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Spojité modely v populační dynamice

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I confirm that I am the sole author of this bachelor thesis under the guidance of doc. RNDr. Jan Tomeček, Ph.D., and that I have not used any sources other than those listed in the bibliography.

In Olomouc on ....

signature

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Terminology

- $\mathbb{R}$ stands for the set of all real numbers,
  $\mathbb{N}$ stands for the set of all natural numbers.

- If we choose $n \in \mathbb{N}$, then $\mathbb{R}^n$ stands for the set of all n-tuples of real numbers.

- The set $C(J)$ stands for a set of vector functions $\mathbf{x}(t)$, whose components $x_1(t), \ldots, x_n(t)$ are continuous on J.
  If we choose $k \in \mathbb{N}$, then $\mathbf{x} \in C^k(J)$ means that components $x_1(t), \ldots, x_n(t)$ have continuous k^{th} derivatives on J.

- The set $C(G)$, $C(J \times G)$, stands for a set of vector functions $\mathbf{f}$, $\boldsymbol{\varphi}$, whose components are continuous on G, $J \times G$, respectively.
  If we choose $k \in \mathbb{N}$, then $\mathbf{x} \in C^k(J)$ means that components $x_1(t), \ldots, x_n(t)$ have continuous k^{th} derivatives on J.

Introduction

Imagine a species in the nature, imagine growth and decline of its population. But what is the reason for these changes in the population size, and are we able to make at least simple anticipation of the evolution? We know that this community is not the only one in the nature, and thus some coexistence or, vice versa, some tendencies for competing to exclude other species are required. Would we be able to describe at least basic principles of these coexistences or competitions in such a way as to be able to predict the evolution of population size?

This bachelor thesis will present and describe few population models to show that cases mentioned above are possible to model using differential equations. To show that dynamical systems give us an opportunity to model, analyse and make at least slight predictions of evolution or behaviour of some biological community. Due to the scope of the thesis, we will be interested in continuous dynamical systems.

The thesis is divided into 3 chapters. The first one is purely theoretical, there are presented some basics of scalar and planar dynamical systems, on which the following chapters build. The second one presents few models falling into Scalar dynamical systems, as well as it contains elaborated exercises dealing with the given topic. The third chapter is focused on applications of planar dynamical systems. The chapter consists of description of two population models and of elaborated exercises related to the models and their application. All these exercises were taken from [3], chapter 6.

Due to the limited range of this thesis, there are analysed and described only some selected models in population dynamics, although there exist many more.

Chapter 1

Dynamical systems

A mathematical model of some system that is changing over time is called *a dynamical system*.

If we are observing evolution of some dynamical system continuously, we are talking about *a continuous dynamical system*. On the other hand, if the evolution of dynamical system is observed at separate instants of time, it is known as *a discrete dynamical system*.

Dynamical systems can also be classified from another point of view, whether their states are described by a real number or by an n-dimensional vector of real numbers. The system in which only one variable is observed is called *a scalar dynamical* system and is more described in Section 1.1. If we follow the time evolution of two variables, we call such system *a planar dynamical system*, described in Section 1.2.

Now we will introduce the basic terms used in the theory of dynamical systems [1].

Definition 1.1. Let G be an open subset of the space $\mathbb{R}^n$ and a vector function $\boldsymbol{\varphi}(t, \mathbf{x})$ mapping the set $\mathbb{R} \times G$ into G. Furthermore, let $\boldsymbol{\varphi} \in C(\mathbb{R} \times G)$ and have the following properties:

- $\boldsymbol{\varphi}(0, \mathbf{x}^0) = \mathbf{x}^0$ for each $\mathbf{x}^0 \in G$;

[1] Theorems and Definitions are taken from [1].

- $\boldsymbol{\varphi}(t+s, \mathbf{x}^0) = \boldsymbol{\varphi}(t, \boldsymbol{\varphi}(s, \mathbf{x}^0))$ for each $t, s \in \mathbb{R}, \mathbf{x}^0 \in G$;

- for each $t \in \mathbb{R}$ there is an inverse mapping to the mapping $\boldsymbol{\varphi}(t, \bullet)$ and is equal to $\boldsymbol{\varphi}(-t, \bullet) : G \to G$.

Then the mapping $\boldsymbol{\varphi} : \mathbb{R} \times G \to G$ is called *a flow*. For each fixed $t \in \mathbb{R}$, we will name a mapping

$$\boldsymbol{\varphi}(t, \bullet) : G \to G$$

a dynamical system in $\mathbb{R}^n$. The space $\mathbb{R}^n$ will be called *a phase space*.

Consider a system of n autonomous ordinary differential equations of the first order

$$\begin{cases} x_1'(t) = f_1(x_1, \dots, x_n), \\ \vdots \\ x_n'(t) = f_n(x_1, \dots, x_n). \end{cases} \tag{1.1}$$

Functions $f_1, \dots, f_n$ are functions of n real variables. This system can be equivalently written in a vector form of

$$\mathbf{x}'(t) = \mathbf{f}(\mathbf{x}(t)), \tag{1.2}$$

where $\mathbf{f} = (f_1, \dots, f_n)$, $\mathbf{x} = (x_1, \dots, x_n)$, $\mathbf{x}' = (x_1', \dots, x_n')$.

Definition 1.2. *By a solution of the equation* (1.2) on the interval $J \subset \mathbb{R}$ we understand a vector function $\mathbf{x}(t) = (x_1(t), \dots, x_n(t)) \in C^1(J)$ such that the equation (1.2) holds for each $t \in J$.

A basic condition that we can specify for individual solutions of equation (1.2) is *an initial (Cauchy) condition*

$$x_1(0) = x_1^0, \dots, x_n(0) = x_n^0, \tag{1.3}$$

where the point $\mathbf{x}^0 = (x_1^0, \dots, x_n^0) \in \mathbb{R}^n$ is called *an initial point of solution*. The equivalent vector form of the condition (1.3) is

$$\mathbf{x}(0) = \mathbf{x}^0. \tag{1.4}$$

Definition 1.3. Finding the solution of the equation (1.2) under the given initial condition (1.4) is called *Cauchy('s) initial value problem*. We will denote it as the problem (1.2), (1.4).

The problem is to find a solution of the equation (1.2) on an interval $J \subset \mathbb{R}$ satisfying the condition (1.4). Such solution will be marked as $\boldsymbol{\varphi}(\bullet, \mathbf{x}^0)$. According to Definition 1.2 and formula (1.4), the function $\boldsymbol{\varphi}$ satisfies the following equalities

$$\boldsymbol{\varphi}(t, \mathbf{x}^0) = \mathbf{f}(\boldsymbol{\varphi}(t, \mathbf{x}^0)) \quad \text{for each } t \in J, \tag{1.5}$$

$$\boldsymbol{\varphi}(0, \mathbf{x}^0) = \mathbf{x}^0. \tag{1.6}$$

The proof of the following theorem will not be included into this thesis, but it can be found in [1].

Theorem 1.1. *(Basic theorem on existence and uniqueness) Let G be an open subset in $\mathbb{R}^n$ containing point $\mathbf{x}^0$. Further let $\mathbf{f} \in C^1(G)$.*

Then the problem (1.2), (1.4) has the unique solution $\boldsymbol{\varphi}(t, x^0)$ defined on a maximal interval $I_{x^0} = (a_{x^0}, b_{x^0}) \subset \mathbb{R}$ containing 0.

Definition 1.4. Let $\varphi(\bullet, \mathbf{x}^0)$ be a solution of the Cauchy initial value problem (1.2), (1.4). The set $\{(t, \varphi(t, \mathbf{x}^0)) : t \in I_{x^0}\}$ is called *a graph* of the solution.

Definition 1.5. Let $\varphi(\bullet, \mathbf{x}^0)$ be a solution of the Cauchy initial value problem (1.2), (1.4). The set $\{\varphi(t, \mathbf{x}^0) : t \in I_{x^0}\}$ is called *an orbit* of the solution.

Definition 1.6. *A critical point* of the equation (1.2) is a point $\overline{\mathbf{x}} = (\overline{x_1}, \ldots, \overline{x_n}) \in \mathbb{R}^n$ satisfying the system of equations

$$\begin{cases} f_1(x_1, \ldots, x_n) = 0, \\ \vdots \\ f_n(x_1, \ldots, x_n) = 0. \end{cases}$$

If a point $\overline{\mathbf{x}}$ is not a critical point, it is called *a regular point* of the equation (1.2).

Definition 1.7. *A phase portrait* of the equation (1.2) is a set of orbits of all equations' solution curves along with arrows indicating variance of point $\varphi(t, \mathbf{x}^0)$ on the orbit for increasing t. The space $\mathbb{R}^n$ containing a phase portrait of the equation is called *a phase space*.

Definition 1.8. A critical point $\overline{\mathbf{x}} \in G \subset \mathbb{R}^n$ of the equation (1.2) is called *stable*, if the following statement holds

$$\begin{cases} \forall \epsilon > 0 \ \exists \delta > 0 \ \forall \mathbf{x}^0 \in G : \parallel \overline{\mathbf{x}} - \mathbf{x}^0 \parallel < \ \delta \ \Rightarrow \parallel \varphi(t, \mathbf{x}^0) - \overline{\mathbf{x}} \parallel < \ \epsilon \\ \hfill \text{for each } t \geq 0. \end{cases} \tag{1.7}$$

Definition 1.9. A critical point $\overline{\mathbf{x}} \in G \subset \mathbb{R}^n$ of the equation (1.2) is called *unstable*, if the following statement holds

$$\begin{cases} \exists \epsilon > 0 \ \forall \delta > 0 \ \exists \mathbf{x}^0 \in G : \parallel \overline{\mathbf{x}} - \mathbf{x}^0 \parallel < \ \delta \wedge \ \parallel \varphi(t, \mathbf{x}^0) - \overline{\mathbf{x}} \parallel \geq \ \epsilon \\ \hfill \text{for at least one } t > 0. \end{cases} \tag{1.8}$$

Definition 1.10. A critical point $\overline{\mathbf{x}} \in G \subset \mathbb{R}^n$ of the equation (1.2) is called *asymptotically stable*, if it is stable and the following statement holds

$$\exists r > 0 \ \forall \mathbf{x}^0 \in G : \parallel \overline{\mathbf{x}} - \mathbf{x}^0 \parallel < \ r \ \Rightarrow \ \lim_{t \to \infty} \parallel \varphi(t, \mathbf{x}^0) - \overline{\mathbf{x}} \parallel = \ 0. \tag{1.9}$$

1.1. Scalar dynamical systems

If we put a dimension $n = 1$ in definitions and theorems above, we get dynamical systems in $\mathbb{R}$ which are called *scalar dynamical systems*. The equation (1.2) has for $n = 1$ the following form

$$x'(t) = f(x(t)). \tag{1.10}$$

Theorem 1.2. *Let be $f \in C^1(\mathbb{R})$. The solution $\varphi(t, x_0)$ of the equation (1.10), defined on (a_{x0}, b_{x0}), either converge to the critical point of the equation (1.10) for $t \to \infty$ (if $b_{x0} = \infty$), or has an infinite limit for $t \to b_{x0} \leq \infty$.*

Theorem 1.3. *Let be $f \in C^1(\mathbb{R})$ and $\overline{x} \in G$ be a critical point of the equation (1.10). If $f'(\overline{x}) < 0$, then $\overline{x}$ is asymptotically stable. If $f'(\overline{x}) > 0$, then $\overline{x}$ is unstable.*

Definition 1.11. A critical point $\overline{x} \in G$ of the equation (1.10) is called *hyperbolic*, if $f'(\overline{x}) \neq 0$. A critical point $\overline{x} \in G$ of the equation (1.10) is called *non-hyperbolic*, if $f'(\overline{x}) = 0$.

1.2. Planar dynamical systems

If we put a dimension $n = 2$ in definitions and theorems from the beginning of Chapter 1, we get planar dynamical systems, which arise from system of two autonomous ordinary differential equations of the first order

$$\begin{cases} x_1'(t) = f_1(x_1, x_2), \\ x_2'(t) = f_2(x_1, x_2), \end{cases} \tag{1.11}$$

where a mapping $\mathbf{f} = (f_1, f_2)$ has continuous partial derivatives on an open set $G \subset \mathbb{R}^2$. The system (1.11) can be written in an equivalent vector notation

$$\mathbf{x}'(t) = \mathbf{f}(\mathbf{x}(t)). \tag{1.12}$$

According to Definition 1.6, the point $\overline{\mathbf{x}} = (\overline{x}_1, \overline{x}_2) \in G$ is a critical point of the equation (1.12), if and only if

$$f_1(\overline{x}_1, \overline{x}_2) = 0, \qquad f_2(\overline{x}_1, \overline{x}_2) = 0.$$

1.2.1. Planar linear dynamical systems with a constant matrix in canonical form

This chapter includes equations of the form

$$\mathbf{x}' = \mathbf{J} \cdot \mathbf{x}(t). \tag{1.13}$$

for any two-dimensional constant matrix J in Jordan canonical form. The phase space, as defined in Definition 1.7, is in that case $\mathbb{R}^2$.

Theorem 1.4. *Let J be a matrix with the complex conjugate eigenvalues $\lambda_{1,2} = \alpha \pm i\beta$, where $\alpha \neq 0$, $\beta \neq 0$. Then the equation (1.13) has one of the four phase portraits on Figure 1.1.*

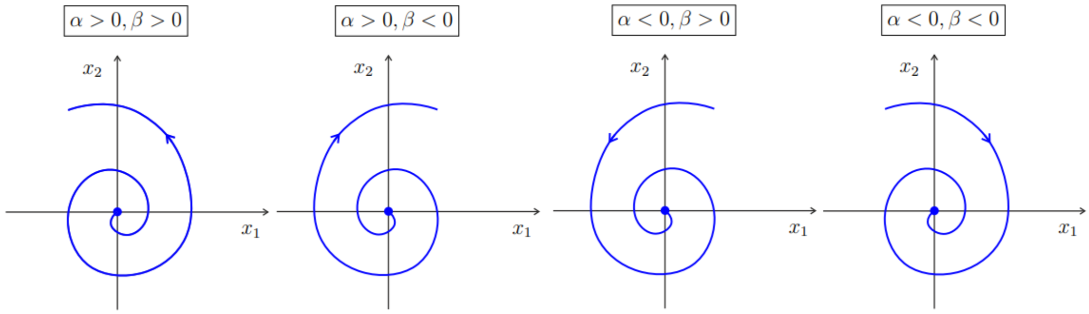

Figure 1.1: The picture was taken from [1].

Theorem 1.5. *Let J be a matrix with purely imaginary eigenvalues $\lambda_{1,2} = \pm i\beta$, where $\beta \neq 0$. Then the equation (1.13) has one of the four phase portraits on Figure 1.2.*

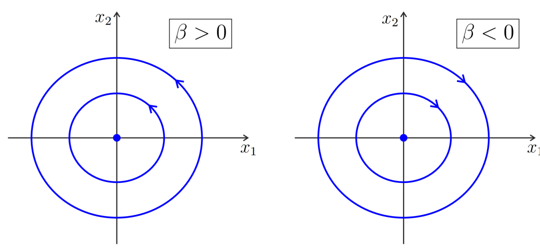

Figure 1.2: The picture was taken from [1].

1.2.2. Planar non-linear dynamical systems

Definition 1.12. A critical point $\overline{\mathbf{x}} \in G$ of the equation (1.12) is called *hyperbolic*, if the Jacobian matrix

$$\mathrm{D}\mathbf{f}(\overline{\mathbf{x}}) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1}(\overline{x}_1, \overline{x}_2) & \frac{\partial f_1}{\partial x_2}(\overline{x}_1, \overline{x}_2) \\ \frac{\partial f_2}{\partial x_1}(\overline{x}_1, \overline{x}_2) & \frac{\partial f_2}{\partial x_2}(\overline{x}_1, \overline{x}_2) \end{pmatrix} \tag{1.14}$$

has both eigenvalues with non-zero real components.

Definition 1.13. A critical point $\overline{\mathbf{x}} \in G$ of the equation (1.12) is called *non-hyperbolic*, if the Jacobian matrix (1.14) has at least one eigenvalue with zero real component.

Definition 1.14. Let $\overline{\mathbf{x}} \in G$ be a critical point of the equation (1.12). The equation

$$\mathbf{y}' = \mathrm{D}\mathbf{f}(\overline{\mathbf{x}})\mathbf{y} \tag{1.15}$$

is called *a linear variational equation* to the equation (1.12) at the point $\overline{\mathbf{x}}$.

Theorem 1.6. *Let $\overline{\mathbf{x}} \in G$ be a hyperbolic critical point of the equation (1.12). If the eigenvalues of the Jacobian matrix $\mathrm{D}\mathbf{f}(\overline{\mathbf{x}})$ have negatives real parts, then the critical point $\overline{\mathbf{x}}$ is asymptotically stable.*

Theorem 1.7. *Let $\overline{\mathbf{x}} \in G$ be a hyperbolic critical point of the equation (1.12). If at least one eigenvalue of the Jacobian matrix $D\mathbf{f}(\overline{x})$ has a positive real component, then the critical point $\overline{\mathbf{x}}$ is unstable.*

Definition 1.15. A critical point $\overline{\mathbf{x}}$ of the equation (1.12) is called *a source (sink)*, if there exists a neighbourhood U of the point $\overline{\mathbf{x}}$ such that for each point $\mathbf{x^0} \in U$ the entire positive part (negative part) of the orbit of the solution $\varphi(t, \mathbf{x^0})$ stays in U and moreover

$$\lim_{t\to\infty} \varphi(t, \mathbf{x^0}) = \overline{\mathbf{x}} \qquad \left(\lim_{t\to-\infty} \varphi(t, \mathbf{x^0}) = \overline{\mathbf{x}}\right).$$

Definition 1.16. A critical point $\overline{\mathbf{x}}$ of the equation (1.12) is called *a saddle*, if there exist points $\mathbf{x^0} \neq \overline{\mathbf{x}}$ and $\mathbf{x^1} \neq \overline{\mathbf{x}}$ such that

$$\lim_{t\to\infty} \varphi(t, \mathbf{x^0}) = \overline{\mathbf{x}} \qquad \text{and} \qquad \lim_{t\to-\infty} \varphi(t, \mathbf{x^1}) = \overline{\mathbf{x}}.$$

Theorem 1.8. *Let $\overline{\mathbf{x}} \in G$ be a hyperbolic critical point of the non-linear equation (1.12). Then the point $\overline{\mathbf{x}}$ is*

- *a source,*
- *a sink,*
- *a saddle*

if the critical point $(0, 0)$ of the linear variational equation (1.15) is such.

Definition 1.17. A critical point $\overline{\mathbf{x}}$ of the equation (1.12), which is a sink or a source is called *a spiral*, if there exists a neighbourhood U of the point $\overline{\mathbf{x}}$ such that for each point $\mathbf{x^0} \in U$ either the positive or the negative part of the orbit of the solution $\varphi(t, \mathbf{x^0})$ circulates around the point $\overline{\mathbf{x}}$ infinitely. It means that when transformed into polar coordinates $r(t)$ and $\theta(t)$,

$$\lim_{t\to\infty} |\theta(t)| = \infty \qquad \text{or} \qquad \lim_{t\to-\infty} |\theta(t)| = \infty.$$

If the orbits circulate around the point $\overline{\mathbf{x}}$ only a finite number of times, then the point $\overline{\mathbf{x}}$ is called *a node*.

Theorem 1.9. *(Method of linearization) Let $\mathbf{f} \in C^2(G)$ and let $\overline{\mathbf{x}} \in G$ be a hyperbolic critical point of the non-linear equation* (1.12).
Then the point $\overline{\mathbf{x}}$ is

- *a node-source,*
- *a spiral-source,*
- *a node-sink,*
- *a spiral-sink,*
- *a saddle*

if the critical point $(0, 0)$ of the linear variational equation (1.15) *is such.*

Chapter 2

Application of scalar dynamical systems

2.1. Exponential growth (Malthusian model)

Thomas Robert Malthus is largely famous for his idea of limiting the growth of the population. In 1798, he published *An Essay on the Principle of Population* where his model, also called *Exponential growth*, is presented. Malthus' thesis is based on the observation that there is an asymmetry between population growth and resources production growth. In the mathematical language it means that while the population increases exponentially, the resources increase only arithmetically. So it follows that even though there were not any war or epidemic or something different able to decrease the population size, a famine will be necessary. This famine could last until the population level decreases below the available resources. Malthus also proposed several ways, quite drastic ways, to regulate the population. These rules as well as any other policy of demographic regulation is called Malthusianism.

The model assumes that the birth and death rates are proportional to the size of the population. The concepts of fertility rate (number of births per unit of time and individual) β and mortality rate (number of deaths per unit time and per individual) δ are introduced and assumed to be constant in time.

The rate of change of population size $N(t)$ is then the difference, i.e

$$N'(t) = \beta N(t) - \delta N(t), \tag{2.1}$$

but the rate is mostly known in the form of a differential equation

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t), \quad r = \beta - \delta, \tag{2.2}$$

with an initial condition $N(0) = N_0 > 0$.
The differential equation (2.2) is called *Exponential growth* or *Malthusian growth model*. However the model is better known in the form of the solution of equation (2.2).

To find this solution we can use the method of separation of variables [1]. This way we get functions

$$f(t) = r \quad \text{and} \quad g(N) = N,$$

for which we have

$$D(f) = \mathbb{R} \quad \text{and} \quad D(g) = \mathbb{R},$$

therefore it makes sense to look for a solution only in the set $\mathbb{R}^2$. But since this is a population model, it only makes sense to consider non-negative N, therefore we will look for a solution in the set

$$\Omega = \mathbb{R} \times (0, \infty).$$

Now we need to check if there are any critical points. Definition 1.6 implies that a critical point of a differential equation is an expression of a solution whose value does not change over time. In other words, we have to find for which N holds

$$\frac{\mathrm{d}N}{\mathrm{d}t} = 0.$$

[1] Explanation of method of separation of variables can be found in [2]

The equality applies only for $N = 0$, i.e. the system has one critical point $N = 0$, which is anyway outside the investigated space Ω.

Let write the equation (2.2) in the form

$$N'(t) = rN(t), \quad r \in \mathbb{R},\, t \in \mathbb{R}.$$

After modification it is possible to apply integration

$$\int \frac{N'(t)}{N(t)}\,\mathrm{d}t = \int r\,\mathrm{d}t.$$

In order to proceed, we use a substitution $\omega = N(t)$ and $\mathrm{d}\omega = N'(t)\,\mathrm{d}t$, consequently we have

$$\int \frac{\mathrm{d}\omega}{\omega} = rt + c_1, \quad c_1 \in \mathbb{R}.$$

Then we can continue by logarithmization

$$\ln|N(t)| = rt + c_1, \quad c_1 \in \mathbb{R}.$$

Since $N(t) > 0$, $\forall t \in \mathbb{R}$, we can remove the absolute value, thus

$$\ln(N(t)) = rt + c_1, \quad c_1 \in \mathbb{R}.$$

By expressing $N(t)$ from the equation we get a general solution

$$N(t) = e^{rt+c_1}, \quad t \in \mathbb{R}, \quad c_1 \in \mathbb{R},$$

or otherwise

$$N(t) = ce^{rt}, \quad t \in \mathbb{R}, \quad c \in \mathbb{R}^+.$$

But we need to find such solution suiting the initial condition $N_0 = N(0)$. If we compute $N(0)$, we get such $c = N_0$, which suits the initial condition. Hence the wanted solution of the equation (2.2) is

$$N(t) = N_0 e^{rt}, \quad t \in \mathbb{R}, \tag{2.3}$$

where

- $N(0) = N_0$ is the initial population size,
- $r = \beta - \delta$ is the population growth rate, sometimes called Malthusian parameter,
- t is the time.

We know that the parameter r is equal to the difference $\beta - \delta$. It implies that if fertility exceeds mortality, i.e. $\beta > \delta$, the Malthusian model predicts *exponential* population growth, shown in Figure 2.1. Contrariwise if $\beta < \delta$, the population must decrease until it is extinguished. This type of the model is called *Exponential decay* and is represented on Figure 2.2.

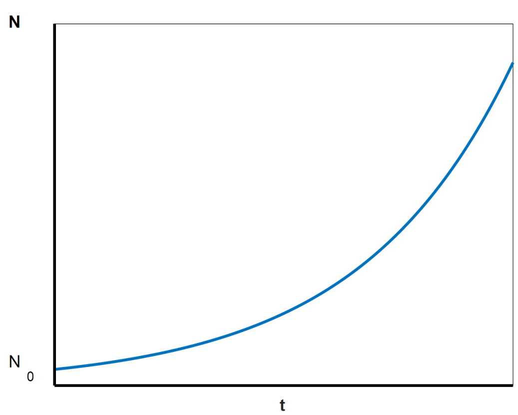

Figure 2.1: Exponential growth $N(t) = N_0 e^{rt}, r > 0$, with an initial population N_0

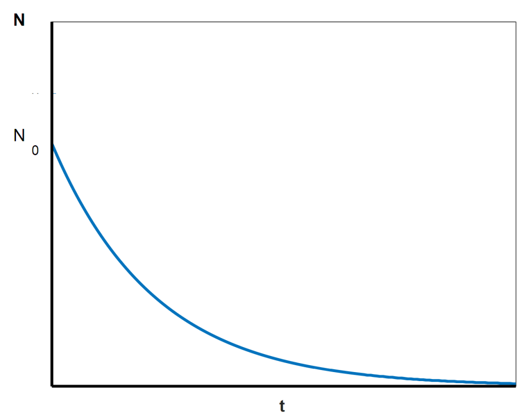

Figure 2.2: Exponential decay $N(t) = N_0 e^{rt}, r < 0$, with an initial population N_0

In the real world, examples of exponential growth are very limited, because expansion runs into other real-world constraints such as space and food resources. Nevertheless, this principle can be observed, for example, in Radioactive decay. Or the model can be used, for example, to model the initial growth phase of bacterial populations in an optimal environment or as a basic model of economic growth. However, this model is quite simple to be considered for populations interacting with their environment, such as ours.

2.2. Logistic growth

In 1838, Pierre François Verhulst, inspired by Malthus, proposed his own model called *Logistic growth.* Whereas Malthus introduced fertility and mortality rates to be constant, Verhulst came with an idea that the larger the population, the lower fertility rate and the higher death rate. It means that if the growth reaches maximum rate for a certain size of population, then the rate begins to slow down until it stops completely when the population reaches a critical size K. The parameter K is interpreted as the maximum number of individuals that the environment is able to support.

The model considers a non-constant intrinsic growth rate

$$g(N) = r\left(1 - \frac{N}{K}\right), \tag{2.4}$$

where we can see that the rate $g(N)$ depends on the population size N. We also see that as the population size N increases, the rate $g(N)$ decreases. Once the critical population size K is reached, the growth rate will be null, because the term $\left(1 - \frac{N}{K}\right)$ will be equal to zero.

The model is mathematically described by the following equation

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\left(1 - \frac{N(t)}{K}\right), \tag{2.5}$$

where

- $N(t)$ represents the size of the population over time,
- $r > 0$ is a growth rate per capita,
- K is a critical size of the population, also known as carrying capacity,
- N_0 represents the initial population.

The solution of the model and its properties are studied and shown in Example 2.2.1 originally from [3].

Problem 2.2.1. Let's consider the following equation

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N. \tag{2.6}$$

(a) Assuming that $N(0) = N_0$, integrate equation (2.6) and show that its solution is given by

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}}. \tag{2.7}$$

(b) Show that the solution given by (2.7) has the following properties:

(1) $\lim_{t \to \infty} N(t) = K$,

(2) the graph is convex for t such that $N_0 < N(t) < K/2$,

(3) the graph is concave for t such that $K/2 < N(t) < K$,

(4) if $N_0 > K$, the graph is convex.

Solution

ad(a): The equation (2.6) can be solved by the method of separation of variables [2]. Thus we obtain functions

$$f(t) = r \quad \text{and} \quad g(N) = \left(1 - \frac{N}{K}\right)N$$

for which we have

$$D(f) = \mathbb{R} \quad \text{and} \quad D(g) = \mathbb{R}.$$

It follows that it makes only sense to find a solution in the set $\mathbb{R}^2$. However, we are investigating a population model, therefore we will look for a solution only in the set

$$\Omega = \mathbb{R} \times (0, \infty).$$

In order to solve the equation (2.6), we must find its critical points. According to Definition 1.6, the critical point is the point at which the population reaches an equilibrium. It means we solve

$$\frac{\mathrm{d}N}{\mathrm{d}t} = 0.$$

[2]Explanation of method of separation of variables can be found in [2]

We found that it holds if and only if $N = 0$ or $1 - \frac{N}{K} = 0$, which implies that we have two critical points $N = 0$ and $N = K$.

First, we will focus on finding the solution in $\Omega_1 = \mathbb{R} \times (0, K)$, it means we have to find a function N whose graph is a subset of Ω_1. We come out of the equation (2.6) which will be denoted as $N'(t)$ in the following part. Thus we have

$$N'(t) = r\left(1 - \frac{N(t)}{K}\right) N(t).$$

The equation must be rearranged, so that it could be integrated. So we acquire

$$\int \frac{N'(t)}{\left(1 - \frac{N(t)}{K}\right) N(t)}\,\mathrm{d}t = \int r\,\mathrm{d}t.$$

If we use a substitution $\omega = N(t)$ and $\mathrm{d}\omega = N'(t)\,\mathrm{d}t$, we have

$$\int \frac{\mathrm{d}\omega}{\left(1 - \frac{\omega}{K}\right)\omega} = rt + c, \quad c \in \mathbb{R},$$

and we can continue by logarithmization

$$\ln|N(t)| - \ln\left|1 - \frac{N(t)}{K}\right| = rt + c, \quad c \in \mathbb{R}. \tag{2.8}$$

The absolute values can be removed because the following conditions are satisfied

1. $N(t) > 0 \quad \forall t \in \mathbb{R}$,
2. $(1 - \frac{N(t)}{K}) > 0$, this condition applies, since $N(t) < K$ suits Ω_1.

To find out the solution $N(t)$, we need to rearrange the equation (2.8) which yields

$$\ln\left(\frac{N(t)}{1 - \frac{N(t)}{K}}\right) = rt + c.$$

Then we need to find an antilogarithm and simplify so that we get

$$N(t) = e^{rt+c}\left(1 - \frac{N(t)}{K}\right),$$

and finally express $N(t)$ which leads to

$$N(t) = \frac{e^{rt+c}}{1 + \frac{e^{rt+c}}{K}} = \frac{Ke^{rt+c}}{K + e^{rt+c}}. \tag{2.9}$$

We found a general solution, but now we want to find such value of K for which the solution suits the initial condition $N_0 = N(0)$. Thus we make the substitution $N(0)$ and then, we can express $K = \frac{N_0 e^c}{e^c - N_0}$. If we put this found K into $N(t)$, we obtain the required solution

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}}, \quad t \in \mathbb{R}.$$

Then, we will focus on finding the solution in $\Omega_2 = \mathbb{R} \times (K, \infty)$, it means that we will search for a function N whose graph is a subset of Ω_2. Using similar procedures as in the previous part, we obtain

$$\ln |N(t)| - \ln \left| 1 - \frac{N(t)}{K} \right| = rt + c,$$

where $c \in \mathbb{R}$. There we can also remove the absolute values, because the following conditions are satisfied

1. $N(t) > 0 \quad \forall t \in \mathbb{R}$,
2. $(1 - \frac{N(t)}{K}) < 0$, this condition applies, as $N(t) > K$ suits Ω_2.

After removing the absolute values and simplification, we have

$$\ln \left(\frac{N(t)}{\frac{N(t)}{K} - 1} \right) = rt + c,$$

which can be further modified so that we get the general solution

$$N(t) = \frac{-e^{rt+c}}{1 - \frac{e^{rt+c}}{K}} = \frac{-Ke^{rt+c}}{K - e^{rt+c}}.$$

Again, we operate with the initial condition $N_0 = N(0)$ and we want to find a solution suiting that condition. Thus, after expressing $K = \frac{N_0 e^c}{N_0 - e^c}$ from $N(0)$ and substituting it in $N(t)$, the wanted solution is acquired

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}}, \quad t \in \mathbb{R}.$$

ad(b):

To confirm the property **(1)**, we have to compute

$$\lim_{t\to\infty} \frac{KN_0}{N_0 + (K - N_0)e^{-rt}} = \frac{KN_0}{N_0} = K.$$

Thus the statement of the model, that the population size tends to its maximum number K over time t, is proved.

The proof of properties **(2)**, **(3)**, **(4)** requires calculation of second derivative of the function $N(t)$, i.e. we need to compute

$$N''(t) = \left((rN(t))' \left(1 - \frac{N(t)}{K}\right) + rN(t)\left(1 - \frac{N(t)}{K}\right)'\right)(N'(t))^2,$$

which can be simplified by expanding and rearranging, hence we get

$$N''(t) = r^2 N(t)\left(1 - \frac{N(t)}{K}\right)\left(1 - \frac{2N(t)}{K}\right)(N'(t))^2.$$

Then it is necessary to find inflexion points and, for each interval, determine concavity or convexity. To find inflexion points, we have to solve $N''(t) = 0$, which is satisfied for $N(t) = 0$, $N(t) = K$ or $N(t) = \frac{K}{2}$. Now it remains to take any value of variable N from each interval, $\left(0; \frac{K}{2}\right)$, $\left(\frac{K}{2}; K\right)$, $(K; \infty)$, substitute it in $N''(t)$ and find out the sign of the result. It can be written in a table for clarity, as shown in Figure 2.3.

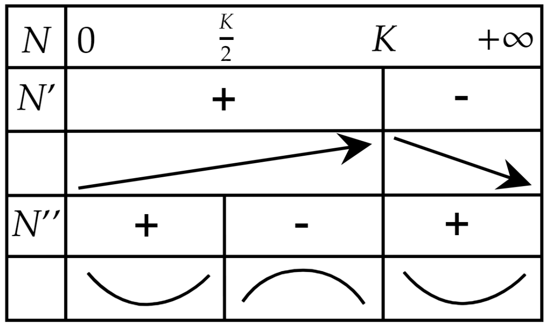

Figure 2.3: The sign table for function N where $N' = N'(t)$ and $N'' = N''(t)$

Now we are able to make following conclusions.

For t such that $N_0 < N(t) < \frac{K}{2}$, the value of $N''(t)$ is positive, so the graph is convex. In Figure 2.4 it applies for $t \in (0; t_i)$.

For t such that $\frac{K}{2} < N(t) < K$, the value of $N''(t)$ is negative, so the graph is concave. In Figure 2.4 it applies for $t \in (t_i; \infty)$.

For t such that $K < N(t)$, the value of $N''(t)$ is positive, so the graph is convex. In Figure 2.4 it applies for $t \in (0, \infty)$.

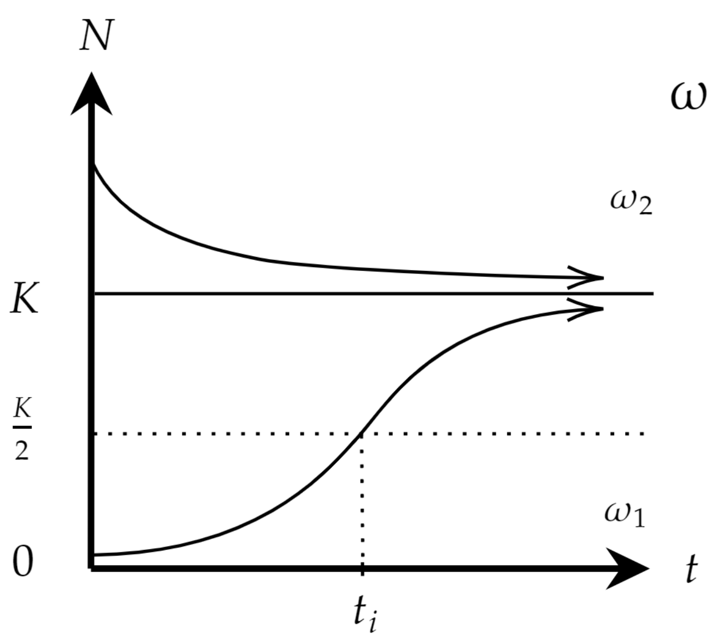

Figure 2.4: Representation of the size of the population N over time t, where t_i is an inflexion point of the function N

In example 2.2.1, we have derived the solution of the *Logistic growth* model together with its properties. Its graphical representation can be seen in Figure 2.5, which shows the population dynamics given by the model.

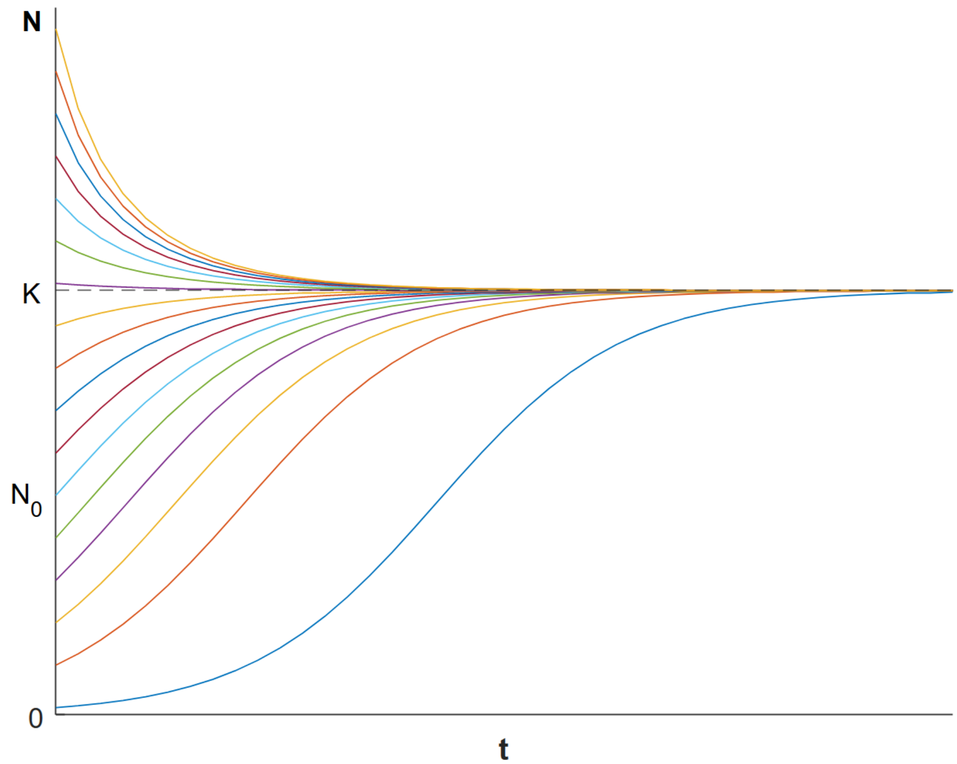

Figure 2.5: Representation of the population size N over time t where $K = 120$ and $r = 1.2$

This model is already more suitable for modelling population growths than the *Exponential growth model*, because it takes into account environmental constraints. For example, yeast, a microscopic fungus used to make bread and alcoholic beverages, can produce a classic S-shaped curve when grown in a test tube. Yeast growth levels off as the population hits the limit of the available nutrients. But we can also mention an example from the real world where a logistic growth curve fits the population dynamics, and that is the population growth of the harbor seal in Washington State in the 1980s and 1990s [3].

[3]This phenomenon is discussed in the survey [9].

Chapter 3

Application of planar dynamical systems

3.1. Lotka-Volterra model

It is a mathematical model describing oscillations in a biological system, where one species is a prey and the second one is a predator.

The dynamics of predator-prey system is mathematically expressed by a pair of first-order non-linear differential equation developed independently by Alfred J. Lotka and Vito Volterra.

The model was initially proposed by Alfred J. Lotka in the theory of autocatalytic chemical reactions in 1910. In 1920, Lotka extended the model, via Andrey Kolmogorov, to "organic systems" using a plant species and a herbivorous animal species as an example and in 1925 he used the equations to analyse predator–prey interactions in his book on biomathematics.

In 1926, Voltera developed the same set of equations to describe maritime phenomenon observed by Umberto D'Ancona - D'Ancona studied the fish catches in the Adriatic Sea and he had noticed that the percentage of predatory fish caught had increased during the years of World War I (1914–18). This puzzled him, as the fishing effort had been very much reduced during the war years.

The Lotka–Volterra model has been used to explain the dynamics of natural populations of predators and prey, such as the lynx and snowshoe hare data of the Hudson's Bay Company, that traded in animal furs in Canada, and the moose and wolf populations in Isle Royale National Park.

List of simplifying assumptions made by Volterra:

1. Prey population have an unlimited supply of food at all time.
2. Prey grow in an unlimited way when predators do not keep them under control.
3. Predators depend on the presence of their prey to survive, because the growth rate of the predator population is proportional to food intake (the rate of predation).
4. The rate of predation depends on the likelihood that a victim is encountered by a predator.

As we are interested in evolution over time, we notice $X(t)$ number of preys and $Y(t)$ number of predators over time t. Both are therefore functions from $\mathbb{R}^+$ to $\mathbb{N}$, but in order to have mathematical tools we prefer to work with continuous variables. This is why we consider two new quantities

$$x(t) = \frac{X(t)}{X_0} \quad \text{and} \quad y(t) = \frac{Y(t)}{Y_0}, \tag{3.1}$$

where X_0 (respectively Y_0) is a fixed number of prey (respectively predators). The quantities x and y are therefore proportions of prey and predators. The variations of $x(t)$ and $y(t)$ are hence small quantities, so that we can assume that $x(t)$ and $y(t)$ are continuous functions from $\mathbb{R}^+$ to $\mathbb{R}$.

For the rest, we will make the additional regularity presumption by assuming these functions are differentiable. Consider the rates of change over an interval $\triangle t$

$$\frac{\frac{\triangle x(t)}{\triangle t}}{x(t)} = \frac{\frac{\triangle X(t)}{\triangle t}}{X(t)}. \tag{3.2}$$

If we suppose that the variations of $x(t)$ are small compared to $X(t)$, we can go to the limit

$$\lim_{\triangle t \to 0} \frac{\frac{\triangle x(t)}{\triangle t}}{x(t)} = \frac{x'(t)}{x(t)}. \tag{3.3}$$

In the absence of predators, the prey have a constant growth rate (we assume abundant food and lack of competition) and it is represented by

$$\frac{x'(t)}{x(t)} = a. \tag{3.4}$$

After rearrangement we acquire a Malthus-type equation $\frac{\mathrm{d}x}{\mathrm{d}t} = ax$, $a > 0$, which gives by integration the geometrical law of increase $x(t) = x_0 e^{at}$ [1]. This corresponds to assumption 2, i.e. the prey grow in an unlimited way when predators do not keep them under control.

Likewise, predators tend to disappear in the absence of prey for lack of food. This mortality rate is expressed by

$$\frac{y'(t)}{y(t)} = -c. \tag{3.5}$$

It remains to take into account the interactions between the two species.

The predation rate (the rate of decline of prey due to predators) is assumed to be proportional to the number of predators. Hence the equation (3.4) has the form

$$\frac{x'(t)}{x(t)} = a - by(t), \quad a, b > 0. \tag{3.6}$$

The rate of change in the number of predators is proportional to the amount of food available to them, i.e. the number of prey. Adequate form of the equation (3.5) is then

$$\frac{y'(t)}{y(t)} = -c + dx(t), \quad c, d > 0. \tag{3.7}$$

By adding the initial conditions (beginning population of each species) we obtain set of equations called Lotka-Volterra equations

$$\begin{cases} x' = x(a - by) \\ y' = y(-c + dx) \end{cases} \quad \text{and} \quad (x(0), y(0)) = (x_0, y_0), \quad x_0, y_0 > 0, \tag{3.8}$$

[1] *Malthusian exponential growth* is discussed in Section 2.1.

which can be written into the more known form

$$\begin{cases} \frac{dx}{dt} = ax - bxy \\ \frac{dy}{dt} = -cy + dxy \end{cases} \quad \text{and} \quad (x(0), y(0)) = (x_0, y_0), \quad x_0, y_0 > 0. \tag{3.9}$$

The term xy approximates the likelihood of an encounter between predators and prey since both species move about randomly and are uniformly distributed over their habitat. The ratio b/d is analogous to predation efficiency, i.e. the efficiency of converting a unit of prey mass into a unit of predator mass.

To summarize the meaning of each parameter of the Lotka-Volterra equations:

- $a > 0$ represents growth rate of preys,
- $b > 0$ represents predation coefficient,
- $c > 0$ represents mortality rate of predators,
- $d > 0$ represents reproductive rate of the predator per prey.

The system of Lotka-Volterra equations has two steady states

$$(\overline{x_1}, \overline{y_1}) = (0, 0), \tag{3.10}$$

$$(\overline{x_2}, \overline{y_2}) = \left(\frac{c}{d}, \frac{a}{b}\right). \tag{3.11}$$

Here we can see that the steady-state level of prey is not dependent on its own growth rate or mortality, but rather on parameters associated with the predator ($\overline{x_2} = c/d$). Inversely, the same applies for predator.
To find out a character of the steady states $(\overline{x_1}, \overline{y_1})$ and $(\overline{x_2}, \overline{y_2})$, we use the Jacobian matrix of partial derivatives of the right part of the system

$$J(x, y) = \begin{pmatrix} a - by & -bx \\ dy & dx - c \end{pmatrix}. \tag{3.12}$$

Let us consider the critical point $(\overline{x_1}, \overline{y_1})$. If we substitute the critical point in the Jacobian matrix (3.12), we get

$$J(\overline{x_1}, \overline{y_1}) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \tag{3.13}$$

and we are able to compute eigenvalues of the matrix

$$\lambda_1 = a \quad \text{and} \quad \lambda_2 = -c.$$

The critical point is hence hyperbolic by Definition 1.12. It suggests that we can apply Theorem 1.7, according to which the critical point is unstable.
According to the classification of phase portraits in [1], Chapter 6, the critical point $(\overline{x_1}, \overline{y_1})$ appears to be a saddle, because it satisfies the condition $\lambda_1\lambda_2 < 0$, by which the saddle point is characterized there. To verify this statement, if we set $x = 0$, $\frac{\mathrm{d}y}{\mathrm{d}t}$ will be negative, therefore y decline $\forall t > 0$. However, if we set $y = 0$, $\frac{\mathrm{d}x}{\mathrm{d}t}$ will be positive, therefore x increases $\forall t > 0$. These two cases are shown in Figure 3.1. Based on these behaviours, and the assertion of Definition 1.16, we can certainly say that the critical point $(0, 0)$ is a saddle.

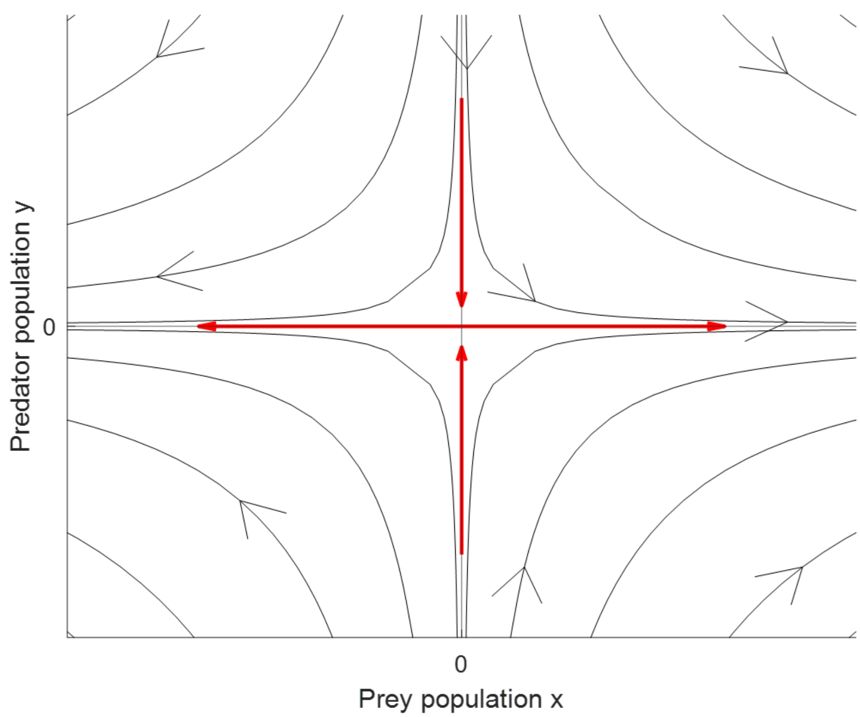

Figure 3.1: The saddle critical point $(0, 0)$.

Consequently, it is easy to conclude that the natural extinction of the prey population is not possible. This follows already from the very nature of the critical point, which is instability, i.e. for populations sizes however close to this critical point, there will be no extinction, the populations will always recover.

Let us now consider the second critical point $(\overline{\mathrm{x}_2}, \overline{\mathrm{y}_2}) = \left(\frac{c}{d}, \frac{a}{b}\right)$. We again substitute the critical point into the Jacobian matrix (3.12), so we get

$$J(\overline{x_1}, \overline{y_1}) = \begin{pmatrix} 0 & -\frac{bc}{d} \\ \frac{ad}{b} & 0 \end{pmatrix}, \tag{3.14}$$

which allows us to calculate the eigenvalues

$$\lambda_{1,2} = \pm i\sqrt{ca}.$$

The critical point is hence non-hyperbolic by Definition 1.13. Since the eigenvalues of $J(\overline{\mathrm{x}_2}, \overline{\mathrm{y}_2})$ are pure imaginary and $\det J(\overline{x_1}, \overline{y_1}) > 0$, the critical point $(\overline{x_1}, \overline{y_1})$ appears to be a center, following the classification of phase portraits in [1], Chapter 6. A verification can be done simply by resolving the system (3.9). If we take the equations of the system (3.9) and divide the second equation by the first one, we acquire

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{y}{a - by}\frac{dx - c}{x}.$$

Using the method of separation of variables [2] we have

$$\int \frac{a - by}{y}\,\mathrm{d}y = \int \frac{dx - c}{x}\,\mathrm{d}x,$$

which yields

$$a \ln|y| - by = dx - c\ln|x| + c_1, \quad c_1 \in \mathbb{R}. \tag{3.15}$$

Since the model is the population one, we are only interested in solutions for which $x > 0$ and $y > 0$ hold. Consequently we can remove the absolute value from (3.15) and after rearrangement we get

$$a \ln y + c \ln x - by - dx = c_1, \quad c_1 \in \mathbb{R}. \tag{3.16}$$

Let us denote

$$L(x, y) = a \ln y + c \ln x - by - dx.$$

[2] Explanation of method of separation of variables can be found in [2]

Then obviously, the solution of the system (3.9) is a pair $(x(t), y(t))$, satisfying $x(t) > 0$ and $y(t) > 0$, so that there exists $c_1 \in \mathbb{R}$ such that

$$L(x(t), y(t)) = c_1, \quad \forall t \in \mathbb{R}.$$

In other words, the orbits of the system lie at the levels of the function $L(x, y)$ and are represented in Figure 3.2.

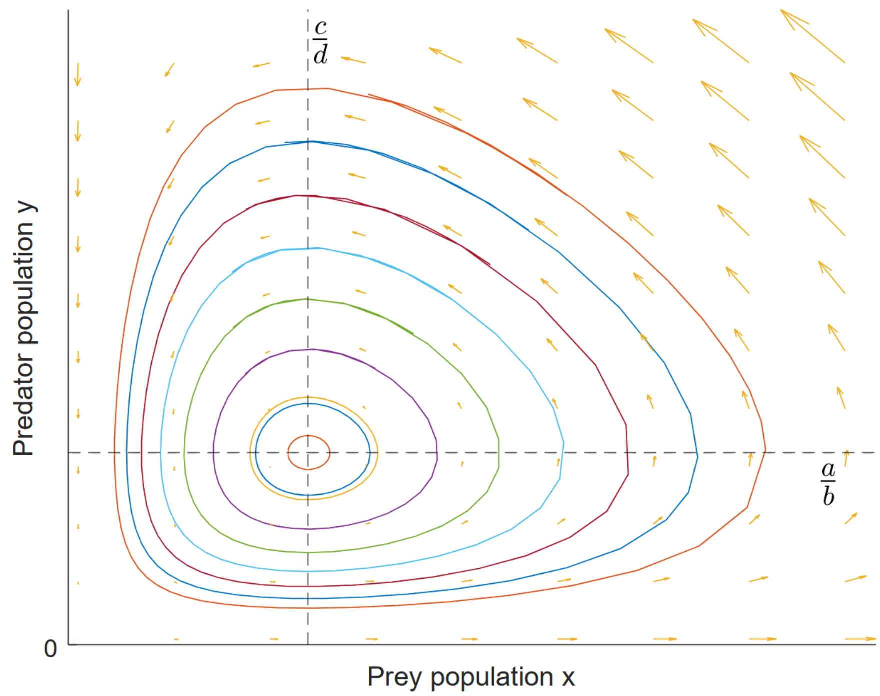

Figure 3.2: A neutral stability predicted by Lotka-Volterra equation.

We can clearly see that the orbits oscillate periodically around the critical point $\left(\frac{c}{d}, \frac{a}{b}\right)$. These periodicity is better illustrated in Figure 3.3.

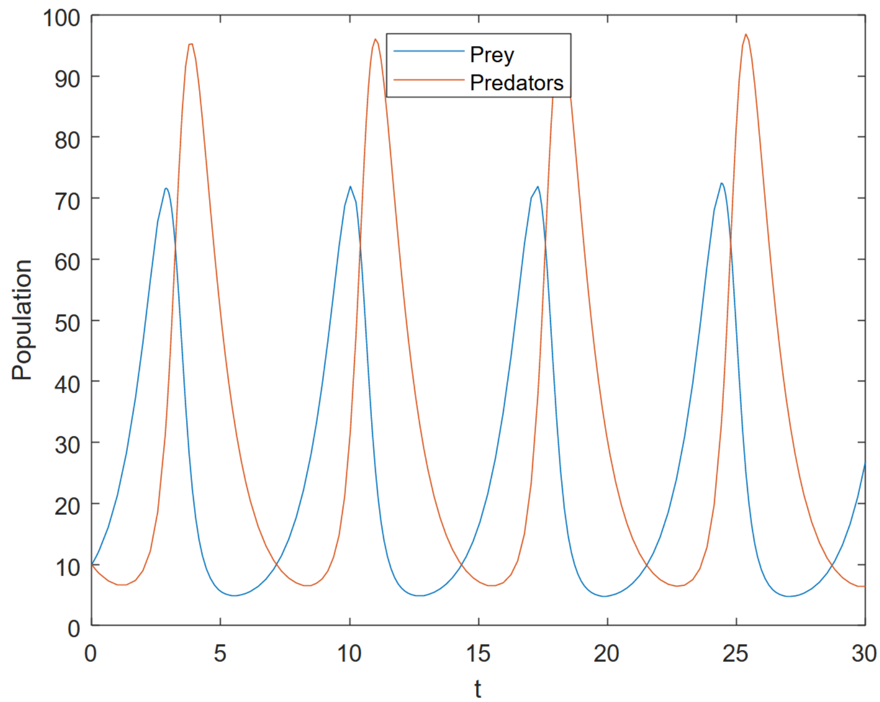

Figure 3.3: $a = 1,\ b = 0.03,\ c = 1,\ d = 0.04$

Already according to Figure 3.2, the critical point $\left(\frac{c}{d}, \frac{a}{b}\right)$ seems to be a center. However, we can also check it by considering how many times an orbit of the system (3.9) intersects the line $x = \frac{c}{d}$. On the nullcline $x = \frac{c}{d}$, we observe that

$$L\left(\frac{c}{d}, y\right) = a \ln y - by + c \ln \frac{c}{d} - c.$$

Let us denote

$$f(y) = L\left(\frac{c}{d}, y\right)$$

and examine the monotony of the function f on its domain $(0, \infty)$, which is at the same time the interval of our interest because, as already mentioned, we are only interested in positive values of y. Thus we need to compute its first derivative

$$f'(y) = \frac{b}{y}\left(\frac{a}{b} - y\right).$$

Obviously,

- $f'(y) > 0$ for $y \in \left(0, \frac{a}{b}\right)$,

- $f'(y) < 0$ for $y \in \left(\frac{a}{b}, \infty\right)$,

thus the function $f(y)$ is increasing on the interval $\left(0, \frac{a}{b}\right)$ and decreasing on $\left(\frac{a}{b}, \infty\right)$, and the point $\frac{a}{b}$ is therefore a point at which the function $f(y)$ has a strict local maximum. Moreover

$$\lim_{t \to 0^+} f(y) = -\infty,$$
$$\lim_{t \to \infty} f(y) = -\infty.$$

Hence it must be true that the equation $f(y) = C$ has at most two solutions for any given constant $C \in \mathbb{R}$. Specifically

- no solution, if $C > f\left(\frac{a}{b}\right)$,
- one solution, if $C = f\left(\frac{a}{b}\right)$,
- two solutions, if $C < f\left(\frac{a}{b}\right)$.

Consequently, trajectory of the orbits of the system (3.9), defined by the prescription (3.16), intersects the line $x = \frac{c}{d}$ at most twice for any value of the constant c_1. Therefore, the trajectory cannot be a spiral because the set of the solutions of the equation $f(y) = C$ is not infinite, and hence the critical point $\left(\frac{c}{d}, \frac{a}{b}\right)$ must be a center.

To interpret the model, let us recall that the size of the predator population is completely dependent on the size of the prey population, and vice versa.
If there is enough prey, the predator population begins to grow. As the number of predators increases, the amount of prey caught increases so that the prey does not reproduce fast enough and the prey population starts to decrease. This fact means that predators will die out due to lack of food. This will eventually benefit the prey, as the environment will again be safer for them and their population will start to grow again. And so the whole scenario repeats periodically.
In this model, therefore, natural extinction of populations is not possible.

The model is the simplest one from predator-prey models and its idea consists of the interaction of two populations in a permanent environment. Even if we don't find many such environments in the real life, the model can be used as a helpful diagnostic tool. For example, as noted in [3], we could use this model together with minor variants to test out a set of assumptions and so identify stabilizing and destabilizing influences. Moreover, the model served as a basis for other models that were created by modifying this model.

3.2. Lotka-Volterra model with a refuge

It may be interesting to consider that some prey may hide from predators. Such a model can be conceived in several ways, especially in terms of how we define the amount of prey that can be hidden. Here we will analyse one of the possible models.

Problem 3.2.1. Suppose that prey have a refuge from predators into which they can retreat. Assume the refuge can hold a fixed number of prey. How would you model this situation and what predictions can you make?

Solution

Already known parameters:

- a ... growth rate of preys,
- b ... predation coefficient,
- c ... mortality rate of predators,
- d ... reproductive rate of the predator per prey.

We consider a new parameter:

- p ... the amount of prey that the refuge can hold.

We define a function

$$\Psi(x) = max\{0; x-p\} = \begin{cases} 0 & \text{for} \quad x \leq p \\ x-p & \text{for} \quad x > p \end{cases}$$

representing the amount of prey available for predation.

Thus our model has the following form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax - b\Psi(x)y,$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = -cy + d\Psi(x)y.$$

Here we can notice that the right-hand sides of the system are not from C^1, it means for the right sides of the equations in the system above holds $f \notin C^1(\mathbb{R}^2)$. However as the function $\Psi(x)$ is Lipschitz continuous, it also applies for the right-hand sides f on $\mathbb{R}^2$. And therefore the assertion of Theorem 1.1 is valid in this case.

As we are analysing a population model, we are interested in results for $x > 0$ and $y > 0$.

First, we analyse the model having presumptions

$$\begin{aligned} 0 \leq x \leq p, \\ y \geq 0, \end{aligned}$$

which lead us to consider following form of the system of equations

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax, \tag{3.17}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -cy. \tag{3.18}$$

This means that since the entire prey amount can be hold by the refuge, we do not assume any predation. Thus the prey population increases, however, the predator population declines due to lack of food.
The equilibrium in the model occurs when the amount of both populations does not change, thus we can easily deduce that the corresponding critical point is $(\overline{x_1}, \overline{y_1}) = (0, 0)$. The Jacobian matrix of partial derivatives of the system's right sides

$$\begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix}. \tag{3.19}$$

will help us to investigate stability of this critical point. Normally the next step is to substitute the point into the equation (3.19), but we already have the matrix in required form. Afterwards, we have to compute eigenvalues of the matrix,

$$(a - \lambda)(-c - \lambda) = 0 \quad \Leftrightarrow \quad \lambda_1 = a \quad \vee \quad \lambda_2 = -c.$$

In this case, we can just claim that the critical point is a saddle, because we already proved it for the critical point (3.10), in the previous model, having the same eigenvalues of the Jacobian matrix. We can also make the same conclusion as for the critical point (3.10), which is that the natural extinction of the populations is not possible.

The solution of the system will be found by resolving

$$\int \frac{\mathrm{d}x}{x} = \int a\,\mathrm{d}t,$$

$$\int \frac{\mathrm{d}y}{y} = -\int c\,\mathrm{d}t.$$

Using logarithmization we get

$$\ln|x| = at + q,$$

$$\ln|y| = -ct + r,$$

where q, $r \in \mathbb{R}$. The absolute value can be removed because, as mentioned in the beginning, we are only interested in $x > 0$ and $y > 0$. And after rearranging the expression we arrive to the solution

$$x = e^{at+q},$$

$$y = e^{-ct+r}.$$

Therefore, the dynamics of this model is possible to illustrate by Figure 3.4.

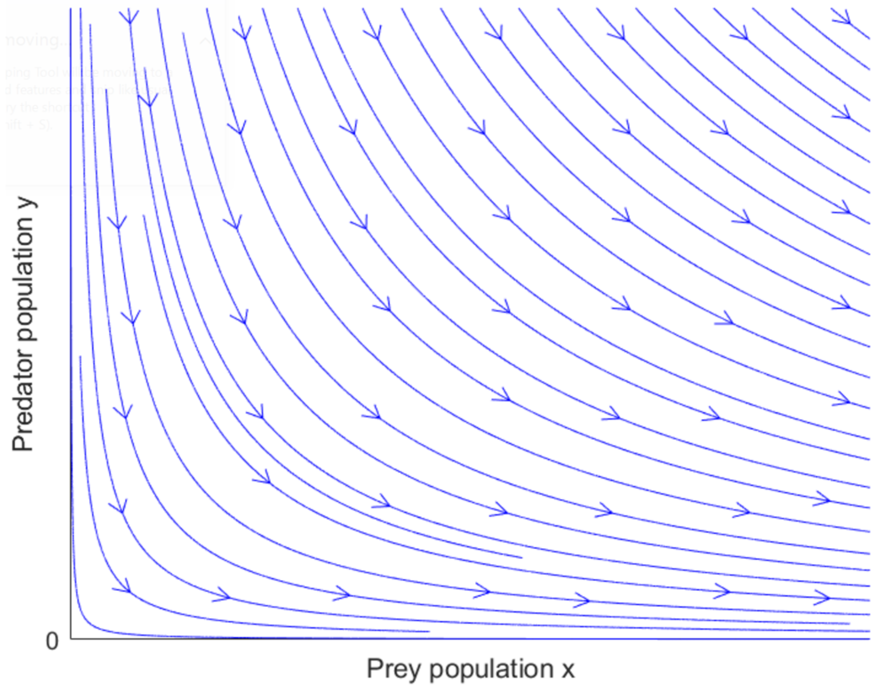

Figure 3.4: The phase portrait of the system (3.17), (3.18) under conditions $0 \le x \le p$ and $y \ge 0$. Used values of parameters are $a = 1$, $c = 1$.

Now, we focus on the model assuming

$$x > p,$$
$$y \ge 0,$$

thus our system of equations has a form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax - b(x-p)y, \tag{3.20}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -cy + d(x-p)y. \tag{3.21}$$

As we are mainly interested in the stability analysis, it is mandatory to find critical points of the system. We already know from Definition 1.6 that a system achieves its equilibrium in moment when the amount of the population does not change. Therefore we solve

$$ax - b(x-p)y = 0, \tag{3.22}$$

$$-cy + d(x-p)y = 0. \tag{3.23}$$

The solution of the equality (3.22) can be found simply. It applies for $y = 0$ or $x = \frac{c}{d} + p$.

However, finding the solution of (3.23) is no longer so trivial. But we can take benefit of the fact, that it makes sense to look for solutions only for x and y such that $\frac{\mathrm{d}y}{\mathrm{d}t} = 0$, i.e. for $y = 0$ and $x = \frac{c}{d} + p$.

This way, we discovered following critical points

$$
\begin{aligned}
(\overline{x_1}, \overline{y_1}) &= (0, 0),\\
(\overline{x_2}, \overline{y_2}) &= \left(\frac{c}{d} + p, \frac{ac + adp}{bc}\right).
\end{aligned}
$$

But due to given assumptions, $x > p$, $y \geq 0$, we are interested only in the second critical point $(\overline{x_2}, \overline{y_2})$.

In order to examine the stability and the type of the critical point $(\overline{x_2}, \overline{y_2})$, let us linearize the system of equations (3.20), (3.21). It means that we first compute the Jacobian matrix of the system

$$
J(x, y) = \begin{pmatrix} a - by & -bx + bp \\ dy & dx - c - dp \end{pmatrix}
$$

and then determine the value of $J(\overline{x_2}, \overline{y_2})$, which is

$$
J(\overline{x_2}, \overline{y_2}) = \begin{pmatrix} -\frac{adp}{c} & -\frac{bc}{d} \\ \frac{acd + ad^2 p}{bc} & 0 \end{pmatrix}.
$$

The non-linear system (3.20), (3.21), can be now locally, i.e. about the steady state $(\overline{x_2}, \overline{y_2})$, replaced by the linear variational equation, as defined by Definition 1.14.

Now we need to know the eigenvalues of the matrix $J(\overline{x_2}, \overline{y_2})$ to be able to decide about the stability and type of the critical point $(\overline{x_2}, \overline{y_2})$. So, if we put

$$
\det(J(\overline{x_2}, \overline{y_2}) - \lambda E) = 0,
$$

where E is the identity matrix, we get the quadratic equation

$$
\lambda^2 + \lambda \frac{adp}{c} + ac + adp = 0, \tag{3.24}
$$

whose discriminant is

$$\triangle = \frac{(adp)^2 - 4c^2(ac + adp)}{c^2}.$$

Obviously we cannot make any decision about the sign of the discriminant at this moment, consequently we need to make an examination to be able to decide whether the eigenvalues λ_1, λ_2 of the matrix $J(\overline{x_2}, \overline{y_2})$ are real numbers or complex numbers. So, let us examine whether $\triangle < 0$, i.e.

$$\frac{(adp)^2 - 4c^2(ac + adp)}{c^2} < 0,$$

that is

$$\frac{(adp)^2}{4ac^2(c + dp)} < 1. \tag{3.25}$$

Hence, clearly, if the inequality (3.25) holds, the eigenvalues

$$\lambda_1 = -\frac{adp}{2c} + \frac{1}{2c}\sqrt{(adp)^2 - 4c^2(ac + adp)},$$
$$\lambda_2 = -\frac{adp}{2c} - \frac{1}{2c}\sqrt{(adp)^2 - 4c^2(ac + adp)},$$

would not be real numbers. In such case, the eigenvalues λ_1, λ_2 have the form $\alpha \pm \beta i$, where $\alpha < 0$ and $\beta > 0$.

Otherwise, when the condition (3.25) is not met, the eigenvalues λ_1, λ_2 would be real. But what about their signs? Naturally, the eigenvalue λ_2 is always a negative number. However concerning the eigenvalue λ_1, its sign is not apparent at first sight. So let us assume that the eigenvalue λ_1 is negative, then it would have to be true that

$$-\frac{adp}{2c} + \frac{1}{2c}\sqrt{(adp)^2 - 4c^2(ac + adp)} < 0,$$

which can be modified such that

$$\sqrt{(adp)^2 - 4c^2(ac + adp)} < adp,$$

that is

$$4c^2(ac + adp) > 0. \tag{3.26}$$

Which we know is true since $a, c, d, p \in \mathbb{R}^+$. Therefore, we can conclude that if the condition (3.25) does not hold, then $\lambda_1, \lambda_2 \in \mathbb{R}^-$.

Now, let us focus on the first case, where $\lambda_1, \lambda_2 = \alpha \pm \beta i$, $\alpha < 0$, $\beta > 0$. Since these critical points have non-zero real components, clearly, by Definition 1.12, they are hyperbolic. Consequently we can apply Theorem 1.6, according to which λ_1, λ_2 are asymptotically stable.

Following the classification of phase portraits in [1], Chapter 6, the critical point $(\overline{x_2}, \overline{y_2})$ we can find out type of the critical point. As

$$\det J(\overline{x_2}, \overline{y_2}) > 0 \quad \text{and} \quad \operatorname{tr} J(\overline{x_2}, \overline{y_2}) < 0,$$

the critical point is a sink. Concretely, it is a spiral-sink point, since the characteristic condition

$$4\det J(\overline{x_2}, \overline{y_2}) > (\operatorname{tr} J(\overline{x_2}, \overline{y_2}))^2$$

holds and it is true that

$$\lambda_{1,2} = \alpha \pm i\beta, \quad \alpha < 0, \quad \beta \neq 0.$$

According to Theorem 1.9, we can assert that also the critical point of the non-linear system (3.20), (3.21) is a spiral-sink point, because the type of the critical point of the non-linear system is same as the type of the null critical point of the corresponding linearized system.

The phase portrait of the system around this critical point is represented in Figure 3.5.

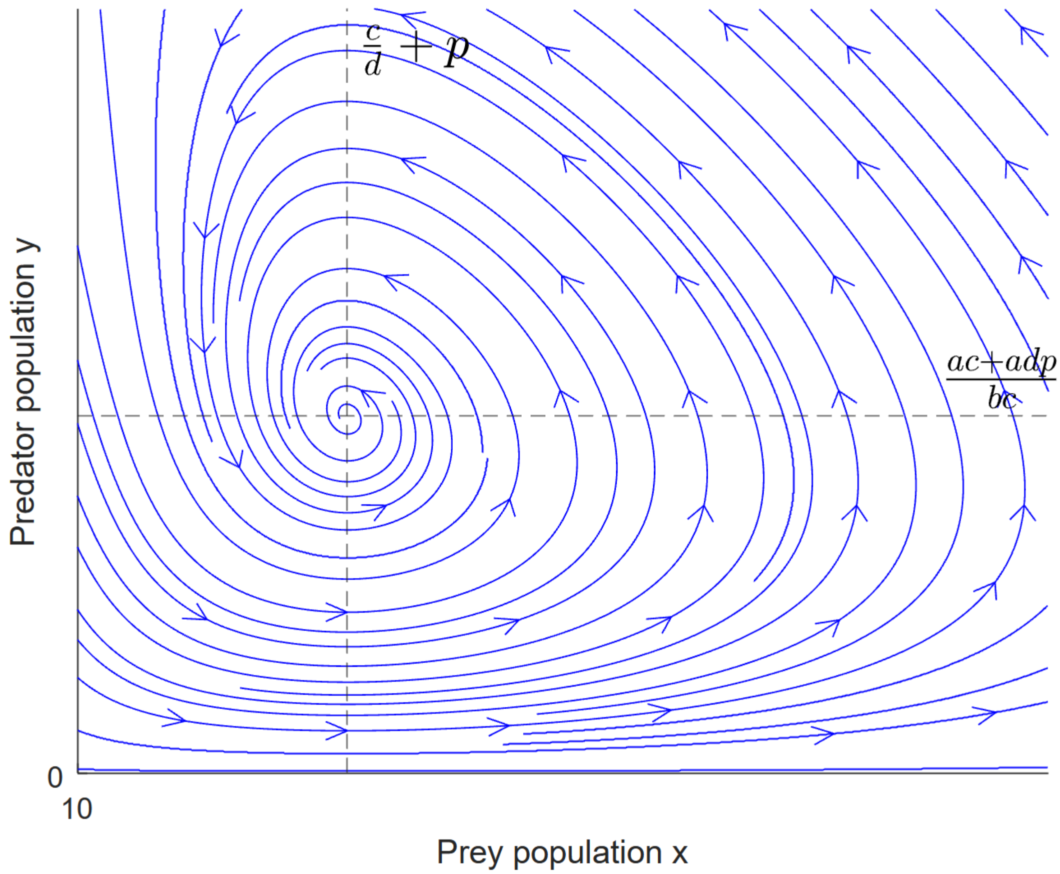

Figure 3.5: The phase portrait of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

The representation of the population dynamics of this system is shown by Figure 3.6. It is obvious that the population stabilizes over time, since the critical point $(\overline{x_2}, \overline{y_2})$ is a spiral-sink. This behaviour is clearly visible in Figure 3.7.

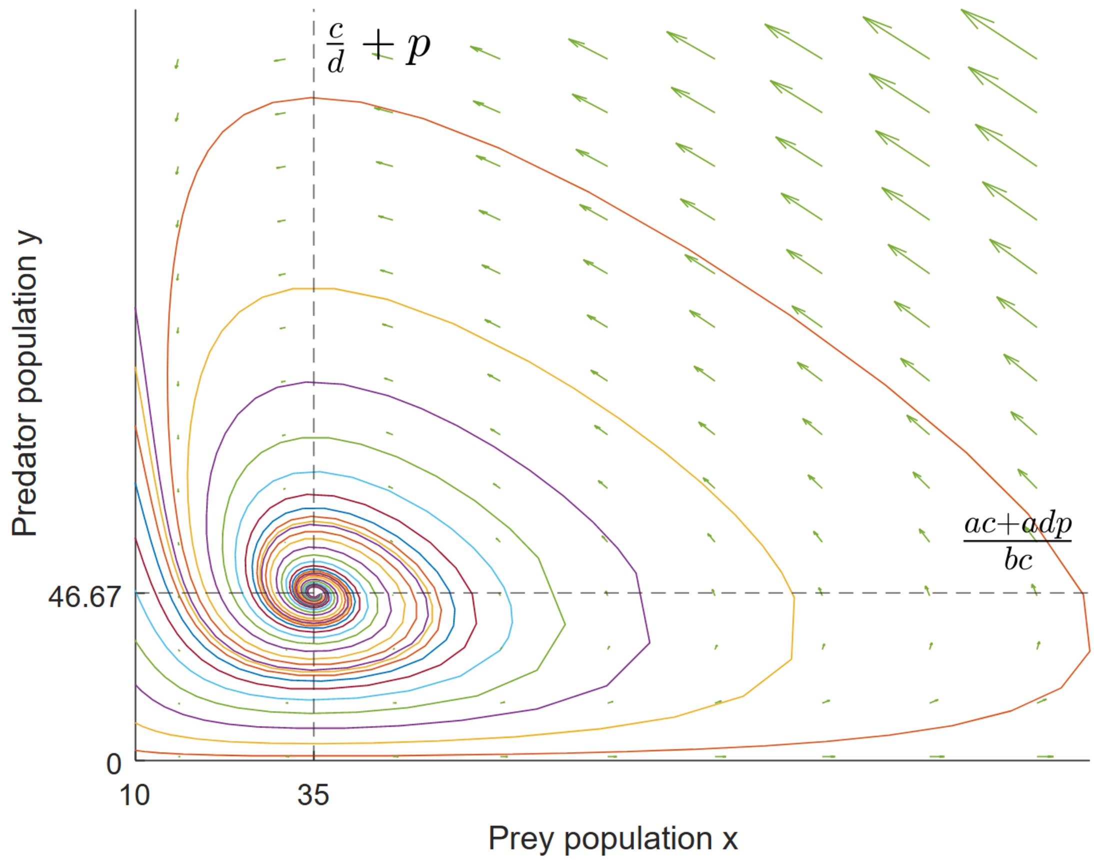

Figure 3.6: Representation of the population dynamics of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

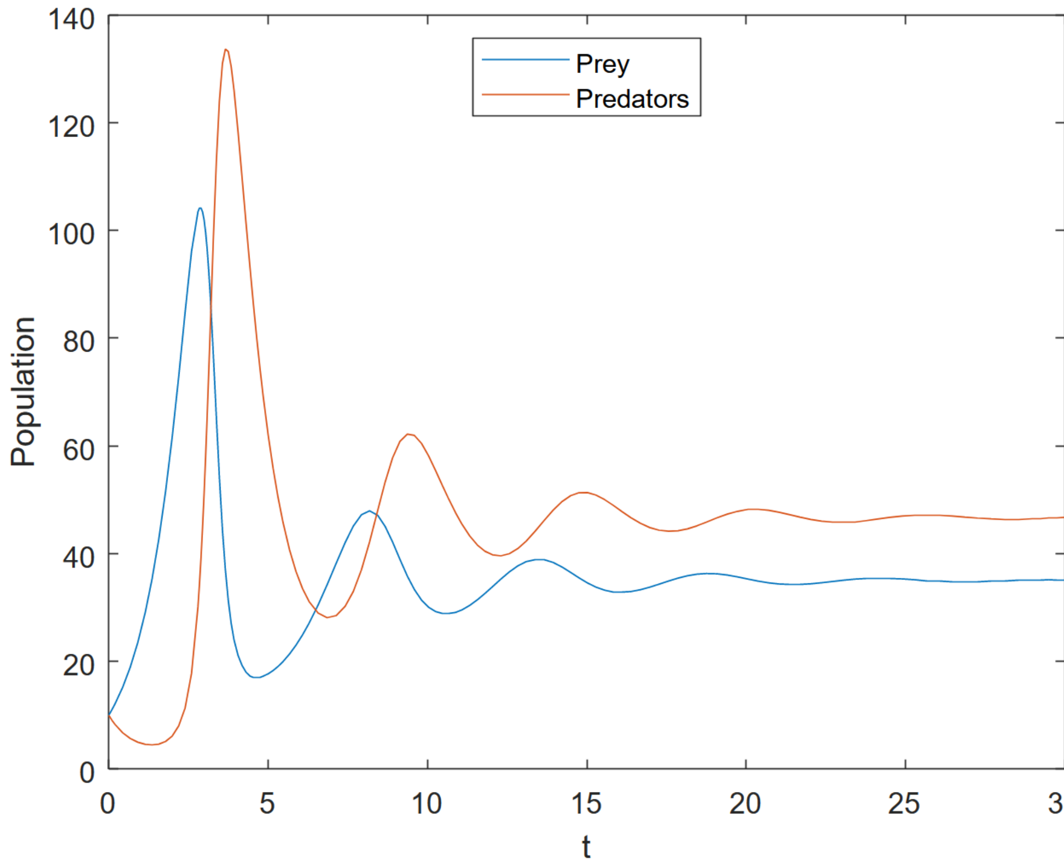

Figure 3.7: Oscillations of populations in population dynamics of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, for initial populations $x_0, y_0 = 10$, in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

Now, let examine the case where $\lambda_1, \lambda_2 \in \mathbb{R}^-$. Also these critical points have non-zero real components, thus, by Definition 1.12, they are hyperbolic. This allows us to apply Theorem 1.6, according to which λ_1, λ_2 are asymptotically stable. If we use again the classification of phase portraits in [1], Chapter 6, we realize that the critical point is a sink since

$$\det J(\overline{x_2}, \overline{y_2}) > 0 \quad \text{and} \quad \mathrm{tr} J(\overline{x_2}, \overline{y_2}) < 0.$$

Moreover,

$$4\det J(\overline{x_2}, \overline{y_2}) < (\mathrm{tr} J(\overline{x_2}, \overline{y_2}))^2$$

and

$$\lambda_1, \lambda_2 < 0, \quad \lambda_1 \neq \lambda_2,$$

holds, which suggests that the critical point is a node-sink type.

Also there we can claim that the critical point of the non-linear system (3.20), (3.21) is of the same type as the one of the linearized system, i.e. a node-sink, which is guaranteed by Theorem 1.9.

The phase portrait of the neighbourhood of the critical point is shown by Figure 3.8.

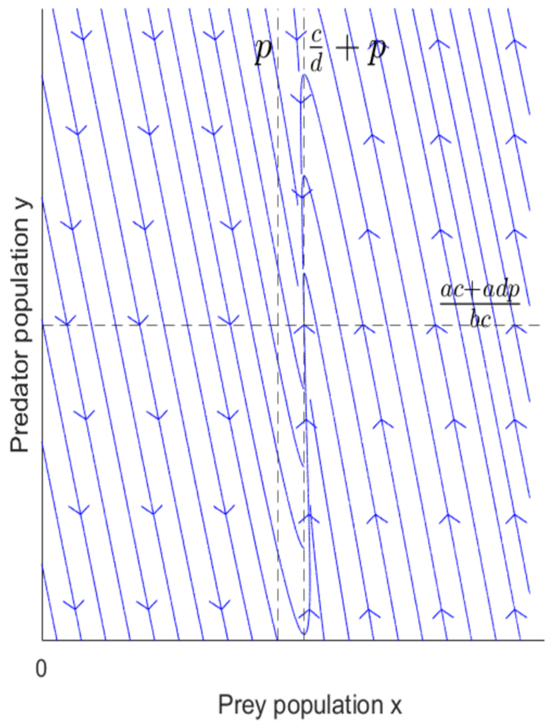

Figure 3.8: The phase portrait of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, in the case when $\triangle > 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1.5$, $d = 0.09$, $p = 150$.

The population dynamics of this system is depicted in Figure 3.9. Also in this case the stabilisation of the population occurs. Moreover, it happens much faster than in the previous system, i.e. the system (3.20), (3.21), where λ_1, λ_2 are complex numbers in form $\alpha \pm \beta i$, $\alpha < 0$, $\beta > 0$. It is well illustrated in Figure 3.10.

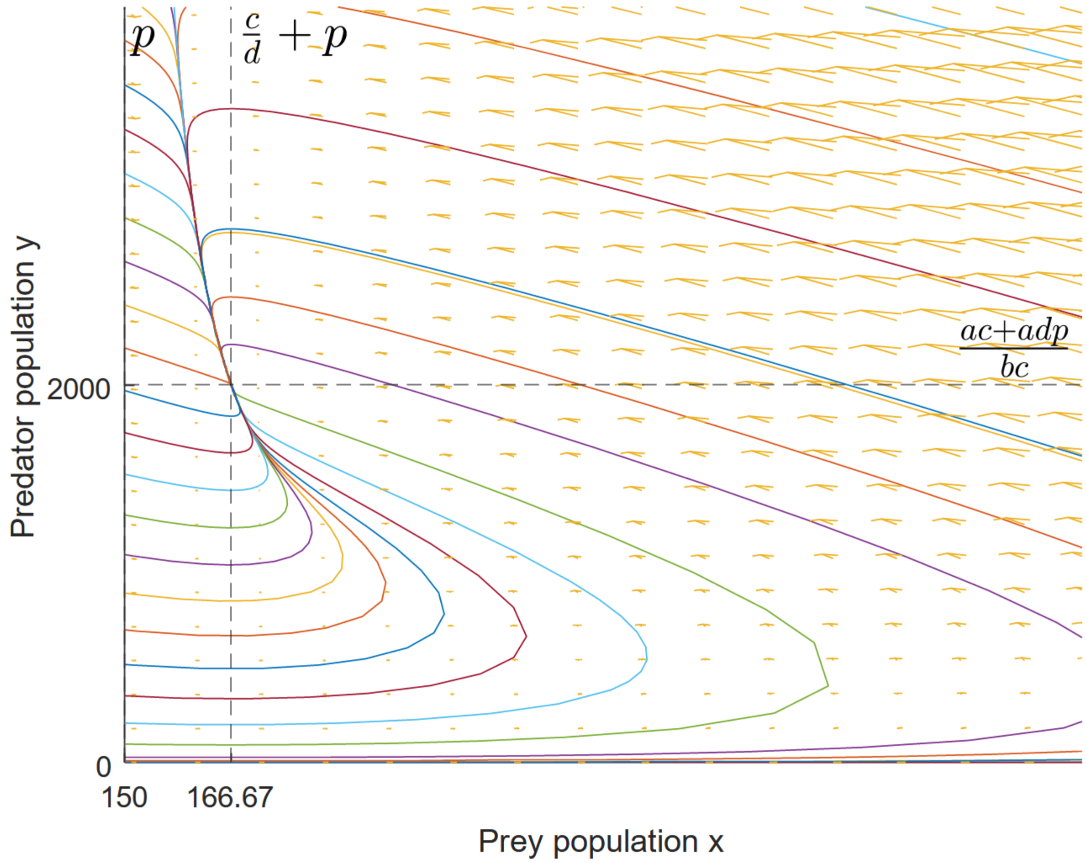

Figure 3.9: Representation of the population dynamics of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, in the case when $\triangle > 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1.5$, $d = 0.09$, $p = 150$.

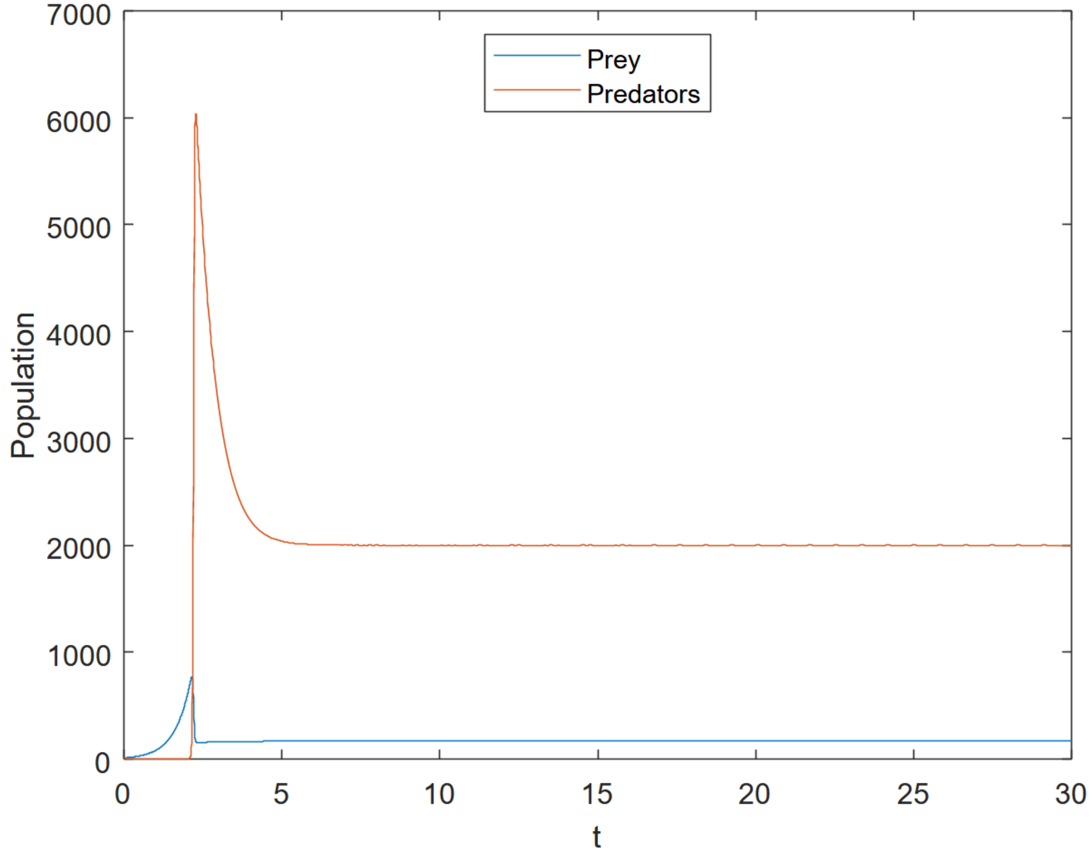

Figure 3.10: Oscillations of populations in population dynamics of the system (3.20), (3.21), under conditions $x > p$ and $y \neq 0$, for initial populations $x_0, y_0 = 10$, in the case when $\triangle > 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1.5$, $d = 0.09$, $p = 150$.

To summarize, the examined type of Lotka-Volterra model with a refuge stabilizes over time for any initial population $x_0, y_0 > 0$, i.e. the population size converges to the steady state value $\left(\frac{c}{d} + p, \frac{ac+adp}{bc}\right)$. Even when the population is anywhere close to 0, there is always a recovery and stabilization. The final representation of the model having parameters a, b, c, d, p such that the condition (3.25) holds is shown in Figure 3.11. On the other hand, when the condition (3.25) is not satisfied, the final representation of the model is depicted in Figure 3.12.

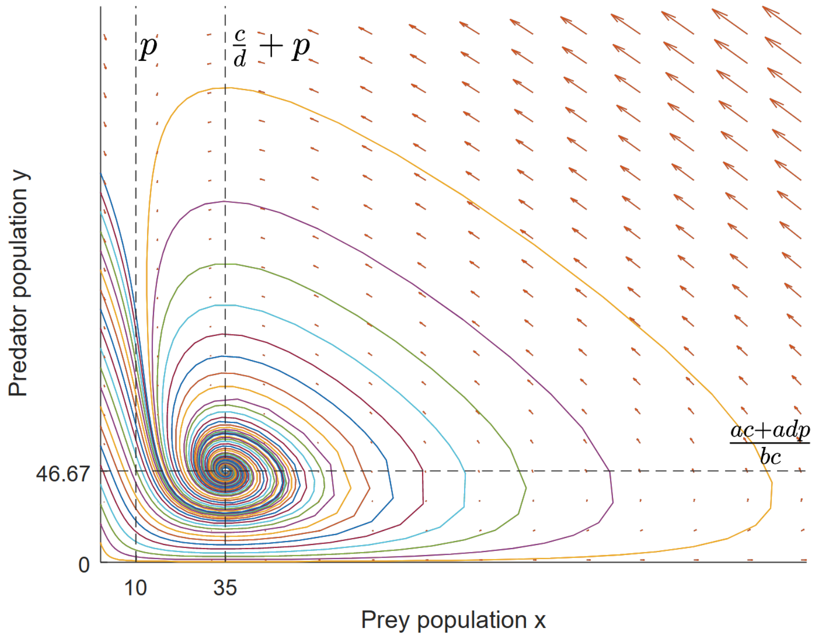

Figure 3.11: Representation of the population dynamics in the Lotka-Volterra model with a refuge in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

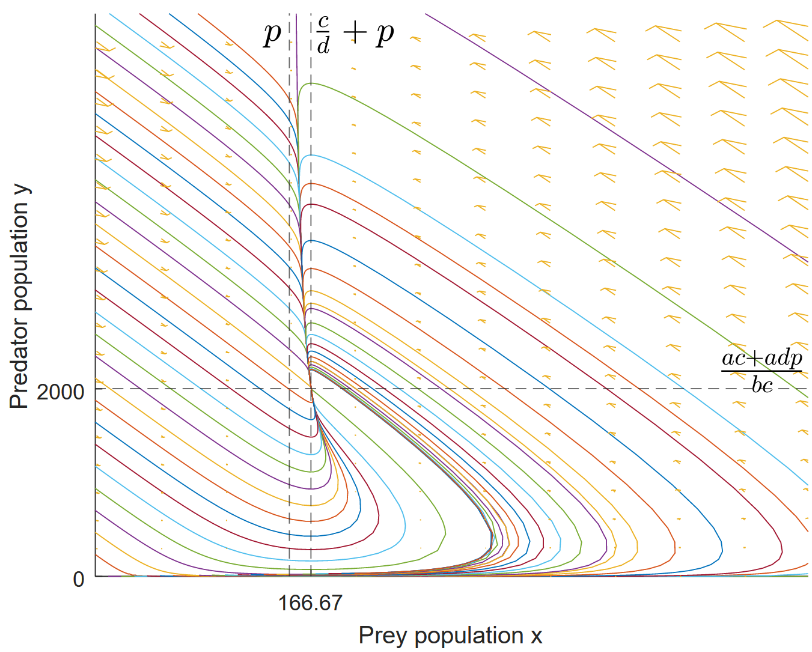

Figure 3.12: Representation of the population dynamics in the Lotka-Volterra model with a refuge in the case when $\triangle > 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1.5$, $d = 0.09$, $p = 150$.

What is interesting in this model is that when the prey population size exceeds the number of prey that the refuge can hold, the amount of prey is never again reduced below that number. This can be verified by substituting of $x = p$ in (3.20), (3.21), which yields

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ap,$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = -cy.$$

As $a, p > 0$, then $\frac{\mathrm{d}x}{\mathrm{d}t} > 0$. It follows that if the function $x(t)$ reaches the value p, it is only possible that the function is increasing, never decreasing. This behaviour is marked by red arrows in Figures 3.13 and 3.14.

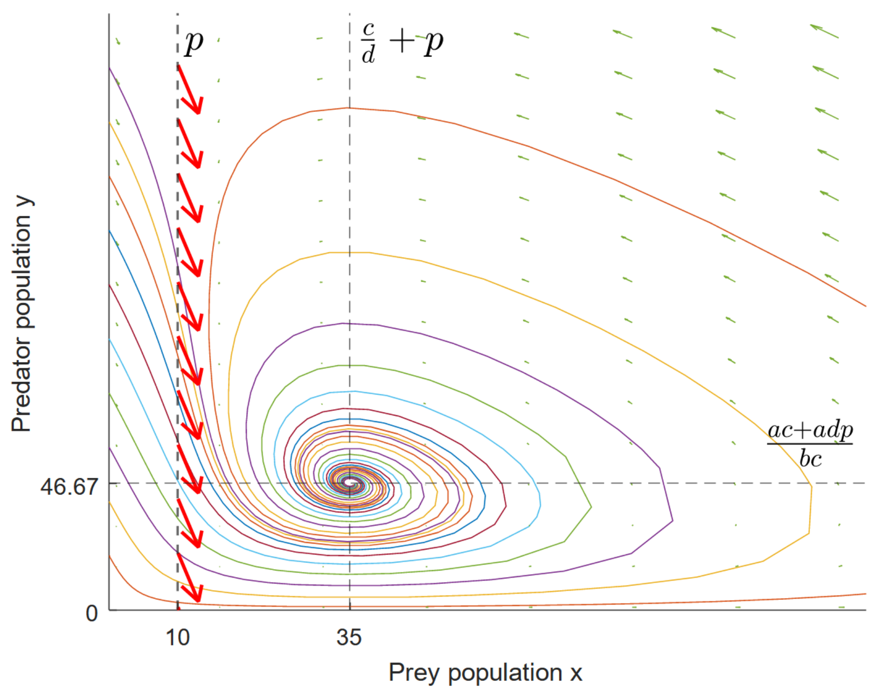

Figure 3.13: Representation of the population dynamics in the Lotka-Volterra model with a refuge in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

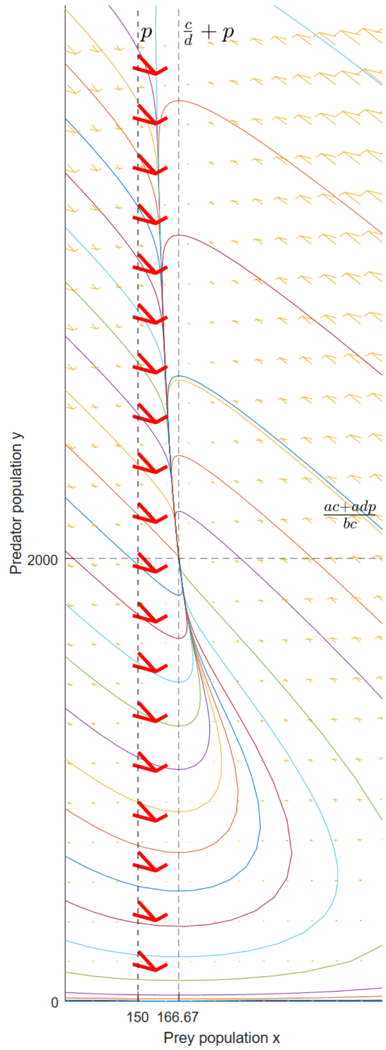

Figure 3.14: Representation of the population dynamics in the Lotka-Volterra model with a refuge in the case when $\triangle < 0$. Used values of parameters are $a = 1$, $b = 0.03$, $c = 1$, $d = 0.04$, $p = 10$.

Finally, if we compare the Lotka-Volterra model with a refuge and the neutral Lotka-Volterra stability model, described in Section 3.1, we can notice several differences.

First one can be found in the parameters on which the equilibrium of a population depends. Let us recall the populations steady state in the neutral Lotka-Volterra stability model

$$\left(\frac{c}{d}, \frac{a}{b}\right)$$

and in Lotka-Volterra model with a refuge

$$\left(\frac{c}{d} + p, \frac{a}{b} + \frac{adp}{bc}\right).$$

For the prey population it is almost the same, the equilibrium is still related only to the parameters associated with predators, only shifted by the value of the number of prey that the refuge can hold. But, concerning the equilibrium of the predator population, this state of the population depends on the parameters associated with the prey as well as the predators, i.e. in addition to the parameters a and b, it also depends on c and d. And, moreover, it depends on parameter p too. In other words, in that case, the behaviour of predator population influences their own steady state value.

Second difference is quite obvious from the above analysis. The populations which oscillate and never stabilize in the neutral Lotka-Volterra model, in the case of the model with a refuge finally find an equilibrium point and stabilize.

However, what they have in common is that the natural extinction is not possible. No matter how small the populations are, there will always be a recovery.

Conclusion

We have presented several models describing a population dynamics. It should be noted that these were continuous models. The first part of the thesis consists of some theory of dynamical systems. In the second part, the reader could get acquainted with two scalar models, namely *the Exponential growth* and *the Logistic growth*. And finally, the *Lotka-Volterra* model was introduced, together with its modification, in which the model considers the prey refuge, where the refuge can hold a fixed number of prey.

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Contents of the attached CD

The enclosed CD contains the MATLAB source codes of the images that appear in the thesis. This section provides the mapping of the files to figures in the thesis.

The file

* `ExponentialGrowth_1.m` refers to Figure 2.1,
* `ExponentialGrowth_2.m` refers to Figure 2.2,
* `LogisticGrowth.m` refers to Figure 2.5,
* `LotkaVolterra_CP1_SaddlePoint.m` refers to Figure 3.1,
* `LotkaVolterra_OrbitsWithDirections.m` refers to Figure 3.2,
* `LotkaVolterra_PopulationsOverTime.m` refers to Figure 3.3,
* `LotkaVolterraRefuge_OtoP_PhasePortrait.m` refers to Figure 3.4,
* `LotkaVolterraRefuge_PtoInf_CPSpiral_PhasePortrait.m` refers to Figure 3.5,
* `LotkaVolterraRefuge_PtoInf_CPSpiral_OrbitsWithDirections.m` refers to Figure 3.6,
* `LotkaVolterraRefuge_PtoInf_CPSpiral_PopulationsOverTime.m` refers to Figure 3.7,

* `LotkaVolterraRefuge_PtoInf_CPNode_PhasePortrait.m` refers to Figure 3.8,

* `LotkaVolterraRefuge_PtoInf_CPNode_OrbitsWithDirections.m` refers to Figure 3.9,

* `LotkaVolterraRefuge_PtoInf_CPNode_PopulationsOverTime.m` refers to Figure 3.10,

* `LotkaVolterraRefuge_OtoInf_CPSpiral_OrbitsWithDirections.m` refers to Figure 3.11,

* `LotkaVolterraRefuge_OtoInf_CPNode_OrbitsWithDirections.m` refers to Figure 3.12,

* `LotkaVolterraRefuge_OtoInf_CPSpiral_OrbitsWithDirections_HghltArrows.m` refers to Figure 3.13,

* `LotkaVolterraRefuge_OtoInf_CPNode_OrbitsWithDirections_HghltArrows.m` refers to Figure 3.14.