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FAKULTETA ZA MATEMATIKO, NARAVOSLOVJE IN INFORMACIJSKE TEHNOLOGIJE

Zaključna naloga
(Final project paper)

Bifurkacije ravnovesnih stanj vektorskih polj in uporaba v sistemih plenilec-plen

(Bifurcations of equilibria of vector fields with applications to predator-prey systems)

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Izvleček: V zaključni nalogi obravnavamo bifurkacije ravnovesnih stanj vektorskih polj in prikažemo uporabo v sistemih plenilec-plen. Predstavimo transkritično, sedelno-vozelno, viličasto bifurkacijo ter bifurkacijo Poincare-Andronov-Hopf in izpeljemo pogoje za nastanek vsake od navedenih bifurkacij. Kot primer uporabe predstavimo in analiziramo tri modele, ki opisujejo interakcijo plenilcev in njihovega plena.

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Abstract: In the final project paper we study bifurcations of equilibria of vector fields and present some applications in predator-prey systems. We introduce the notion of the transcritical, saddle-node, pitchfork and the Poincare-Andronov-Hopf bifurcation and present the conditions for each of these bifurcations. As an example of applications, we present and study three models describing the interactions of predators and their prey.

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To my family, for their love and support. To my mentor, for her time and assistance. To FAMNIT, for providing me with this opportunity.

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iff	if and only if
i.e.	that is
s.t.	such that
LAS	locally asymptotically stable

1 Introduction

Mathematical models in natural sciences often come in the form of a system of ordinary differential equations

$$\dot{x}(t) = f(x, \mu), \qquad x \in \mathbb{R}^n, \mu \in \mathbb{R}^p. \tag{1.1}$$

Here, $x(t)$ denotes the state variable of the system (for instance, the densities of the modeled populations at time t, the concentrations of the chemicals at time t etc.) and μ denotes the vector of the parameters of the system (for example, the *per capita* death rates of individuals, the rate of reactions between the molecules etc.). More often than not, such mathematical models are nonlinear (i.e. f is nonlinear) and explicit solutions are difficult, if not impossible, to obtain. In order to obtain some knowledge about the dynamics of the system, we must resort to other methods.

Some information about the dynamics can obtained by studying the equilibria of (1.1). Equilibria are solutions which are constant over time: for a given $\mu_0 \in \mathbb{R}^p$ the vector $x_0 \in \mathbb{R}^n$ is an equilibrium of (1.1) if $f(x_0, \mu_0) = 0$. From the point of view of the dynamics, equilibria are not of particular interest. However, we can ask: what happens with the solutions of the system, if the initial state of the system is in the vicinity of an equilibrium? To answer this question, we perform linear stability analysis and in such a way, some information about the system dynamics can be gained. But how do equilibria of the system and their stability properties change when the parameter is varied?

Such a question arises naturally when modelling natural phenomena (for example, we may wish to know how the dynamics of a disease in a host population may change when the transmissibility of the infection changes or how the outcome of a chemical reaction depends on reaction rates). The branch of mathematics studying the change in the qualitative or the topological structure of vector fields and other dynamical systems is called *the bifurcation theory*. The basics of the bifurcation theory and its applications in predator-prey systems are the topic of this final project.

In Chapter 2, we introduce the preliminary theory needed to start this work, with important results from the theory of dynamical systems and differential equations.

In Chapter 3, we present the bifurcations of equilibria of continuous dynamical systems in the form of a system of differential equations. We analyze and derive the saddle-node, transcritical and pitchfork bifurcations, and provide the conditions for the

Poincare-Andronov-Hopf bifurcation.

Finally, in Chapter 4, we focus on applications and present three models describing the interactions between predators and their prey. We analyze their dynamics and discuss the bifurcations occurring in the three models.

2 Preliminaries

In this section, we aim to deliver preliminary theory which will be needed later on. We start with an important theorem from multivariate calculus.

Theorem 2.1. ***(Implicit function theorem [3])*** *Let $A \subseteq \mathbb{R}^n \times \mathbb{R}^m$ be an open set and let $f : A \to \mathbb{R}^m$ be a $\mathbf{C}^r$ function. Let $(x_0, y_0) \in A$, $f(x_0, y_0) = 0$ and assume that $Df(x_0, y_0)$ (the Jacobian of f at (a, b)) is invertible. Then there is an open neighborhood $U \subseteq \mathbb{R}^n$ of x_0 and a neighborhood V of y_0 in $\mathbb{R}^m$ and a unique function $f : U \to V$ such that*

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

for all $x \in U$. Furthermore f is of class $\mathbf{C}^r$.

The topic of this final project are dynamical systems which come in the form of a parametrized system of differential equations,

$$\dot{x}(t) = f(x, \mu), \quad x \in \mathbb{R}^n, \mu \in \mathbb{R}. \tag{2.1}$$

Here, $x(t)$ denotes the state variable at time t and μ is a parameter of the system. Typically, the systems of interest are nonlinear (i.e. f) is nonlinear, which makes it difficult to get explicit solutions. We will be particularly interested in a particular type of solutions, called equilibria. To this end, we for a moment ignore the dependence of f on a parameter μ.

Definition 2.2. Let $\dot{x}(t) = f(x)$, $x \in \mathbb{R}^n$. A constant solution x_0 that satisfies $f(x_0) = 0$ is called an *equilibrium* or *steady state.*

That means that the equilibria are the solutions of the system that stay constant over time. They are not interesting dynamically, but are useful for getting more information about the system. We can now ask ourselves: what happens with the solutions of the system, if the initial state is close to an equilibrium? Do solutions approach the equilibrium or move away from it? To study this, we introduce the notions of stability [6].

Definition 2.3. Let x_0 be a steady state of $\dot{x}(t) = f(x)$. Then x_0 is *locally stable* if for every $\epsilon > 0$ there exists $\delta > 0$ s.t. for every solution $x(t)$ of $\dot{x} = f(x)$ with initial state $x(0)$ we have: if $\| x(0) - x_0 \| < \delta$ then $\| x(t) - x_0 \| < \epsilon$ for all $t > 0$.

A steady state which is not locally stable is an *unstable* steady state.

Definition 2.4. Let x_0 be an equilibrium of $\dot{x}(t) = f(x)$. Then x_0 is locally asymptotically stable (LAS) if x_0 is locally stable and exists a constant $b > 0$ s.t. if $\| x(0) - x_0 \| < b$ then $\lim_{t\to\infty} \| x(t) - x_0 \| = 0$.

The definitions describe different types of stability, but do not give us a concrete method to determine whether the equilibrium is stable or unstable. To determine whether an equilibrium is stable, we consider the dynamics in the vicinity of x_0. Let

$$y = x - x_0.$$

If $f \in \mathbf{C}^2$, Taylor expansion gives us

$$\dot{y}(t) = \dot{x}(t) = f(x) = f(x_0 + y) = f(x_0) + Df(x_0)y + \mathcal{O}(|y|^2).$$

To determine the stability of x_0 we therefore consider the associated linear system

$$\dot{y}(t) = Df(x_0)y. \tag{2.2}$$

We know the solution of (2.2) [6]: if $y(0)$ is the initial state of $y(t)$, the solution is given by

$$y(t) = e^{Df(x_0)t}y(0).$$

The method described above is called linearization. We know that the stability of solutions of linear system are determined by the eigenvalues of their associated matrix [6]. But what does this tell us about the stability of the equilibrium for the nonlinear system? We have the following

Theorem 2.5. ***(Hartman-Grobman theorem [4])*** *Let $E \subseteq \mathbb{R}^n$ be an open set containing the origin, and let ϕ be the solution of the system $\dot{x}(t) = f(x)$. Suppose that $f(0) = 0$ and that $A = Df(0)$ has no eigenvalue with zero real part. Then there exists a homeomorphism H of an open set U containing the origin onto an open set V containing the origin s.t. for each $x \in U$, there is an open interval $I \subseteq R$ containing zero s.t. for all $x \in U$ and $t \in I$*

$$H \circ \phi(x) = e^{At}H(x).$$

In another words, the Hartman-Grobman theorem states that the linearized and the original system have qualitatively the same dynamics near the equilibrium, provided that the Jacobian has no eigenvalue with real part equal to zero. Such equilibria are given a special name.

Definition 2.6. Let $\dot{x}(t) = f(x), x \in \mathbb{R}^n$ be a system of differential equations, and x_0 its equilibrium. We say that x_0 is *hyperbolic* if all eigenvalues of $Df(x_0)$ have nonzero real parts. Otherwise, x_0 is non-hyperbolic.

We then have the following [6].

Theorem 2.7. *Let $x = x_0$ be an equilibrium of $\dot{x}(t) = f(x)$. Suppose that all of the eigenvalues of $Df(x_0)$ have negative real parts. Then x_0 is LAS. If at least one of the eigenvalues has a positive real part, the equilibrium is unstable.*

As a special case, let us turn to the systems of two nonlinear differential equations

$$\begin{aligned} \dot{x} &= f(x,y) \\ \dot{y} &= g(x,y), \;\; x, y \in \mathbb{R}. \end{aligned} \tag{2.3}$$

We turn to them because they will be frequently used in the remainder of the text, and they have also have some special properties that will be used in this paper.

Theorem 2.8. *Suppose that $X_0 = (x_0, y_0)$ is an equilibrium of (2.3). We have*

1. *Equilibrium X_0 is LAS if the trace of $D(X_0)$ is negative and the determinant of $D(X_0)$ is positive.*
2. *Equilibrium X_0 is unstable if the trace of $D(X_0)$ is positive or the determinant of $D(X_0)$ is negative.*

Before we continue, we introduce some terminology. If X_0 is an equilibrium of (2.3), and its Jacobian has one positive and one negative eigenvalue we call it a *saddle*. If both eigenvalues are positive, it is called an unstable node. If both eigenvalues are negative, it is called a stable node. If the Jacobian has a pair of pure imaginary eigenvalues, then X_0 is a *center*. If it has a pair of complex eigenvalues with a positive real part, it is called an unstable focus, and if it has a pair of complex eigenvalues with a negative real part, it is called a stable focus.

As we previously mentioned, two dimensional systems have some special properties associated with them. One of those properties is that solutions of (2.3) have a limited behaviour. The theory studying that is called the Poincare-Bendixon theory. We will not go into details, and just introduce the basics we need for our work.

Definition 2.9. Let $\phi(t, x(0))$ be the solution of (2.3), which satisfies the starting condition $\phi(0, x(0)) = x(0)$ (we also call ϕ the flow of the system described above). We mark the orbit (trajectory) of the system, which starts in $x(0)$ by $\Gamma(x(0))$.

$\Gamma(x(0))$ is defined by

$$\Gamma(x(0)) = \{X \in \mathbb{R}^2 : X = \phi(t, x(0)), t \in \mathbb{R}\}.$$

The positive orbit $\Gamma^+(x(0))$ is

$$\Gamma^+(x(0)) = \{X \in \mathbb{R}^2 : X = \phi(t, x(0)), t \geq 0\}.$$

One of the properties that an orbit can possess is periodicity.

Definition 2.10. Periodical solution ϕ of the system $\dot{x}(t) = f(x), \ x \in \mathbb{R}^n$ is nonconstant solution, which satisfies $\phi(t, x(0)) = \phi(t + T, x(0))$ for all t. We call the smallest such T the *period* of the solution.

We are also interested in the behavior of orbits as t approaches infinity.

Definition 2.11. The ω-limit set, $\omega(x(0))$ is the set of points, which are approached by the positive orbit, i.e.

$$x \in \omega(x(0)) \iff \exists \{t_n\}_{n=1}^{\infty}, \ \lim_{n\to\infty} t_n = \infty; \ \lim_{n\to\infty} \phi(t_n, x(0)) = x.$$

We have the following

Theorem 2.12. ***(Poincare-Bendixon theorem)*** *Let Γ^+ be a positive orbit of (2.3) contained in compact set $B \subset \mathbb{R}^2$. If $\omega(x_0)$ has no equilibria, then one of the following holds:*

1. *$\Gamma^+(x(0))$ is periodic orbit*
2. *$\omega(x(0))$ is periodic orbit.*

The periodic orbits, just like equilibria, can also be stable or unstable.

Definition 2.13. Periodical orbit of $\phi(t, x(0))$ is said to be *stable* if for every $\epsilon > 0$, there exists $\delta > 0$ s.t. for every other solution $\phi(t, y(0))$ of (2.3) satisfying $|\phi(t_0, x(0)) - \phi(t_0, y(0))| < \delta$, then $|\phi(t, x(0) - \phi(t, y(0))| < \epsilon$ for every $t > t_0, t_0 \in \mathbb{R}$.

Periodic orbit, which is not stable is an *unstable periodic orbit.*

Definition 2.14. Periodical orbit of $\phi(t, x(0))$ is said to be asymptotically stable if it is stable and for every other solution $\phi(t, y(0))$ of $\phi(t, y(0))$ there exists a constant $b > 0$ such that, if $|\phi(t_0, x(0)) - \phi(t_0, y(0))| < b$, then $\lim_{t\to\infty} |\phi(t, x(0) - \phi(t, y(0))| = 0$

In the fourth chapter, we will see an example of such behavior. To see such examples, we will plot *phase portraits*, geometrical representations of flows of a dynamical system in a phase space (space of all possible states of the system). In addition to flows, our plots will also include two different classes of curves:

1. x-*isoclines* are the curves given with by $f(x, y) = 0$
2. y-*isoclines* are the curves given with by $g(x, y) = 0$.

Clearly, the equilibria are the intersections of x and y isoclines.

Before we start with the next chapter, we will briefly mention the *center manifold theory*, which is the main tool that enables us to analyze stability around the non-hyperbolic equilibria. We will first state the notion of central subspace.

Definition 2.15. The central subspace E^c is defined as

$$E^c = \text{span}\{e_1, \ldots, e_c\},$$

where $\{e_1, \ldots, e_c\}$ are the (generalized) eigenvectors corresponding to eigenvalues of Jacobian of $\dot{x}(t) = f(x)$ having real part equal to zero.

The empty central subspace corresponds to non-hyperbolic equilibria. For systems with non-empty central subspace, there exists a space called the center manifold, which enables us to analyze their dynamics.

Theorem 2.16. ***(Center manifold theorem [4])*** *Let $\dot{x}(t) = f(x)$ and $f \in \mathbf{C}^r$. Suppose that $f(0) = 0$ and that $Df(0)$ has k eigenvalues with negative real part, j eigenvalues with positive real part, and $m = n - k - j$ eigenvalues with zero real part. Then there exists an m-dimensional center manifold $W^c(0)$ of class $\mathbf{C}^r$ tangent to the center subspace E^c of $Df(0)$ which is invariant under the flow ϕ of f.*

The existence of central manifold enables to restrict the flow of the system to the central manifold. On it, we are able to analyze dynamics around the non-hyperbolic equilibria. We will not state how to restrict the flow. For that, refer to ([6]).

3 Bifurcations of equilibria of vector fields

Consider a parametrized vector field

$$\dot{x}(t) = g(x, \mu), \qquad x \in \mathbb{R}^n, \qquad \mu \in \mathbb{R}, \tag{3.1}$$

where $g \in \mathbf{C}^r$ (r will be determined by our need for Taylor expansions). Suppose that (3.1) has an equilibrium in (x_0, μ_0), i.e. $g(x_0, \mu_0) = 0$. What do we know about the stability of the equilibrium? How does stability change when the parameter μ changes?

To answer these questions, we will observe the vector field obtained by linearization of (3.1) around the equilibrium (x_0, μ_0). The linearized vector field is given by

$$\dot{y}(t) = Dg(x_0, \mu_0)y. \tag{3.2}$$

If the equilibrium is hyperbolic, then the stability of (x_0, μ_0) in (3.1) is determined by (3.2). We know that $g(x_0, \mu_0) = 0$ and that $Dg(x_0, \mu_0)$ has no eigenvalues on imaginary axis, so $Dfg(x_0, \mu_0)$ is invertible. By the implicit function theorem, there exists a unique $\mathbf{C}^r$ function $x(\mu)$, s.t.

$$g(x(\mu), \mu) = 0$$

for μ's that are close to μ_0 with $x(\mu_0) = x_0$. By continuity of the eigenvalues with respect to parameters, for μ's close to μ_0

$$Dg(x(\mu), \mu)$$

has no eigenvalues on imaginary axis. So, there is a neighborhood of (x_0, μ_0) in which the stability of equilibria remains unaffected. The interesting things start to happen when (x_0, μ_0) is not hyperbolic, i.e. when $Dg(x_0, \mu_0)$ has some eigenvalues with real part equal to zero. In that case, for μ's close to μ_0, we can have the qualitative change in dynamics of our system. The equilibria can be created or destroyed, and new time dependent behavior, like periodic dynamics, can appear.

In order to analyze non-hyperbolic equilibria, we will use the center manifold theory to restrict the vector field to its center manifold, on which we will perform further analysis. Let us turn to our first case, when the linearization gives us system having one zero eigenvalue. From now on, we assume that $(x_0, \mu_0) = (0, 0)$.

3.1 A zero eigenvalue

Suppose that $Dg(x_0, \mu_0)$ has a single zero eigenvalue, with other eigenvalues having non-zero real parts. Then the orbit structure around (x_0, μ_0), is determined by the center manifold equation, which we write as

$$\dot{x}(t) = f(x, \mu), \qquad x \in \mathbb{R}, \mu \in \mathbb{R}, \tag{3.3}$$

where $f \in \mathbf{C}$. The (3.3) satisfies

$$f(0,0) = 0 \qquad \text{and} \qquad \frac{\partial f}{\partial x}(0,0) = 0,$$

i.e. $(0,0)$ is non-hyperbolic equilibrium. We will now analyze and derive few specific examples of bifurcations.

3.1.1 Saddle-node bifurcation

One type of bifurcation that can happen is called a saddle-node bifurcation. We introduce it with an example. Consider the vector field

$$\dot{x}(t) = f(x, \mu) = \mu - x^2, \qquad x \in \mathbb{R}, \mu \in \mathbb{R}. \tag{3.4}$$

We notice that

$$f(0,0) = 0 \qquad \text{and} \qquad \frac{\partial f}{\partial x}(0,0) = 0. \tag{3.5}$$

The set of equilibria of (3.4) is given by

$$\mu - x^2 = 0,$$

meeaning we have no equilibria for $\mu < 0$, and for $\mu > 0$, equilibria are given with $\pm\sqrt{\mu}$. From there, we conclude that $\mu = 0$ is a bifurcation point. Linearization of (3.4) gives us $Df(x) = -2x$, so $x = \sqrt{\mu}$ is a stable equilibrium, and $x = -\sqrt{\mu}$ is an unstable equilibrium. Hence, as the parameter goes from negative values to positive values, the system undergoes a saddle-node bifurcation where two equilibria appear; one of them is stable, the other unstable.

We will now derive the general conditions under which the saddle-node bifurcation will appear. In order for our system to undergo saddle-node bifurcation, we need the curve of equilibria to satisfy two properties:

1. To be tangent to the line $\mu = 0$ at $x = 0$, i.e.,

$$\frac{d\mu}{dx}(0) = 0. \tag{3.6}$$

2. To lay entirely on one side of $\mu = 0$, which will be satisfied if we have

$$\frac{d^2\mu}{dx^2}(0) \neq 0. \tag{3.7}$$

Now, let us consider a general, one-parameter family of scalar fields

$$\dot{x}(t) = f(x, \mu), \qquad x \in \mathbb{R}, \mu \in \mathbb{R}. \tag{3.8}$$

By the assumption, we have a non hyperbolic equilibrium at (x_0, μ_0)=(0,0) i.e.,

$$f(0,0) \quad \text{and} \quad \frac{\partial f}{\partial x}(0,0) = 0. \tag{3.9}$$

If we also have that

$$\frac{\partial f}{\partial \mu}(0,0) \neq 0, \tag{3.10}$$

then, by implicit function theorem, there exists a unique function

$$\mu = \mu(x), \quad \mu(0) = 0, \tag{3.11}$$

defined for x small enough such that $f(x, \mu(x)) = 0$. Now, we want to derive conditions in terms of derivatives of f at (0,0), so that (3.6) and (3.7) are met. Along with (3.9) and (3.10), they imply that we have a saddle-node bifurcation at bifurcation point $(0, 0)$. We can derive (3.6) and (3.7) with derivatives of f at the bifurcation point, by implicitly differentiating f along the curve of equilibria. From (3.10), we have that

$$f(x, \mu(x)) = 0. \tag{3.12}$$

If we differentiate (3.12) with respect to x we get

$$\frac{df}{dx}(x, \mu(x)) = 0 = \frac{\partial f}{\partial x}(x, \mu(x)) + \frac{\partial f}{\partial \mu}(x, \mu(x))\frac{d\mu}{dx}(x). \tag{3.13}$$

If we evaluate 3.13 at $(\mu, x) = (0, 0)$, we obtain

$$\frac{d\mu}{dx}(0) = -\frac{\frac{\partial f}{\partial x}(0,0)}{\frac{\partial f}{\partial \mu}(0,0)}, \tag{3.14}$$

and from there we see that (3.9) and (3.10) imply that

$$\frac{d\mu}{dx}(0) = 0,$$

or that curve of equilibria is tangent to $\mu = 0$ at $x = 0$. By differentiating (3.13) again with respect to x we get

$$\begin{aligned} \frac{d^2 f}{dx^2}(x, \mu(x)) = 0 = \frac{\partial^2 f}{\partial x^2}(x, \mu(x)) + 2\frac{\partial^2 f}{\partial x \partial \mu}(x, \mu(x))\frac{d\mu}{dx}(x) \\ + \frac{\partial^2 f}{\partial \mu^2}(x, \mu(x))\left(\frac{d\mu}{dx}(x)\right)^2 + \frac{df}{d\mu}(\mu, \mu(x))\frac{d^2\mu}{dx^2}(x). \end{aligned} \tag{3.15}$$

Evaluating (3.15) at $(\mu, x) = (0,0)$ and using (3.14) gives us

$$\frac{\partial^2 f}{\partial x^2}(0,0) + \frac{\partial f}{\partial \mu}(0,0)\frac{d^2\mu}{dx^2}(0) = 0, \tag{3.16}$$

which is the same as

$$\frac{d^2\mu}{dx^2}(0) = -\frac{\frac{\partial^2 f}{\partial x^2}(0,0)}{\frac{\partial f}{\partial \mu}(0,0)}. \tag{3.17}$$

Thus, (3.17) is non-zero provided that we have

$$\frac{\partial^2 f}{\partial x^2}(0,0) \neq 0.$$

So, the required conditions for saddle-node bifurcation were derived. The simplest form (more formally called the normal form) of the center manifold for the systems where it occurs is

$$\dot{x}(t) = \mu \pm x^2.$$

The bifurcation diagram for $\dot{x}(t) = \mu - x^2$ is given below. From the diagram we see that, for the given value of μ we have the following cases:

1. For $\mu < 0$, we have no equilibria.

2. For $\mu > 0$, we have two equilibria $\pm\mu$, where the positive equilibrium is stable and the negative is unstable.

3. $\mu = 0$ is a bifurcation point.

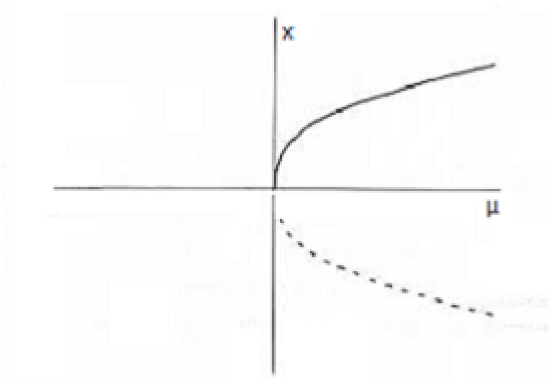

Figure 1: Bifurcation diagram for saddle-node bifurcation (full line - stable equilibria, dashed line - unstable equilibria).

The saddle-node bifurcation is also known as the blue-sky bifurcation, due to the sudden (diss)appearance of equilibria at the bifurcation point.

3.1.2 Transcritical bifurcation

The next bifurcation we will consider is the transcritical bifurcation. Consider the vector field

$$\dot{x}(t) = f(x, \mu) = \mu x - x^2, \qquad x \in \mathbb{R}, \mu \in \mathbb{R}. \tag{3.18}$$

It is easy to see that

$$f(0,0) = 0 \qquad \text{and} \qquad \frac{\partial f}{\partial x}(0,0) = 0. \tag{3.19}$$

The lines of equilibria of (3.18) are given by

$$x = 0 \qquad \text{and} \qquad x = \mu.$$

Linearization of (3.18) gives us $Df(x) = \mu - 2x$, so if $\mu < 0$ equilibrium $x = 0$ is stable and $x = \mu$ is unstable, and if $\mu > 0$ then $x = 0$ is unstable and $x = \mu$ stable. The equilibria change their stabilities at $\mu = 0$, so $\mu = 0$ is the bifurcation point of our system.

Now, let us derive the general conditions for transcritical bifurcation. Conditions needed for the transcritical bifurcation to occur are the following:

1. Two curves of equilibria points passing through $(x_0, \mu_0) = (0, 0)$, one given by $x = \mu$, and other by $x = 0$.
2. Both curves of equilibria existing on both sides of $\mu = 0$.
3. The stability along each curve of equilibria changes after passing through $\mu = 0$.

We consider the same family of scalar fields as in the previous bifurcation, and $(x, \mu) = (0, 0)$ is a non-hyperbolic equilibrium. Since we want to have two curves of equilibria through the origin, we need to have

$$\frac{\partial f}{\partial \mu}(0,0) = 0, \tag{3.20}$$

or by implicit function theorem we will have just one line of equilibria through the origin.

In this example, we require that $x = 0$ is one curve of equilibria, and therefore our system is of the form

$$\dot{x}(t) = f(x, \mu) = xF(x, \mu), \quad x \in \mathbb{R} \quad \mu \in \mathbb{R}, \tag{3.21}$$

where F is defined as

$$F(x, \mu) := \begin{cases} \frac{f(x,\mu)}{x} & \text{if } x \neq 0 \\ \frac{\partial f}{\partial x}(0, \mu) & \text{if } x = 0 \end{cases} \tag{3.22}$$

Now, we seek under which conditions F has a curve of equilibria through $(x, \mu) = (0, 0)$. These conditions will be expressed with derivatives of F, which can be expressed using derivatives of f.

By using (3.22), it is easy to see that

$$F(0,0) = 0 \tag{3.23}$$

$$\frac{\partial F}{\partial x}(0,0) = \frac{\partial^2 f}{\partial x^2} \tag{3.24}$$

$$\frac{\partial^2 F}{\partial x^2}(0,0) = \frac{\partial^3 f}{\partial x^3}(0,0) \tag{3.25}$$

and

$$\frac{\partial F}{\partial \mu}(0,0) = \frac{\partial^2 f}{\partial x \partial \mu}(0,0). \tag{3.26}$$

If we assume that (3.26) is not equal to zero, we can use implicit function theorem to show that there exists a function $\mu(x)$, such that $F(x, \mu(x)) = 0$ If we want that our function is not equivalent to $x = 0$, and to exist on both sides of $\mu = 0$, we need that

$$0 < \left| \frac{d\mu}{dx}(0) \right| < \infty.$$

After performing implicit differentiation on F, just like in the case of saddle node bifurcation, we get

$$\frac{d\mu}{dx}(0) = -\frac{\frac{\partial F}{\partial x}(0,0)}{\frac{\partial F}{\partial \mu}(0,0)} \tag{3.27}$$

By using equations (3.23-3.26), (3.27) becomes

$$\frac{d\mu}{dx}(0) = -\frac{\frac{\partial^2 f}{\partial x^2}(0,0)}{\frac{\partial^2 f}{\partial x \partial \mu}(0,0)}. \tag{3.28}$$

After performing those operations, we have established the required criteria for the transcritical bifurcation. The normal form for the transcritical bifurcation is

$$\dot{x}(t) = \mu x \pm x^2.$$

We provide the bifurcation diagram for the $\mu x - x^2$.

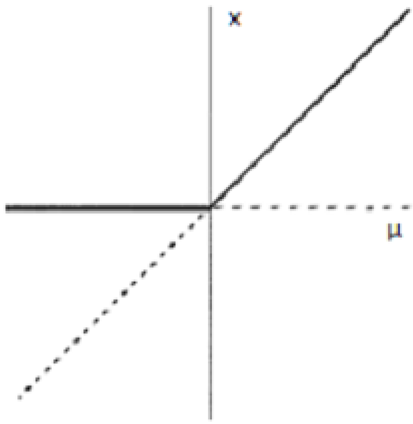

Figure 2: Bifurcation diagram for transcritical bifurcation (full line - stable equilibria, dashed line - unstable equilibria).

3.1.3 Pitchfork bifurcation

The last bifurcation of scalar fields is the pitchfork bifurcation. Consider the vector field

$$\dot{x}(t) = f(x, \mu) = \mu x - x^3, \qquad x \in \mathbb{R}, \mu \in \mathbb{R}. \tag{3.29}$$

It is easy to see that

$$f(0,0) = 0, \qquad \text{and} \qquad \frac{\partial f}{\partial x}(0,0) = 0. \tag{3.30}$$

The equilibria are given by

$$x = 0 \qquad \text{if } \mu < 0$$

and

$$x = 0 \qquad \text{and} \qquad x = \pm\sqrt{\mu} \qquad \text{if } \mu > 0.$$

Linearization gives us $Df(x) = \mu - 3x^2$. For $\mu < 0$ the equilibrium $x = 0$ is stable. For $\mu > 0$, $x = 0$ is an unstable equilibrim, while the equilibria $x = \pm\sqrt{\mu}$ are stable. Again, $\mu = 0$ is a bifurcation point.

Now, let us perform the general analysis. The pitchfork bifurcation will have the following characteristics:

1. Two curves of equilibria through $(\mu, x) = (0, 0)$, one given by $x = 0$, the other one by $\mu = x^2$.

2. The curve $x = 0$ exists on both sides of $\mu = 0$, the curve $\mu = x^2$ exists on one side of $\mu = 0$.

3. The points on the curve $x = 0$ have different stability types on the opposite sides of $\mu = 0$, and equilibria of $x^2 = \mu$ have the same stability type.

We assume that we have the same family of scalar fields, which have the non-hyperbolic equilibrium at $(x, \mu) = (0, 0)$. Like with transcritical bifurcation, we need that

$$\frac{\partial f}{\partial \mu}(0,0) = 0. \tag{3.31}$$

and since $x = 0$ is a curve of equilibria, our scalar field has the form

$$\dot{x}(t) = xF(x, \mu), \quad x \in \mathbb{R}, \mu \in \mathbb{R} \tag{3.32}$$

where

$$F(x,\mu) := \begin{cases} \frac{f(x,\mu)}{x} & \text{if } x \neq 0 \\ \frac{\partial f}{\partial x}(0,\mu) & \text{if } x = 0 \end{cases} \tag{3.33}$$

To get the second curve, we need that

$$F(0,0) = (0,0) \tag{3.34}$$

with

$$\frac{\partial F}{\partial \mu}(0,0) \neq 0. \tag{3.35}$$

Due to the implicit function theorem, for some neighborhood of x exists a unique function $\mu(x)$ such that $F(x, \mu(x)) = 0$. In order for the curve to satisfy the properties mentioned above, we need that

$$\frac{d\mu}{dx}(0) = 0 \tag{3.36}$$

and

$$\frac{d^2\mu}{dx^2}(0) \neq 0. \tag{3.37}$$

After performing implicit differentiation of F, we see that properties are satisfied, since

$$\frac{d\mu}{dx}(0) = -\frac{\frac{\partial F}{\partial x}(0,0)}{\frac{\partial F}{\partial \mu}(0,0)} = 0 \tag{3.38}$$

and

$$\frac{d^2\mu}{dx^2}(0) = -\frac{\frac{\partial^2 F}{\partial x^2}(0,0)}{\frac{\partial F}{\partial \mu}(0,0)} \neq 0 \tag{3.39}$$

If we use (3.33) (3.38) (3.39), we can express it in terms of derivatives of f in this form

$$\frac{d\mu}{dx}(0) = -\frac{\frac{\partial^2 F}{\partial^2 x}(0,0)}{\frac{\partial F}{\partial \mu}(0,0)} = 0 \tag{3.40}$$

and

$$\frac{d^2\mu}{dx^2}(0) = -\frac{\frac{\partial^3 f}{\partial x^3}(0,0)}{\frac{\partial^2 f}{\partial x \partial \mu}(0,0)} \neq 0. \tag{3.41}$$

Therefore, we have established the conditions needed for occurrence of the pitchfork bifurcation. The normal form for the families undergoing pitchfork bifurcation is

$$\dot{x}(t) = \mu x \pm x^3.$$

We provide the bifurcation diagram for $\mu x - x^3$.

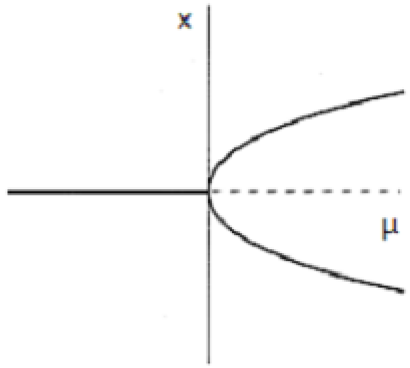

Figure 3: Bifurcation diagram for pitchfork bifurcation (full line - stable equilibria, dashed line - unstable equilibria).

3.2 A pure imaginary pair of eigenvalues : Poincare-Andronov-Hopf bifurcation

We will now turn to the the next possible type of bifurcation, the Poincare-Andronov-Hopf bifurcation. It received its name from the names of the first mathematicians that were studying it. After observing the bifurcations of zero eigenvalue, we consider a system where the linearization around the equilibrium has a pair of pure imaginary eigenvalues. For this bifurcation, we will only provide partial analysis. Example where this bifurcation occurs will be provided in the fourth chapter. Let us consider the following family of vector fields

$$\dot{x}(t) = g(x, \mu), \quad x \in \mathbb{R}^n, \mu \in \mathbb{R} \tag{3.42}$$

and we assume that g is at least C^5 around the equilibrium $0 = g(x_0, \mu_0)$. We want to know how the orbit structure changes as μ is varied. We assume that the linearized vector field has a pair of complex eivenvalues, and that the rest of eigenvalues have non-zero real parts. Since the equilibrium is non-hyperbolic, we don't have information about the orbit structure at the equilibrium and the orbit structures of points close to it. But, by center manifold theory, we know that the orbit structure near (x_0, μ_0) is determined by restriction of g to its center manifold. On the center manifold (3.42) has the following form (see [6]):

$$\begin{bmatrix}\dot{x}(t)\\ \dot{y}(t)\end{bmatrix} = \begin{bmatrix}\mathrm{Re}\lambda(\mu) & -\mathrm{Im}\ \lambda(\mu)\\ \mathrm{Im}\ \lambda(\mu) & \mathrm{Re}\lambda(\mu)\end{bmatrix}\begin{bmatrix}x\\ y\end{bmatrix} + \begin{bmatrix}f^1(x,y,\mu)\\ f^2(x,y,\mu)\end{bmatrix}, \tag{3.43}$$

where $(x, y, \mu) \in \mathbb{R} \times \mathbb{R} \times \mathbb{R}$, f^1 and f^2 are non-linear in x and y and $\lambda(\mu), \overline{\lambda(\mu)}$ are the eigenvalues of vector field linearized about the equilibrium. Eigenvalues will be denoted by

$$\lambda(\mu) = \alpha(\mu) \pm i\omega(\mu), \quad \text{with} \quad \alpha(0) = 0, \omega(0) \neq 0. \tag{3.44}$$

The normal form of (3.43) (see [6]) is

$$\begin{aligned}\dot{x}(t) &= \alpha(\mu)x - \omega(\mu)y + (\alpha(\mu)x - b(\mu)y)(x^2 + y^2) + \mathcal{O}(|x^5|, |y^5|),\\ \dot{y}(t) &= \omega(\mu)x + \alpha(\mu)y + (b(\mu)x + a(\mu)y)(x^2 + y^2) + \mathcal{O}(|x^5|, |y^5|)\end{aligned} \tag{3.45}$$

In polar coordinates, it is given by

$$\begin{aligned}\dot{r}(t) &= \alpha(\mu)r + a(\mu)r^3 + \mathcal{O}(r^5),\\ \dot{\theta}(t) &= \omega(\mu) + b(\mu)r^2 + \mathcal{O}(r^4).\end{aligned} \tag{3.46}$$

We expand its Taylor series around $\mu = 0$, since we are interested in the dynamics near that point. Then (3.46) becomes

$$\begin{aligned}\dot{r}(t) &= \alpha'(0)\mu r + a(0)r^3 + \mathcal{O}(\mu^2 r, \mu r^3, r^5),\\ \dot{\omega}(t) &= \omega(0) + \omega'(0)\mu + b(0)r^2 + \mathcal{O}(\mu^2, \mu r^2, r^4)\end{aligned} \tag{3.47}$$

where we differentiate with respect to μ and $\alpha(0) = 0$. By neglecting the higher order terms , and easing the notation, we get the system

$$\begin{aligned}\dot{r}(t) &= d\mu r + ar^3,\\ \dot{\theta}(t) &= \omega + c\mu + br^2,\end{aligned} \tag{3.48}$$

where $d := \alpha'(0),\ \ a := a(0),\ \ \omega := \omega(0),\ \ c := \omega'(0),\ \ b := b(0)$.

How do we analyze the dynamics of this system? In scalar fields, we would just find the equilibria and study the nature of their stability. But, in (3.47) we proceed differently. We look for the values of $r > 0$ and μ such that $\dot{r} = 0$, but $\dot{\theta} \neq 0$, which will correspond to periodic orbits of (3.47), which will be emphasized in the next lemma.

Lemma 3.1. *For $-\infty < \frac{\mu d}{a} < 0$ and sufficiently small μ,*

$$(r(t), \theta(t)) = \left(\sqrt{\frac{-\mu d}{a}}, \left(\omega + \left(c - \frac{bd}{a}\right)\mu\right)t + \theta_0\right), \tag{3.49}$$

is a periodic orbit of 3.47.

Proof. To show that (3.49) is a periodic orbit, we only need to ensure that $\dot{\theta} \neq 0$. And because ω is a constant independent from μ, this immediately follows if μ is sufficiently small. □

Stability questions are interpreted in the next lemma.

Lemma 3.2. *The periodic orbit (3.49) is*

- *Asymptotically stable for $a < 0$;*
- *Asymptotically unstable for $a > 0$.*

Proof. The proof is omitted, as it relies on theory which is beyond the scope of our work. □

We notice that because $r > 0$, (3.49) is the only periodical orbit possible for (3.47). Regarding the stability of the periodic orbit, and if it exists for $\mu > 0$ or $\mu < 0$, from (3.49), we observe that we have four possibilities:

Theorem 3.3. *Consider the normal form (3.47). We assume that the origin is a equilibrium which is*

$$\begin{aligned} &\textit{stable at} \quad \mu = 0 \quad \textit{for} \quad a < 0 \\ &\textit{unstable at } \mu = 0 \quad \textit{for} \quad a > 0. \end{aligned}$$

Then, for different d and a, we distinguish between the following cases:

1. $\mathbf{d} > \mathbf{0}, \mathbf{a} > \mathbf{0}$. *In this case, the origin is an unstable equilibrium for $\mu > 0$ and asymptotically stable equilibrium for $\mu < 0$, with an unstable periodic orbit for $\mu < 0$.*

2. $\mathbf{d} > \mathbf{0}, \mathbf{a} < \mathbf{0}$. *In this case, the origin is an asymptotically stable equilibrium for $\mu < 0$ and an unstable equilibrium for $\mu > 0$, with an asymptotically stable periodic orbit for $\mu > 0$.*

3. $\mathbf{d} < \mathbf{0}, \mathbf{a} > \mathbf{0}$. *In this case, the origin is an unstable equilibrium for $\mu < 0$ and an asymptotically stable equilibrium for $\mu > 0$ with an unstable periodic orbit for $\mu > 0$.*

4. $\mathbf{d} < \mathbf{0}, \mathbf{a} < \mathbf{0}$. *In this case, the origin is an asymptotically stable equilibrium for $\mu < 0$ and an unstable equilibrium for $\mu > 0$, with an asymptotically stable periodic orbit for $\mu < 0$.*

Proof. This proof will use the Poincare-Bendixon theorem. We consider truncated normal form (3.48) and the second case. In this case, we have a stable periodic orbit and it exists for $\mu > 0$, and r coordinate is given by $r = \sqrt{\frac{-d\mu}{a}}$. We choose sufficiently small $\mu > 0$ and we consider the annulus A, given by

$$A = \Big\{(r,\theta)|r_1 \leq \sqrt{\frac{-d\mu}{a}} \leq r_2\Big\}.$$

It is not hard to see, that by (3.48), on the boundary of A, our vector field is pointing strictly into the interior of A. Therefore, A is a positive invariant set. Also, A has no equilibria, so by Poincare-Bendixon theorem, A has a stable periodic orbit. But, our goal is to show that this also holds for the (3.47). Let's consider now (3.47). If we take sufficiently small μ and r sufficiently small, the $\mathcal{O}(\mu^2 r, \mu r^3, r^5)$ terms can be made so that they are much smaller than the rest of the normal form. So, by again taking r_1 and r_2 sufficiently small, A will still be a positive invariant set with no equilibria. So, by Poincare-Bendixon theorem, A contains a stable periodic orbit. The proof for the other three cases is similar (when $a > 0$, we just the time reversed flow). □

We state a remark. When $a < 0$, the periodic orbit can exists for either $\mu > 0$ or $\mu < 0$, and in both cases, it is asymptotically stable. The same holds when $a > 0$, except that the periodic orbit is unstable. So, the value of a tells us if we will have stable or unstable periodic orbit. The case when $a < 0$ is referred to as a supercritical bifurcation, and $a > 0$ is referred to as a subcritical bifurcation.

4 Examples from mathematical biology: predator-prey models

The theory of dynamical systems has a wide range of applications in natural sciences, such as biology, physics and chemistry. In this chapter we take a look at some of the well-known models in biology that describe the interactions between a predator population and its prey. This section is partly based on the book of Edelstein-Keshet (see [1]). We will start with the famous Lotka-Volterra model (see [5]).

4.1 Lotka-Volterra model

During and after the World War I, Italian biologist Umberto D'Ancona was observing the structure of fish population in the Adriatic sea. During his observations, he noticed an unexpected phenomena: that in the years during the World War I, when there was less fishing, the population of predator fish increased. Struck by that, he wrote to the famous Italian mathematical Vito Volterra. Volterra answered by using simple mathematical model in form of the system of differential equations. A few years later, Alfred Lotka independently formulated and analyzed the same model in a different context. Before we start with the analysis, in this chapter we will mark derivatives with prime instead of dot notation.

If we denote with $y(t)$ the size of the predator population at time t and by $x(t)$ the size of the population of the prey, we can describe the Volterra's assumptions in the following way:

1. In absence of predators, population grows exponentially, i.e. $\dot{x}(t) = ax$, for $a > 0$.
2. Prey is needed for the survival of the predators: in absence of prey the predator population falls exponentially, i.e. $\dot{y}(t) = -dy$, for $d > 0$.
3. The amount of prey a predator catches in time unit is proportional with the size of the prey's population; bx for some $b > 0$.
4. Caught prey is reflected in the growth of the predator population such that, with some proportionality constant, the caught prey is directly converted to new predators.

The amount of prey a predator catches in time unit is called the *functional response*. The *numerical response* gives us the number of newborn predators for one predator in one time unit, usually as a function of the amount of prey that predator catches. The functional responses are generally classified as Holling type I, II and III functional responses, from the work of C.S. Holling ([2]). In the Lotka-Volterra model, we use the Holling type I response, i.e. the linear functional response.

The assumptions of Volterra lead to the following system:

$$\begin{aligned} \dot{x}(t) &= ax - bxy \\ \dot{y}(t) &= cxy - dy \end{aligned} \tag{4.1}$$

The equilibria are

$$(x_1, y_1) = (0,0) \qquad (x_2, y_2) = \left(\frac{d}{c}, \frac{a}{b}\right).$$

Linearization of (4.1) has the form

$$D(x,y) = \begin{pmatrix} a - by & -bx \\ cy & cx - d \end{pmatrix}. \tag{4.2}$$

The linearizations around equilibria are given by

$$D(x_1, y_1) = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix} \qquad \text{and} \qquad D(x_2, y_2) = \begin{pmatrix} 0 & -\frac{bd}{c} \\ \frac{ac}{b} & 0 \end{pmatrix}.$$

We see that for any positive values of a, b, c, d, (x_1, y_1) is a saddle (unstable equilibrium), whereas (x_2, y_2) is a center. Hence we do not observe any bifurcations in the Lotka-Volterra system. We plot the orbits and the predator-prey population graph for the parameters $a = 8, b = 5, c = 5, d = 1$.

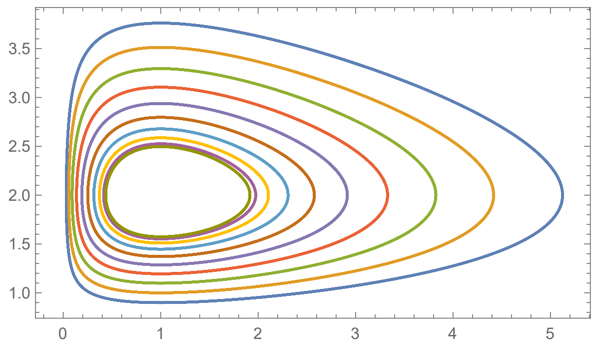

Figure 4: Orbits of the Lotka-Volterra system for parameters $a = 8, b = 5, c = 5, d = 1$.

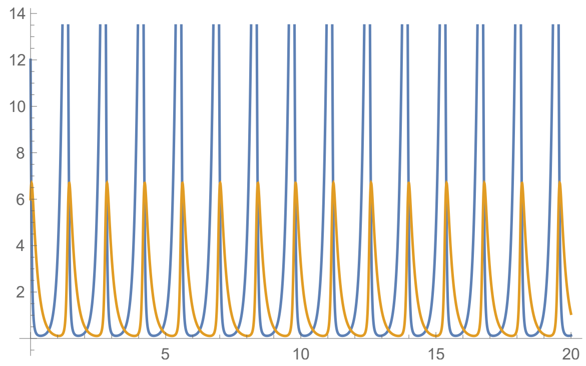

Figure 5: Graph of predator prey functions of Lotka-Volterra system for parameters $a = 8, b = 5, c = 5, d = 1$ (prey-blue, predator-orange).

The Lotka-Volterra model incorporates very simple assumptions regarding the dynamics of the two populations and predicts as model solutions an infinite family of closed curves (see [1]). This family of closed curves is destroyed as soon as more realistic assumptions are considered. In this sense, the model of Lotka-Volterra is not a convincing model of predator-prey interactions. In the following two sections, we take a look at two slightly more realistic models.

4.2 The predator-prey model with logistic growth and Holling type I functional response

We now assume that, in absence of predators, the prey population grows logistically with intrinsic growth rate r $(r > 0)$ and with carrying capacity $K > 0$, meaning that in absence of predators

$$\dot{x}(t) = rx\big(1 - \frac{x}{K}\big).$$

Keeping the other assumptions the same as in the Lotka-Volterra model, we will therefore consider the following model:

$$\begin{aligned} \dot{x}(t) &= rx\Big(1 - \frac{x}{K}\Big) - bxy \\ \dot{y}(t) &= cxy - dy. \end{aligned}$$

There are three equilibria, two of them have no predator population present,

$$(x_1, y_1) = (0, 0) \qquad \text{and} \qquad (x_2, y_2) = (K, 0),$$

and one with both populations present is

$$\Big(x_3, y_3\Big) = \Big(\frac{d}{c}, \frac{r}{b}\Big(1 - \frac{d}{cK}\Big)\Big).$$

We see that (x_3, y_3) is biologically meaningful when $K > \frac{d}{c}$. Linearization around first two equilibria gives us

$$D(x_1, y_1) = \begin{pmatrix} r & 0 \\ 0 & -d \end{pmatrix} \qquad \text{and} \qquad D(x_2, y_2) = \begin{pmatrix} -r & -bK \\ 0 & -d + cK \end{pmatrix}$$

meaning that (x_1, y_1) is always a saddle point. The steady state (x_2, y_2) is a saddle if we have a biologically meaningful third equilibrium, and is LAS otherwise. Linearization around (x_3, y_3) is given by

$$D(x_3, y_3) = \begin{pmatrix} -rx_3 & -bx_3 \\ cy_3 & 0 \end{pmatrix}.$$

Whenever (x_3, y_3) is biologically meaningful, the trace of $D(x_3, y_3)$ is negative and its determinant of positive, meaning that (x_3, y_3) is LAS whenever it is biologically meaningful.

To discuss the bifurcations in our system, let us fix all the parameters but K. We observe that at $K = \frac{d}{c}$ a transcritical bifurcation occurs where equilibria (x_2, y_2) and (x_3, y_3) exchange stability. To demonstrate this with an example, let $r = 2, b = 1, c = 3, d = 6$. The system goes through a transcritical bifurcation at $K = 2$. For $K < 2$, the predator population goes extinct, while the two populations can coexist for $K > 2$.

In Figure 4.2 we provide a bifurcation diagram for y_3 as the function of K.

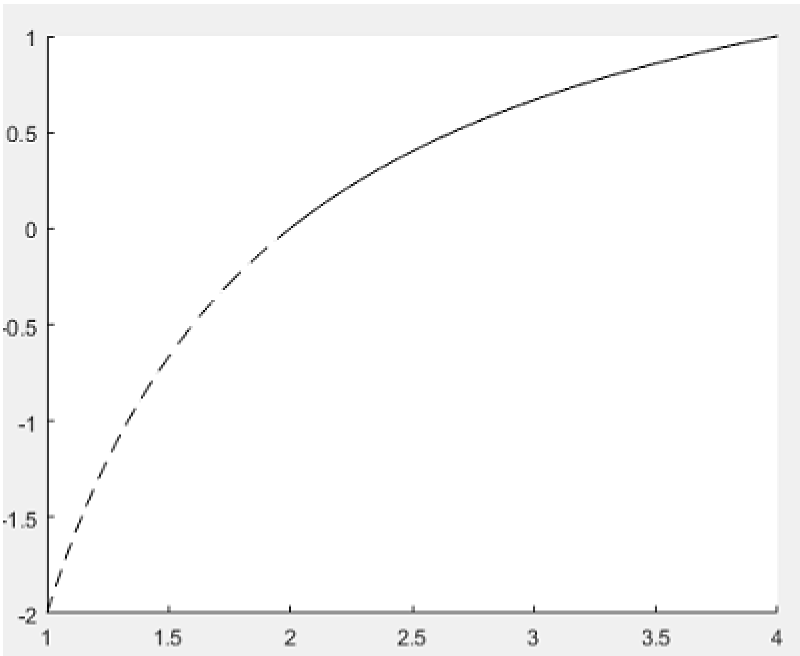

Figure 6: Bifurcation diagram for y_3 as the function of K for parameter values $r = 2, b = 1, c = 3, d = 6$ (full line - stable equilibria, dashed line - unstable equilibria).

4.3 The Rosenzweig-MacArthur model

In the next model, we use the Holling II functional response,

$$g(x) = \frac{bx}{1 + b\beta x}.$$

We set the numerical response to be proportial to the functional response. Keeping the other assumptions from previous system, we get the following system:

$$\begin{aligned} \dot{x}(t) &= rx\Big(1 - \frac{x}{K}\Big) - \frac{bxy}{1 + b\beta x} \\ \dot{y}(t) &= \frac{cxy}{1 + b\beta x} - dy, \end{aligned} \tag{4.3}$$

which is called the Rosenzweig - MacArthur model.

Let us perform the analysis of isoclines and stability analysis of (4.3). The $x-$isoclines are given by

$$x = 0 \ \text{ or } \ y = \frac{r}{b}\Big(1 - \frac{x}{K}\Big)\Big(1 + b\beta x\Big),$$

meanwhile $y-$isoclines are given by

$$y = 0 \ \text{ or } \ x = \frac{d}{c - db\beta}.$$

We have two equilibria with no predators present, namely

$$(x_1, y_1) = (0, 0) \qquad \text{and} \qquad (x_2, y_2) = (K, 0),$$

and one with both populations present is

$$(x_3, y_3) = \Big(\frac{d}{c - db\beta}, \frac{r}{b}(1 - \frac{x_3}{K})(1 + b\beta x_3)\Big).$$

When is (x_3, y_3) biologically meaningful? For that to occur, we first of all need that

$$\frac{d}{c - db\beta} > 0.$$

The second condition is that $x_3 < K$.

In order analyze the stability of equilibria, we will perform the linearization on our system. We set that $f(x) = rx\big(1 - \frac{x}{K}\big)$ and $g(x) = \frac{bx}{1+b\beta x}$. In that form,

$$D = \begin{pmatrix} f'(x) - yg'(x) & -g(x) \\ \gamma y g'(x) & \gamma g(x) - d \end{pmatrix}.$$

Then

$$D(x_1, y_1) = \begin{pmatrix} r & 0 \\ 0 & -d \end{pmatrix} \qquad \text{and} \qquad D(x_2, y_2) = \begin{pmatrix} -r & -\frac{bK}{1+b\beta K} \\ 0 & \frac{cK}{1+b\beta K} - d \end{pmatrix}$$

The first equilibrium is always a saddle. The second is a saddle whenever $\frac{cK}{1+b\beta K}-d>0$ and is LAS whenever $\frac{cK}{1+b\beta K}-d<0$. Linearization around (x_3,y_3) gives us

$$D(x_3,y_3)=\begin{pmatrix} f'(x_3)-y_3g'(y_3) & -g(x_3) \\ \gamma y_3 g'(x_3) & 0 \end{pmatrix}$$

The determinant of $D(x_3,y_3)$ is equal to $\gamma y_3 g(x_3)g'(x_3)$, which is positive. The trace value depends on $f'(x_3)-g'(x_3)y_3$. Now, let us observe $y=\frac{f(x)}{g(x)}$. It is also the x-isocline. We see that

$$y'=\frac{f'g-fg'}{g^2}=\frac{f'-yg'}{g},$$

implying that (x_3,y_3) is LAS whenever it is on the declining part of x-isocline. We see that when trace becomes equal to zero, we will have a pair of imaginary eigenvalues.

To discuss bifurcations, we fix all the parameters but K. In the following example, we set the parameters as : $r=1.1, b=1, c=0.9, d=0.5, \beta=0.8$. By varying the parameter K, we notice that (x_3,y_3) goes from LAS to unstable equilibrium. Because we get a pair of imaginary eigenvalues when trace becomes equal to zero, our system goes through Poincare-Andronov-Hopf bifurcation. We provide a bifurcation diagram for y as a function of K. The point at which Poincare-Andronov-Hopf bifurcation occurs is marked with a circle.

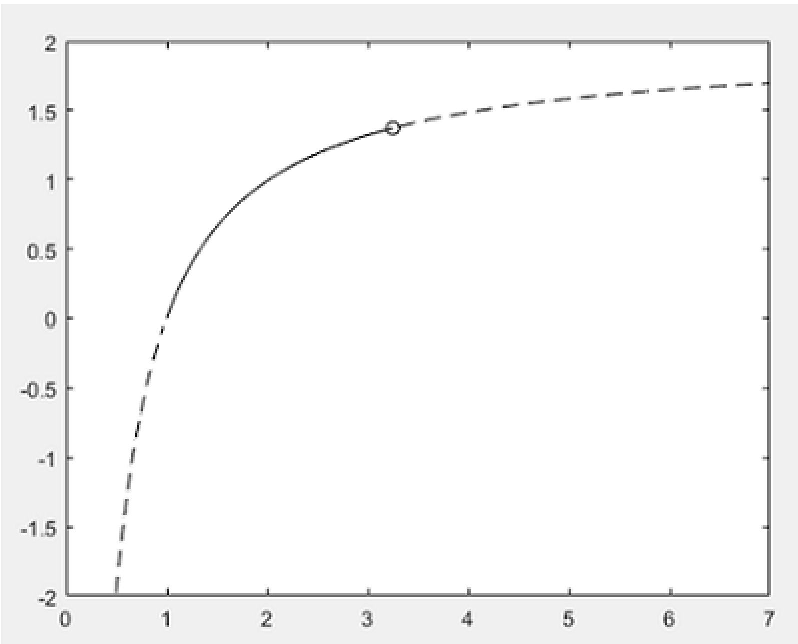

Figure 7: Bifurcation diagram for y as a function of K for parameter values $r=1.1, b=1, c=0.9, d=0.5, \beta=0.8$ (full line - stable equilibria, dashed line - unstable equilibria).

From the graph, we notice that the stability of y changes for the values of $K=1$ and $K=3.25$. When $K=3.25$, the value of y is 1.37, and at that moment trace of the Jacobian of (4.3) at (x_3, y_3) becomes zero, (x_3, y_3) becomes unstable and our system undergoes Poincare-Andronov-Hopf bifurcation. At $K = 1$, (x_3, y_3) goes from unstable to stable equilibrium. At the same time, (x_2, y_2) goes from stable to unstable equilibrium, meaning that our system undergoes transcritical bifurcation. So, the bifurcation points of our system our $K = 1$ and $K = 3.25$. In the figure given below, we will show phase portraits with topologically different dynamics for two different values of K, before and after (x_3, y_3) goes from stable to unstable. From the portraits, we see that Poincare-Andronov-Hopf bifurcation is supercritical.

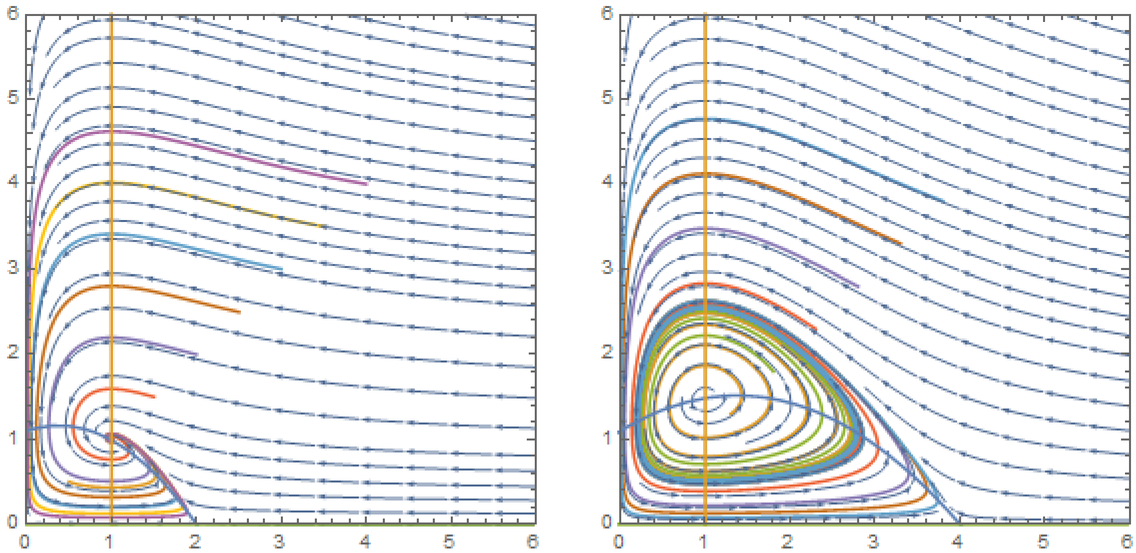

Figure 8: Phase portraits for $K = 2$ and $K = 4$.

5 Conclusion

In this final project paper, we studied the bifurcations of equilibria of vector fields with applications to predator-prey systems. We were mostly following the book by Wiggins (see [6]), for theoretical part, and Edelstein-Kershet's book (see [1]) for applications part. We studied dynamical systems in a form of parametrized system of non-linear differential equations

$$\dot{x}(t) = f(x, \mu), \qquad x \in \mathbb{R}^n, \mu \in \mathbb{R}.$$

In the preliminary section, we presented the main results from the theory of dynamical systems that are needed in the subsequent chapters.

In the third chapter, we wanted to answer two question: how is the stability of equilibria affected as the parameter value changes, and how can we determine the stability of systems around the non-hyperbolic equilibria? To answer our question, we applied center manifold theory. We analyzed and derived conditions for four different bifurcations: saddle-node, transcritical, pitchfork and Poincare-Andronov-Hopf.

The theory developed in the fourth chapter was applied in three examples of predator-prey dynamics. We started from the simplest example of Lotka-Volterra, and moved to more realistic models. We have analyzed the stability of system's equilibria and performed bifurcation analysis by fixing all but one parameter. From all of the work we performed, we were able to deduce, at least for some cases, how shifts in the value of the parameters can lead to change in the dynamics of the system.

6 Povzetek naloge v slovenskem jeziku

Teorija bifurkacij je področje matematike, ki se ukvarja z spremembami kvalitativnih ali topoloških struktur vektorskih polj in ostalih dinamičnih sistemov. V tej nalogi smo študirali bifurkacije ravnovesnih točk vektorskih polj z uporabo v sistemih plenilec-plen.

Študirali smo dinamične sisteme podane v obliki parametriziranih sistemov nelinearnih diferencialnih enačb,

$$\dot{x}(t) = f(x, \mu), \qquad x \in \mathbb{R}^n, \mu \in \mathbb{R}.$$

Osredotočili smo se na ravnovensne točke takih sistemov, torej točke (x_0, μ_0) za katere velja $f(x_0, \mu_0) = 0$. Dinamično gledano, ravnovesne točke niso zanimive. Ampak, ravnovesne točke nam pomagajo spoznati več o dinamiki sistemov, ki imajo začetna stanja v bližini ravnovesnih točk. Da bi spoznali več o dinamiki teh sistemov, smo predstavili različne pojme stabilnosti ravnovesnih točk ter princip linearizacije sistema okoli ravnovesne točke. Povedali smo, v katerih primerih nam linearizacija da popolno informacijo o stabilnosti ravnovesne točke nelinearnega sistema in predstavili nekaj rezultatov za ravninske sisteme.

V tretjem poglavju smo odgovarjali na vprašanje, kako se dinamika spreminja ko spreminjamo vrednosti parametra μ. Motivacijo za to vprašanje smo dobili iz modeliranja naravnih procesov (na primer, kako se spreminja velikost populacije rib glede na intenziteto ribištva). Pokazali smo, da se dinamika kvalitativno ne spreminja okrog hiperboličnih ravnovesnih točk, do kvalitativnih sprememb pa pride, ko so ravnovesne točke nehiperbolične. Predstavili smo transkritično, sedelno-vozelno in viličasto bifurkacijo in za vsako od njih izpeljali pogoje, ki omogočajo njihov nastanek. Nato smo analizirali vektorska polja, pri katerih linearizacija poda matriko s parom imaginarnih lastnih vrednosti. Predstavili smo Poincare-Andronov-Hopfovo bifurkacijo.

V zadnjem poglavju smo uporabili teorijo na treh modelih dinamike plenilec-plen. Začeli smo z modelom Lotka-Volterra in nato predstavili še dva bolj realistična modela; model z logistčno rastjo plena ter funkcionalnim odzivom Holling I in model Rosenzweig-MacArthur. Za vse tri modele smo naredili stabilnostno analizo ravnovesnih stanj, študirali bifurkacije v modelih ter predstavili bifurkacijske diagrame.

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