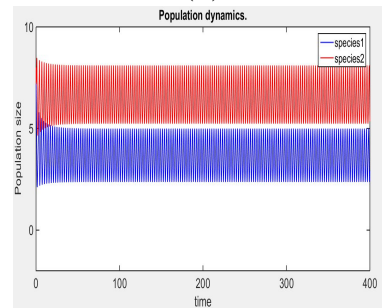
The hypothesis is that for $0 < x \leq b_2$ or $0 < y \leq b_1$, the associated species is mutualistic otherwise the population concerned becomes a competitor at a higher density. When the growth of each population is zero, we obtain a stable equilibrium characterized by the point $(c_1 - x - a_1(y - b_1)^2, c_2 - y - a_2(x - b_2)^2)$.



(a)



(b)



(c)

Figure 10: Chronicles of the competition-cooperation model

The evolution of populations is summarized by the examples in Figure 10 below.

We have the different cases of figures according to the values of the parameters. In Figure (10a) where initial population rates are $x_0 = 12$ and $y_0 = 15$, for example, the populations are in a situation of cooperation while Figure (10b) with initial population rates $x_0 = 40$ and $y_0 = 40$, presents a situation of competition. As for Figure (10c), we see the two preceding cases succeed one another over a long period taking as initial population rates $x_0 = 8$ and $y_0 = 8$. Indeed, when the species are in a situation of cooperation, the numbers increase simultaneously then reach a threshold where they enter into competition in this case the densities of the populations regress until reaching a threshold where the species become cooperative again.

4.4 Lotka-Volterra model with refuge for prey

Consider two populations in predation interaction. Suppose that a proportion $\phi(x, y)$ of prey can find a shelter allowing it to escape from predators. The differential equation system describing this interaction is given by, [28]:

$$\begin{cases} \frac{dx}{dt} = \alpha_1 x - d_1 y(x - \phi(x, y)) \\ \frac{dy}{dt} = -\alpha_2 y + d_2 y(x - \phi(x, y)) \end{cases} \quad (22)$$

Parameters d_1 and d_2 are positive. When all the preys are within reach of the predators, we find the equation (15) which has two points of equilibrium $(0, 0)$ and (x^*, y^*) with,

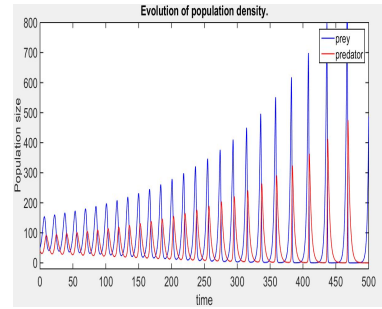
$$x^* = \frac{\alpha_2}{d_2} + \phi(x, y) \text{ and } y^* = \frac{\alpha_1}{d_1} + \frac{\alpha_1 d_2}{\alpha_2 d_1} \phi(x, y)$$

Note that the nature of each equilibrium point depends on the value taken by $\phi(x, y)$ and also on the initial conditions. The figures and the phase portrait describing the behavior of the species which interact according to system (22) are represented by Figure 11. The growth rates considered here are $\alpha_1 = 0.5$ for prey and $\alpha_2 = 0.1$ for predators. We have also taken the parameters $d_1 = 0.1$ and $d_2 = 0.4$, and the initial population rate $x_0 = 50$ and $y_0 = 40$; and used the following value for $\phi(x, y) = mx$ with $m \in]0, 1[$.

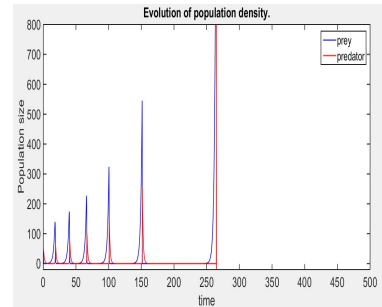
We notice that, the closer the value of m is to 0, the dynamics is close to that of system (15) of which a representation is given in Figure (11a). However, when the value of m is close to 1, we notice that, on Figure (11b), over time the populations of predators tend towards extinction between 250 and 275, while the populations of prey seem to evolve without limit. Figure (11c) shows the phase portrait.

4.5 Lotka-Volterra model with migration

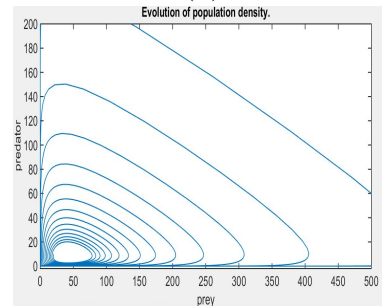
In the model of the prey-predator relationship, if we assume that "the preys have the possibility of moving, that they can go outside their initial environment, either in search of food or to escape their predators, and that predators also have the possibility of going outside their environment in search of preys"; it would then be necessary to take into account the spatial dimension of the problem. Taking this factor into account leads to a



(a)



(b)



(c)

Figure 11: Chronicles of Lotka-Volterra model with refuge for prey

type of spatio-temporal model, which is used in ecology or biology. The dynamics of this interaction is then described by the following system of partial differential equations, [29] :

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + (\alpha_1 - b_1 u - \zeta_1)u \\ \frac{\partial v}{\partial t} = d_2 \Delta v + (\alpha_2 - \zeta_2)v \end{cases} \quad (23)$$

We choose a bounded spatial domain with boundary conditions that can be of the Neumann type for example, in which the populations of prey and predators to be studied are found. In this equation we have

- u and v respectively represent the density of prey and predators at time t and at position

x ;

- Δ is the Laplacian operator; d_1 and d_2 are the diffusion coefficients of prey and predator respectively ;
- ζ_1 and ζ_2 denote the functional responses of the predator to the prey (ie the variations in the number of prey consumed per individual and per day).

The other terms are the same as before.

We obtain four equilibrium points $(0, 0)$, $(1, 0)$, $(0, \bar{v})$ and (u^*, v^*) . The nature of each of them depends on the considered domain and the initial conditions.

This model is suitable for example for the study of a biological invasion, which consists of the rapid numerical and spatial expansion of a population outside its initial environment.

It has moreover been used recently (in France between 2000 and 2003), to study the spread of the horse chestnut leafminer.

Figure 12 presents the chronicle of two species propagating in the same way in space .

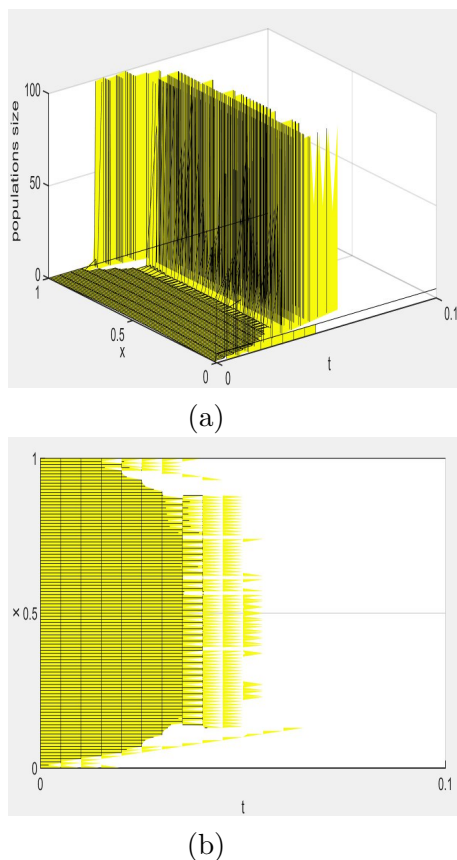


Figure 12: Propagation of two prey-predator species in time and space

The following growth rates are used: $\alpha_1 = 0.5$ for the prey (chestnut trees) and $\alpha_2 = 0.1$ for the predators (miners) with $u_0 = 500$; $v_0 = 300$. The functional response of the predator to the prey is Holling II type. In this case we will take in system (23),

$$\zeta_1 = \frac{b_2 v}{u + h_u} \quad \text{and} \quad \zeta_2 = \frac{c v}{u + h_v}.$$

Thus, the model (23) is rewritten as follows

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2} + \left(\alpha_1 - b_1 u - \frac{b_2 v}{u + h_u} \right) u \\ \frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2} + \left(\alpha_2 - \frac{c v}{u + h_v} \right) v \end{cases} \quad (24)$$

The spread of predators (miners), represented by the black color in Figure (12a), is strong from the start but ends up fading over time under the effect of the resistance of the prey (chestnut trees). Figure (12b) represents a view in the (t, x) plane.

5 Conclusion

Basic biological models of prey-predator interaction have been investigated. We began by presenting the first models of population dynamics which prompted the implementation of other improved models. These are the simple Malthus model which does not take into account the capacity of the environment and the limited existence of the resources of the population, the Verhulst model which takes into account these two hypotheses, then the model of Gompertz on the rate of aging and mortality of the population and finally the model with the Allee effect which takes into account the introduction of a threshold effect in the equation of the logistic model. Then we made an analysis of the Lotka-Volterra model which is a model of evolution of two populations living in community. It is also called prey-predator model.

Finally, five models based on the Lotka-Volterra model were analyzed. These are :

- the model of competition which induces competition between species living in communities;
- the model of cooperation (also called mutualism) which takes into account the fact that the different populations work together for their mutual survival;

- the model of competition and cooperation which gives the possibility for a population to move from mutualism to competition according to the evolution of the density of the population;
- the Lotka-Volterra model with refuge for prey which assumes that a proportion $\phi(x, y)$ of prey can find a shelter allowing it to escape predators ;
- and the Lotka-Volterra model with migration assuming that preys have the possibility of going outside their initial environment, either in search of food or to escape their predators, as well as predators in search of preys.

During our analyses, we carried out numerical tests, thus illustrating the dynamics of the populations according to the different models presented.

In future research, we plan to study the systems of more than three species in a natural environment and their application in the preservation of the ecosystem.

Acknowledgment:

The authors would like to thank all the reviewers for their thoughtful comments and efforts towards improving our manuscript.

References:

- [1] T.R. Malthus, An Essay on the Principle of Population, vol. 2, 6th edition, (1826).
- [2] P. F. Verhulst, Notice on the law that a population follows in its growth (Notice sur la loi que la population poursuit dans son accroissement). *Corr. Math. Phys.*, 10(1838) 113-121.
- [3] J. Hofbauer, V. Hutson and W. Jansen, Coexistence for systems governed by difference equations of Lotka-Volterra type, *J. Math. Biol.* 25 (1987) 553-570.
- [4] V. Volterra, Lessons on the Mathematical Theory of Struggle for Life (Leçons sur la Théorie Mathématique de la Lutte pour la Vie), *Gauthier-Villars, Paris*, (1931).
- [5] E. Ibarguen-Mondragon, M. Vergel-Ortega, & S. Gomez-Vergel, Malthus Model applied to exponential growth of Covid-19. *Rebista Boletin Redipe*, 9(11)(2020) 159-164.
- [6] M. Rayungsari, A. In'am, and M. Aufin, Genetic Algorithm to Estimate Parameters of Indonesian Population Growth Model, in Proceedings of the International Conference on Community Development (ICCD 2020), vol. 477, no. Iccd. Paris, France: Atlantis Press, 2020. ISBN 978-94-6239-253-3 pp. 426–430.
- [7] B. Gompertz, On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philosophical Transactions of the Royal Society of London*, Vol. 115, (1825), pp. 513-583.
- [8] N. Pavlov, G. Spasov, A. Rahnev and N. Kyurkchiev, A New Class Of Gompertz-Type Software Reliability Models, *International Electronic Journal of Pure and Applied Mathematics*, Vol. 12 No. 1, (2018) 43-57.
- [9] A. R. Sheergojria, P. Iqbala, P. Agarwal and N. Ozdemire, Uncertainty-based Gompertz growth model for tumor population and its numerical analysis, *An International Journal of Optimization and Control: Theories & Applications*, Vol.12, No.2 (2022) pp.137150.
- [10] M. Asadi, A. Di Crescenzo, F. A. Sajadi & S. Spina. A generalized Gompertz growth model with applications and related birth-death processes. *Ricerche di Matematica*, (2020),1-36.
- [11] K. Wu, D. Darcet, Q. Wang and D. Sornette, Generalized logistic growth modeling of the COVID-19 outbreak in 29 provinces in China and in the rest of the world, (2020).
- [12] A. M. Kramer, B. Dennis, A. M. Liebhold and J. Drake. The Evidence for Allee Effects. *Population Ecology*, 51(3)(2009),341-354.
- [13] M. N. Kuperman, G. Abramson, Allee effect in models of interacting species. *Chaos, Solitons Fract.* (2021), 153:111512
- [14] P.A. Stephene, W.J. Sutherland, Consequence of the Allee effet for behaviour, ecology and conservation, *Trends Ecol. Evol.*, vol. 14(10)(1999) 401-405.
- [15] J.M. Drake, A.M. Kramer, Allee effects. *Nat Educ Knowl*, 3(10):2, (2011).

- [16] J. Nagumo, S. Arimoto and S. Yoshizawa, *Proc. IRE*, 50(1962)2061–2070.
- [17] A. J. Lotka, Analytical note on certain rhythmic relations in organic systems. *Proc. Natl. Acad. Sci.* 6, (1920) 410-415.
- [18] A. J. Lotka, Elements of Physical Biology. *Williams & Wilkins, Baltimore*, (1925).
- [19] V. Volterra, Fluctuations in the abundance of a species considered mathematically. *Nature* 118 (1926)558–560. *Reprinted in L.A. Real, J.H. Brown (eds.) Foundations of Ecology. University of Chicago Press, (1991) pp. 283–285.*
- [20] T. Blaszak, Lotka-Volterra models of Predator-Prey Relationships, [https://web.mst.edu/huwen/teaching/Predator Prey Tyler Blaszak.pdf](https://web.mst.edu/huwen/teaching/Predator%20Prey%20Tyler%20Blaszak.pdf), *Missouri University of Science and Technology*, (last accessed on 2023-04-25).
- [21] K. Mahtani, An epidemiological application of the Lotka-Volterra model to predict population dynamics of COVID-19, *Parabola*. Vol. 59, Issue 1 (2023).
- [22] F. J. Ayala, M. E. Gilpin And J. G. Ehrenfeld, Competition Between Species: Theoretical Models and Experimental Tests, *Theoretical Population Biology* 4,(1973) 331-356.
- [23] P. Waltman, Competition Models in Population Biology, *SIAM*, PA, (1983).
- [24] J. Hofbauer, K. Sigmund. Evolutionary Games and Population Dynamics, *Cambridge University Press* (1998).
- [25] C. Bergeron, Mathematical vision of the equilibrium of biodiversity (Original : Vision mathématique sur l'équilibre de la biodiversité). *Bulletin AMQ*, Vol. LV, No 4, (2015) 59.
- [26] M. Hernandez. Dynamics of transitions between population interactions : a nonlinear interaction α -function defined. *Proceedings Royal Society of London B*, 265 (1998)pp. 1433-1440.
- [27] Z. Zhang, Mutualism or Cooperation among Competitors promotes Coexistence and competitive Ability, *Ecological Modelling*, 164 (2003) 271-282.
- [28] A. Okubo and S. A. Levin, Diffusion and Ecological Problems : Modern Perspectives, second Edition, *Interdisciplinary Applied Mathematics*, vol. 14, Springer, New York, (2001).
- [29] B. I. Camara, Complexity of prey-predator model dynamics with diffusion and applications (Complexité de dynamiques de modèles proie-prédateur avec diffusion et applications), *PHD Thesis, Université du Havre*, (2009).
<https://theses.hal.science/tel-00460361/document>.

Contribution of Individual Authors to the Creation of a Scientific Article (Ghostwriting Policy)

All authors have contributed equally to creation of this article.

Indeed,

Thierry Bi Boua Lagui and Gossouhon Sitionon carried out the digital simulation and the interpretation of the results of the curves of the different models. Thierry Bi Boua Lagui and Mouhamadou Dosso wrote the article after checking the simulation results. Soma Ouattara has made corrections to the English translation of the article.

Sources of Funding for Research Presented in a Scientific Article or Scientific Article Itself

There is no funding for this article.

Conflict of Interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Creative Commons Attribution License 4.0 (Attribution 4.0 International , CC BY 4.0)

This article is published under the terms of the Creative Commons Attribution License 4.0
https://creativecommons.org/licenses/by/4.0/deed.en_US