The Predator-Prey Model

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Chapter 1

Introduction

Many mathematical models are described with the help of differential equations. In this thesis, the mathematical model which is going to be analyzed and used is the Lotka-Volterra equations. This is also known as the predator-prey equations. An interesting question that can be derived from these equations is what happens with the system's solutions as time passes by. An important factor in understanding what happens to the system's solutions is the understanding of critial points. Such points correspond to constant solutions, or equilibrium solutions.

These critical points and systems of differential equations are going to be explained in more detail later in the thesis. They are of special importance to the Lotka-Volterra equations. The "thesis question" is going to be what happens to the system's solutions as time passes by where the critical points of the system are of special importance.

The Lotka-Volterra equations were developed simultaneously but independently by Alfred J. Lotka and Vito Volterra. They were developed in papers by Lotka in 1925 and by Volterra in 1926. Lotka was an American mathematician, physical chemist and statistician and was born in what is now Ukraine. He is famous for his work in population dynamics and energetics. Lotka is best known for his work of the predator-prey model and as Wikipedia writes (Wikipedia, 2021a), this model is still the basis of many models used in the analysis of population dynamics in ecology. Although he is best known for the predator-prey model, his main interest was demography and he joined the Metropolitan Life Insurance company. From here on he concentrated on life tables and his passion to bring mathematics to the problems of biology. Lotka sought out to apply the principles of physical sciences to biological sciences.

While Volterra was an Italian mathematician and physicist who held professorships at Pisa,Turin, and Rome. He is particularly famous for his contributions to mathematical ecology and integral equations. Volterra is one of the founders of functional analysis. Born in Ancona to a poor jewish family, Volterra showed early promise in mathematics befor attending the university of Pisa. Here he became as Wikipedia writes (Wikipedia, 2021b) a professor in mechanics in 1883. He immediately started working his theory of functionals which lead to his interest and later contributions in integral and integro-differential equations. In 1892, he became professor of mechanics at the University of Turin and in 1900, professor of mathematical physics at the University of Rome La Sapienza. After World War 1, Volterra started focusing on the application of his mathematical ideas to biology. An outcome of this period is the Lotka-Volterra equations.

The Lotka-Volterra equations or predator-prey equations are a pair of first-order nonlinear differential equations. They are used to describe a situation in which one species(the predator) preys on the other species(the prey) while the prey lives on a different source of food. A real life example of this could be foxes and rabbits living in a closed forest. The foxes hunt and prey on the rabbits and the rabbits live on the vegetation in the forest. Volterra himself was motivated by data collected by his son-in-law, Humberto d'Ancona. D'Ancona observed that the percentage of predatory fish caught in the Adriatic sea had increased during World War 1. This baffled d'Ancona because the fishing effort had been reduced during these years. Volterra developed the model and used it to explain D'Ancona observations. It is important to mention that this is a simple model. A model involving only two species do not fully describe the complex relationships among species that actually occur in nature. But the study of simple models is the first step toward an understanding of more complicated phenomena and is therefore very important.

The thesis is based mainly on the book *Elementary Differential Equations* and *Boundary Value Problems*. The book is written by William E. Boyce, Richard C. Diprima and Douglas B. Meade. The theory which is explained later in the thesis are based mainly on this book. While the examples of the predator-prey equations are also from the book, they are solved by me. Every pictures which shows direction fields and trajectories in the examples are made by me in Mathematica. More details on the prey-predator model can be found in the book *Deterministic mathematical models in population ecology* by H.I.Freedman, 1980. Another book is *Mathematical models in population biology and epidemiology* by Brauer and Castillo-Chavez, 2001. You can also find more information about the predator-prey model in other books on population biology.

Chapter 2

Theory

2.1 The Lotka-Volterra equations

The Lotka-Volterra equations denote x and y the populations of the prey and predator at time t. The population change trough time as according to these equations:

$$\frac{dx}{dt} = ax - \alpha xy, \quad \frac{dy}{dt} = -cy + \gamma xy. \tag{2.1}$$

There are made following assumptions in constructing this model as Boyce writes (Boyce et al., 2017, p.426): 1. If there are no predators, y=0, then the prey grows at a rate proportional to the current population:

$$\frac{dx}{dt} = ax, a > 0, \tag{2.2}$$

when y=0. 2. If the population of the prey is zero, the predator dies out: thus

$$\frac{dy}{dt} = -cy, c > 0, \tag{2.3}$$

when x=0. 3. The numbers of encounters between these two species is proportional to the product of their populations. The encounters tends to promote the growth of the predator and to enhibit the growth of the prey. Thus the growth rate of the prey is decreased by a term $-\alpha xy$, while the growth rate of the predator is increased by a term of the form γxy. α and γ are positive constants. The prey equation can be interpreted as: the rate of change of the prey's population is determined by its own growth rate minus the rate at which it is preyed upon.

While the predator equation can be interpreted as: the rate of change of the predator's population depends on the rate of predation of the prey minus its death rate. The predation rate is similiar between the two species, but different constants are used. This shows that the rate of the population growth of the predator is not always equal to the rate at which it consumes its prey.

Before going into more detail about the predator-prey equations it is important to explain the basic theory of systems of first-order linear equations. The predator-prey equations are nonlinear, but it will be apparent later that first-order linear equations play an important role in solving systems of nonlinear differential equations.

2.2 Systems of first order linear equations

The general theory of a system of n first order linear equations

$$x_1' = p_{11}(t)x_1 + ... + p_{1n}(t)x_n + g_1(t) \tag{2.4}$$

$$\vdots \tag{2.5}$$

$$x_n' = p_{n1}(t)x_1 + ... + p_{nn}(t)x_n + g_n(t), \tag{2.6}$$

closely parallels that of a single linear equation of nth order. We write the system (2.5) in matrix notation to discuss it most effectively. That mean we consider $x_1 = x_1(t), ..., x_n = x_n(t)$ to be components of a vector x=x(t);Also, $g_1(t), ..., g_n(t)$ are components of a vector g(t), and $p_{11}(t), ..., p_{nn}(t)$ are elements of an n*n matrix P(t). Then the equation (2.5) takes the form:

$$x' = P(t)x + g(t). \tag{2.7}$$

This use of vectors and matrices saves a great deal of space and facilitates calculations, but it also emphasizes the similarity between system of differential equations and single(scalar) differential equations. "A vector $x = x(t)$ is a solution to (2.7) if its components satisfy the system of equations(2.5)" Boyce et al. (2017). It is appropriate to consider first the homogeneous equation

$$x' = P(t)x, \tag{2.8}$$

which is obtained from equation (2.7) be letting $g(t) = 0$. And just as in single linear differential equation of any order, there are several different ways to solve the non-homogeneous equation (2.7) once the homogeneous equation has been solved. We use the notation

$$x^1(t) = \begin{pmatrix} x_{11}(t) \\ x_{21}(t) \\ \vdots \\ x_{n_1} \end{pmatrix} \quad , \dots , x^k(t) = \begin{pmatrix} x_{1k}(t) \\ x_{2k}(t) \\ \vdots \\ x_{nk}(t) \end{pmatrix}, \tag{2.9}$$

for specific solutions of the system (2.8). The structure of solutions of system (2.8) are given in two theorems. The first one says:

Theorem 1. *If x^1 and x^2 are vector functions that are solutions of the system (2.8), then the linear combination $c_1x^1 + c_2x^2$ is also a solution for any constants c_1 and c_2*

This theorem is called the Principle of Superposition. The other theorem transforms complex valued solutions into real valued:

Theorem 2. *Consider the system (2.8) $x' = P(t)x$, where every element of P is a real valued continuous function. If $x = u(t)+iv(t)$ is a complex-valued solution of equation (2.8), then its real part u(t) and its imaginary parts v(t) are also solutions of this equation.*

It is assumed that P and g are continuous on some interval $\alpha < t < \beta$. By using theorem 1 we can conclude that if $x^1, ..., x^k$ are solutions of equation 2.8, $x = c_1x^1(t) + ... + c_kx^k(t)$ is also a solution for any constants $c_1, ...c_k$. This shows that every finite linear combination of solutions of equation (2.8) is also a solution. A question that now arises is whether all solutions of equation (2.8) can be found this way. It is reasonable to expect that for the system (2.8) of n first-order differential equations it is sufficient to form linear combinations of n properly chosen solutions. Let's consider the matrix X(t) whose columns are the vectors $x^1(t), ..., x^n(t)$ and let $x^1, ..., x^n$ be n solutions of system (2.8). The matrix:

$$X(t) = \begin{pmatrix} x_{11}(t) & \cdots x_{1n}(t) \\ \vdots & \\ & \vdots \\ x_{n1}(t) & \cdots x_{nn}(t) \end{pmatrix}. \tag{2.10}$$

The columns of X(t) are linearly independent for a given value of t if and only if $detX \neq 0$ for that value of t. This determinant is called the Wronskian of the n solutions $x^1, ..., x^n$ and could also be denoted by $W[x^1, ..., x^n]$: $W[x^1, ..., x^n](t)$ =detX(t). If and only if $W[x^1, ..., x^n]$ is not zero at a point, then the solutions $x^1, ..., x^n$ are linearly independent at that point. This leads to the following theorem:

Theorem 3. *If the vector functions $x^1, ..., x^n$ are linearly independent solutions of the system (2.8) for each point in the interval $\alpha < t < \beta$, then each solution x=x(t) of the system (2.8) can be expressed as a linear combination of $x^1, ..., x^n$*

$$x(t) = c_1x^1(t) + \cdots + c_nx^nt \tag{2.11}$$

in exactly one way

This means that all solutions of equation (2.8) can be written in the form (2.11). It is also customary to call the equation (2.11) the general solution if the constants are thought of as arbitrary because then it includes all solutions of the system (2.8). Any set of solutions $x^1, ..., x^n$ of equation (2.8) that is linearly independent at each point in the interval $\alpha < t < \beta$ is called a fundamental set of solutions for that interval. The next theorem provides us with facts that saves a lot time and computation:

Theorem 4. *If $x^1, ..., x^n$ are solutions of equation (2.8) on the interval $\alpha < t < \beta$, then this interval $W[x^1, ..., x^n]$ either is identically zero or else it never vanishes.*

This is Abel's theorem and this means we do not need to evaluate the Wronskian at every point in the interval $\alpha < t < \beta$. It enables us to determine if $x^1, ..., x^n$ form a fundamental set of solutions by evaluating the Wronskian at any point in the interval. The last theorem concerning the theory of systems of first-order linear equations states that the system (2.8) always has at least one fundamental set of solutions. The theorem is:

Theorem 5. *Let*

$$e^1 = \begin{pmatrix} 1 \\ 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, e^2 = \begin{pmatrix} 0 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, ..., e^{(n)} = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix}; \tag{2.12}$$

further, let $x^1, ..., x^{(n)}$ be the solutions of the system (2.8) that satisfy the initial conditions $x^1(t_0) = e^1, ..., x^{(n)}(t_0) = e^{(n)}$ respectively, where t_0 is any point in $\alpha < t < \beta$. Then $x^1, ..., x^{(n)}$ form a fundamental set of solutions of system (2.8).

The theory which has been described so far about systems of first order linear equations is important in solving homogeneous linear systems with constant coefficients. That is the systems of the form

$$x' = Ax, \tag{2.13}$$

where A is a constant $n \times n$ matrix. The theory behind solving these homogeneous linear systems is important in understanding the Lotka-Volterra equations. When $n = 0$, the system reduces to a single first-order equation

$$\frac{dx}{dt} = ax, \tag{2.14}$$

this solution is $x(t) = ce^{at}$. x=0 is the only critical point when a≠0. Critical points are of special importance and that is when the right hand side of equation (2.14) is equal to zero. These points correspond to constant solutions, or equilibrium solutions of equation (2.14) and are often called critical points. For system (2.13), points where $Ax = 0$ correspond to equilibrium solutions and they are again called critical points. We often assume that $\det A \neq 0$, so $x = 0$ is the only equilibrium solution.

When A is a 2×2 constant matrix and x is a 2×1 vector, we can solve the system (2.13) by seeking solutions of the form

$$x = \xi e^{rt}, \tag{2.15}$$

where the exponent r and the vector ξ are to be determined. Substituting the equation (2.15) for x in the system (2.13) gives

$$r\xi e^{rt} = A\xi e^{rt}. \tag{2.16}$$

Canceling $e^{r}t$ we obtain

$$(A - rI)\xi = 0, \tag{2.17}$$

Where I is the $n \times n$ identity matrix. Then to solve the system of differential equations (2.13), we must solve the system of equations (2.17). When we solve this, we determine the eigenvalues and eigenvectors of the matrix A. The vector x given by equation (2.15) is a solution to (2.13) if r is an eigenvalue and ξ an associated eigenvector of the coefficient matrix A. The nature of the eigenvalues and the corresponding eigenvectors determines the nature of the general solution of the system (2.13).

The following possibilities for the eigenvalues of A are: 1. All eigenvalues are real and different from each other. 2. Some eigenvalues occur in complex conjugate pairs. 3. Some eigenvalues, either real or complex, are repeated. We will see later that in our case of the predator-prey equations, it is eigenvalues that are real and different, and eigenvalues in complex conjugate pairs that are relevant. The corresponding solutions to the differential system (2.13) if the n eigenvalues are all real and different are

$$x^1(t) = \xi e^{r_1 t}, ..., x^n(t) = \xi^n e^{r_n t}. \tag{2.18}$$

And the general solution of equation (2.13) is

$$x = c_1 \xi e^{r_1 t} + \cdots + c_n \xi^{(n)} e^{r_n t}. \tag{2.19}$$

If A is real and symmetric, then all the eigenvalues $r_1, ..., r_n$ must be real. And solutions arising from complex eigenvalues are complex-valued. If A is complex, the complex eigenvalues need not occur in conjugate pars, and the eigenvectors are often complex-valued even though the associated eigenvalue may be real-valued. In general though, if A is complex, then all the solutions are complex valued and the general solutions of the differential equation (2.13) are of the form (2.18).

2.3 The phase plane

When A is a 2×2 constant matrix and x is a 2×1 vector, it can be visualized in the $x_1 x_2$ plane. This is called a phase plane. If we evaluate Ax at a large number of points and plotting the resulting vectors, we obtain a direction field of tangent vectors to solutions of the system of differential equations. We could obtain a qualitative understanding of the behavior of solutions from a direction field. However, a more precise information can be obtain by including some solution curves, or trajectories.

Solution of equation (2.13) is a vector function $x = x(t)$ that satisfy the differential equation. This function can be viewed as a parametric representation for a curve in the $x_1 x_2$-plane. This curve is useful to regard as the trajectory, whose velocity $\frac{dx}{dt}$ is specified by the differential equation. The representative set of trajectories is referred to as a phase portrait. In analyzing the system (2.13), we characterize the differential equation according to the geometric pattern formed by its trajectories in the phase portrait. These trajectories vary depending on the nature of the eigenvalues of A. The trajectories are the basic ingredients of the qualitative theory of linear and nonlinear differential equations. These qualitative methods can be applied to more difficult nonlinear systems which is important in the predator-prey equations.

The behaviour of the trajectories for the first case which we are going to analyze are when the eigenvalues are real and have opposite sign. The second case is when the eigenvalues are pure imaginary.

2.3.1 Real Eigenvalues of Opposite Sign

In this case, the general solution of equation (2.13) is

$$x = c_1 \xi^{(1)} e^{r_1 t} + c_2 \xi^{(2)} e^{r_2 t}, \tag{2.20}$$

where $r_1 > 0$ and $r_2 < 0$. If a solution starts at an initial point on the line trough the eigenvector $\xi^{(1)}$, then c=0. Now the solution stays on the line trough $\xi^{(1)}$ for all t, and since $r_1 > 0$, $x \to \infty$ as $t \to \infty$. However if a solution starts at an initial point on the line trough $\xi^{(2)}$, then it always remains on that line and $x \to 0$ as $t \to \infty$ because $r_2 < 0$.

For solutions starting on other initial points,they approach infinity asymptotic to the line determined by the eigenvector $\xi^{(1)}$ corresponding to the positive eigenvalue r_1. That is because the positive exponential in the equation (2.20) is the dominant term for large t. As Boyce writes (Boyce et al., 2017, p.388), the only solutions approaching the critical point at the origin are those that start precisely on the line determined by $\xi^{(2)}$. For large negative t, it is the negative exponential which is dominant. A typical solution is asymptotic to the line trough the eigenvector $\xi^{(2)}$ as $t \to -\infty$. The exceptions are the solutions that lie exactly on the line trought the eigenvector $\xi^{(1)}$. These solutions approach the origin as $t \to \infty$. These characteristics of the critical point is called a saddle point in this case. This point is unstable.

2.3.2 Pure Imaginary Eigenvalues

In this case the eigenvalues are $\lambda - i\mu$ and $\lambda + i\mu$, but $\lambda = 0$. This reduces the eigenvalues to $i\mu$ and $-i\mu$ and the system

$$x' = \begin{pmatrix} \lambda & \mu \\ -\mu & \lambda \end{pmatrix} x \tag{2.21}$$

reduces to

$$x' = \begin{pmatrix} 0 & \mu \\ -\mu & 0 \end{pmatrix} x. \tag{2.22}$$

The trajectories in this case are circles with center at the origin and are traversed clockwise if $\mu > 0$ and counterclockwise if $\mu < 0$. A complete circuit about the origin is made in a time interval of length $2\pi/\mu$ and then all solutions are periodic with period $2\pi/\mu$. The critical point is called a center. It is possible to show that, in general, the trajectories are ellipses centered at the origin when the eigenvalues are pure imaginary. The critical point is stable.

2.4 Stability and Instability

Before going into the theory of using the characteristics of an appropriate linear system to approximate a nonlinear system, we are going to define stability and instability. The importance of critical points are also going to be discussed.

The system $x' = Ax$ where A is a 2×2 matrix is a two-dimensional autonomous system if the elements of the coefficient matrix A are not a function of the independent variable t. To give a precise mathematical definition of stability and instability, we are going to be using the autonomous system of the form

$$x' = f(x). \tag{2.23}$$

We are using the notation $|x|$ to designate the magnitude of the vector x. Points, if any, where f(x)=0 are called critical points of the autonomous system (2.23). As we have seen before at such points, $x' = 0$ also, so critical points correspond to constant, or equilibrium solutions of the system of differential equations. As Boyce writes (Boyce et al., 2017, p.397), a critical point x^0 of the system (2.23) is said to be stable if, given any $\epsilon > 0$, there is a $\delta > 0$ such that every solution $x = x(t)$ of the system

$$\frac{dx}{dt} = F(x, y) \quad \frac{dy}{dt} = G(x, y), \tag{2.24}$$

which at $t = 0$ satisfies

$$|x(0) - x^0| < \delta \tag{2.25}$$

both exists for all positive t and satisfies

$$|x(t) - x^0| < \epsilon, \tag{2.26}$$

for all $t \geq 0$. These mathematical statements say that all solutions that start "sufficiently close" (within the distance of δ) to x^0 stay "close" (within the distance of ϵ) to x^0. A critical point that is not stable is said to be unstable. There is also a condition where a critical point x^0 is said to be asymptotically stable. However, this is not relevant in our predator-prey equations.

Now let's look at an example. In this example we are going to draw direction fields and sketch trajectories corresponding to the solution satisfying the specified initial conditions. It is a two-dimensional autonomous system which is going to be solved:

$$\frac{dx}{dt} = F(x, y), \quad \frac{dy}{dt} = G(x, y); \quad x(0) = 4, \quad y(0) = 2. \tag{2.27}$$

We are also going to indicate the direction of motion for increasing t. The two-dimensional autonomous system are $\frac{dx}{dt} = -x$ and $\frac{dy}{dt} = -3y$. The first thing we have to do is finding the critical points. We do this by setting $\frac{dx}{dy} = 0$ and $\frac{dy}{dt} = 0$. This leads to $-x = 0$ and $-3y = 0$. The only solution is therefore $x = 0$ and $y = 0$ and the only critical point is (0,0). Solving the initial condition for x, $\frac{dx}{dt} = -x \quad x(0) = 4$ gives $\rightarrow x = 4e^{-t}$. Doing the same for y, $\frac{dy}{dt} = -3y \quad y(0) = 2$ gives $\rightarrow \quad y = 2e^{-3t}$. Here we get a situation we have not looked at. The eigenvalues are real and unequal of the

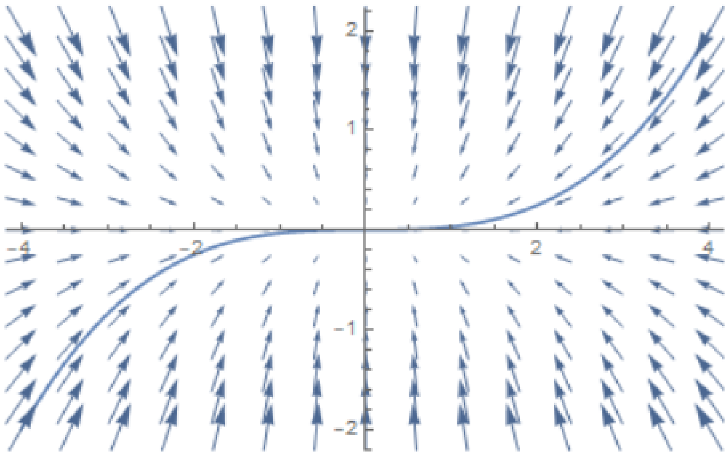

Figure 2.1: Direction fields and trajectory to system (2.28)

same sign. r_1 and r_2 are both negative and this case all solutions approach the critical point at the origin as $t \to \infty$. The last thing is to determine the trajectories. The trajectories of the system (2.27) can sometimes be found by solving a related first-order differential equation. By setting $\frac{dy}{dx} = \frac{G(x,y)}{F(x,y)}$ which is a first-order differential equation in the variables x and y. In our case this gives

$$\frac{dy}{dx} = 3y/x, \quad x(0) = 4, \quad y(0) = 2. \tag{2.28}$$

This leads to $y = x^3/32$. This equation is an equation for the family of trajectories of the system (2.28). Since the eigenvalues are negative, real and unequal, the critical point is asymptotically stable. Then the trajectory we have found is said to be attracted by the critical point. This is because a point P in the xy-plane that the trajectory is passing trough approaches the critical point as $t \to \infty$. The set of all such points P is called the region of asymptotic stability of the critical point. Now the figure 2.1 shows that all solutions approach the critical point (0,0) as $t \to 0$. The critical point is a node and we naturally also see that the trajectory which correspond to our initial condition also approaches the critical point. If we had zoomed in on the critical point, we would have seen that the direction field and pattern of trajectories would have resembled those for a linear system with constant coefficients. It exists visual evidence that a nonlinear system behaves very much like a linear system, at least in the neighborhood of a critical point.

For linear homogeneous systems with constant coefficients, $x' = Ax$, the nature of the critical point at the origin determines to a large extent the behaviour of the trajectories throughout the xy-plane. For predator-prey equations this is no longer true. This is because they are nonlinear autonomous systems. That means that there may be several critical points that are competing, for influence on the trajectories. Furthermore, the nonlinearities in the system are of great importance, especially far away from the critical points. But critical points of nonlinear autonomous systems can be classified just as for linear systems. It is also a fact as we have discussed that nonlinear system behaves very much like a linear system, at least in the neighborhood of a critical point. This will be the next topic of discussion and is important in our understanding of the predator-prey equations.

2.5 Locally Linear Systems

An important theorem which can be derived from the definition of instability, stability and asymptotically stability from the system (2.13) is:

Theorem 6. *The critical point x=0 of the linear system (2.13) 1. is asymptotically stable if the eigenvalues r_1, r_2 are real and negative or have negative real part. 2. is stable, but not asymptotically stable, if r_1, r_2 are pure imaginary; and 3. is unstable if r_1, r_2 are real and either is positive, or if they have positive real part.*

This theorem shows that it is the eigenvalues r_1 and r_2 of the coefficient matrix A that determines the type of critical point at $x = 0$ and its stability characteristics. The eigenvalues of the system (2.13) depends on the coefficients in the system (2.13). If a such a system arises in some applied field, the coefficients comes from the measurements of certain physical quantities. These measurements contains uncertainties, so it is of interest to investigate whether small changes (perturbations) in the coefficients can affect the stability or instability of a critical point and/or significantly alter the pattern of trajectories. It is possible to show that small perturbations in some or all of the coefficients are reflected in small perturbations in the eigenvalues. This will not be shown in this thesis.

To sum it up simply, it is only two cases which small perturbations in the coefficients change the stability or instability and/or type of critical point. The first case is the most sensitive one and that is when $r_1 = i\mu$ and $r_2 = -i\mu$. In this case the trajectories almost always change from ellipses to spirals. The system is asymptotically stable if $\lambda' < 0$, but unstable if $\lambda' > 0$. In this case, small perturbations in the coefficients may well change a stable system into an unstable one and may be expected to change the trajectories from ellipses to spirals. The second case is when r_1 and r_2 are equal. If the separated roots are real, then the critical point is an node and it remains a node. But if the separated roots are complex conjugates, the the critical point changes to a spiral point. The stability of the system in this case is not affected by small perturbations in the coefficients. In all other cases, the stability or instability of the system is not changed, nor the critical point, by small perturbations in the coefficients of the system.

2.6 Linear Approximations to Nonlinear Systems

Lets consider a nonlinear autonomous two-dimensional system

$$x' = f(x). \tag{2.29}$$

The main object in this section is to investigate the behaviour of trajectories of the system (2.29) near a critical point x^0. From earlier we stated that the pattern of trajectories of a nonlinear system close to a critical point resembled the pattern of trajectories of a certain linear system. This suggests that near a critical point we may able to approximate the nonlinear system (2.29) by an appropriate linear system. This is important in our solving of predator-prey equations. The crucial point is whether and how we can find an approximating linear system whose trajectories closely match those of the nonlinear system near the critical point. It is convenient to choose the critical point to be the origin.

First, we consider what it means for a nonlinear system (2.29) to be "close" to linear system (2.13). Suppose that

$$x' = Ax + g(x), \tag{2.30}$$

and that x=0 is an isolated critical point of the system (2.29). This means that there is some circle about the origin within which there are no other critical points. Furthermore, we assume that $\det A \neq 0$, so that x=0 is also an isolated critical point of the linear system $x' = Ax$. For the nonlinear system (2.30) to be close to the linear system $x' = Ax$, we assume that g(x) is small. We assume that the components of g have continuous first partial derivatives and satisfy the limit condition

$$\frac{|g(x)|}{|x|} \to 0 \quad as \quad x \to 0; \tag{2.31}$$

which is, $|g(x)|$ is small in comparison to $|x|$ itself near the origin. This system is called a locally linear system in the neighborhood of the critical point x=0.

As Boyce points out in the book, it may be helpful to express the condition (2.31) in scalar form using polar coordinates. After some computation it follows that condition (2.31) is satisfied if and only if

$$\frac{g_1(rcos\theta, rsin\theta)}{r} \to 0, \frac{g_2(rcos\theta, rsin\theta)}{r} \to 0 \quad as \quad r \to 0 \quad for \quad all \quad 0 \leq \theta \leq 2\pi. \tag{2.32}$$

Now let's look at the general nonlinear system (2.29), which we write in scalar form

$$x' = F(x, y), \quad y' = G(x, y); \tag{2.33}$$

That is, $x = (x, y)^T$ and $f(x) = (F(x, y), G(x, y))^T$. Boyce writes an important theorem concerning the system (2.33) which is:

Theorem 7. *The system (2.33) is locally linear in the neighborhood of a critical point* (x_0, y_0) *whenever the functions F and G have continuous partial derivatives up to order two.*

This theorem means that if the functions F and G are twice differentiable, then the system (2.33) is locally linear. It also means that the linear system that approximates the nonlinear system (2.33) near the critical point (x_0, y_0) is given by:

$$\frac{d}{dt}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} F_x(x_0, y_0) & F_y(x_0, y_0) \\ G_x(x_0, y_0) & G_y(x_0, y_0) \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}, \tag{2.34}$$

where $u_1 = x - x_0$ and $u_2 = y - y_0$. Equation (2.34) gives a simple and general method for finding the linear system corresponding to a locally linear system near a given critical point. The matrix

$$J = J[F, G](x, y) = \begin{pmatrix} F_x(x, y) & F_y(x, y) \\ G_x(x, y) & G_y(x, y) \end{pmatrix}, \tag{2.35}$$

which appears as the coefficient matrix in equation (2.34), is called the Jacobian matrix of the functions F and G with respect to x and y. It is assumed that det J is not zero at (x_0, y_0) so that this point is also an isolated critical point of the linear system (2.34).

Now lets return to the locally linear system (2.30). Since the nonlinear term $g(x)$ is small compared to the linear term Ax when x is small, it is reasonable to hope that the trajectories of the linear system (2.13) are good approximations to those of the nonlinear system (2.30), at minimum near the origin. This is true in many, but not all cases as Boyce points out in a theorem:

Theorem 8. *Let r_1 and r_2 be the eigenvalues of the linear system (2.13), $x' = Ax$, corresponding to the locally linear system (2.30). Then the type and stability of the critical point (0,0) of the linear system (2.13) and the locally linear system (2.30) are as shown in a table.*

The table is not going to be written in this thesis, because not all of these linear systems are relevant to our predator-prey equations. The nonlinear terms are small and do not effect the stability and type of critical point as determined by the the linear terms, except for two cases. On of these cases are relevant in our case and that is when r_1 and r_2 are pure imaginary. Then the small nonlinear term may change the stable center into a spiral point, which may be either asymptotically stable or unstable. It is reasonable to suspect that the small nonlinear term in equation (2.30) might have similar effect in this case. This is so, and that also includes when the eigenvalues are real, equal and positive or real, equal and negative. But theorem 8 tells us that in all other cases the small nonlinear term does not alter the type or stability of the critical point. The second case in our predator-prey equations are when the eigenvalues are real, unequal and have opposite signs. Then the linear system is the same as the locally linear system.

The essential understanding from this discussion is this: Except in two sensitive cases, the type and stability of the critical point of the nonlinear system (2.30) can be determined from a study of the much simpler linear system $x' = Ax$.

In the next part, a study of two examples of the predator-prey equations are going to be shown. In solving these equations, we are going to be using the theory which has been covered so far.

Chapter 3

The predator-prey equations

3.1 The first example

In the first example of the predator prey equations, the system which is going to be analysed is given by

$$F = \frac{dx}{dt} = x(2 - 0.5y), \quad G = \frac{dy}{dt} = y(-0.5 + x). \tag{3.1}$$

From the general equations of the predator-prey equations,

$$\frac{dx}{dt} = ax - \alpha xy = x(a - \alpha y), \quad \frac{dy}{dt} = -cy + \gamma xy = y(-c + \gamma x) \tag{3.2}$$

we see that $a = 2$ and $\alpha = 0.5$ for $\frac{dx}{dt}$ and $c = 0.5$ and $\gamma = 1$ for $\frac{dy}{dt}$. The first step in our analysis of this system is drawing a direction field in Mathematica. From the figure (3.1), it looks like the trajectories encircle the point $(1/2, 4)$. Whether the trajectories are indeed closed curves, or whether they slowly spiral in or out, cannot be determined from the direction field. The origin looks like to be a saddle point.

The next step in the analysis is finding the critical points of the system. The critical points of this system are the solutions of the algebraic equations:

$$x(2 - 0.5y) = 0, \quad y(-0.5 + x) = 0. \tag{3.3}$$

If we assume $x = 0$, then y also have to be zero because we get the equation $-0.5y = 0$. So the first critical point is the origin $(0, 0)$. The second critical point can be solved by solving the equation inside the parentheses. This leads to:

$$2 - 0.5y = 0 \quad \to y = 4. - 0.5 + x = 0 \quad \to x = 0.5. \tag{3.4}$$

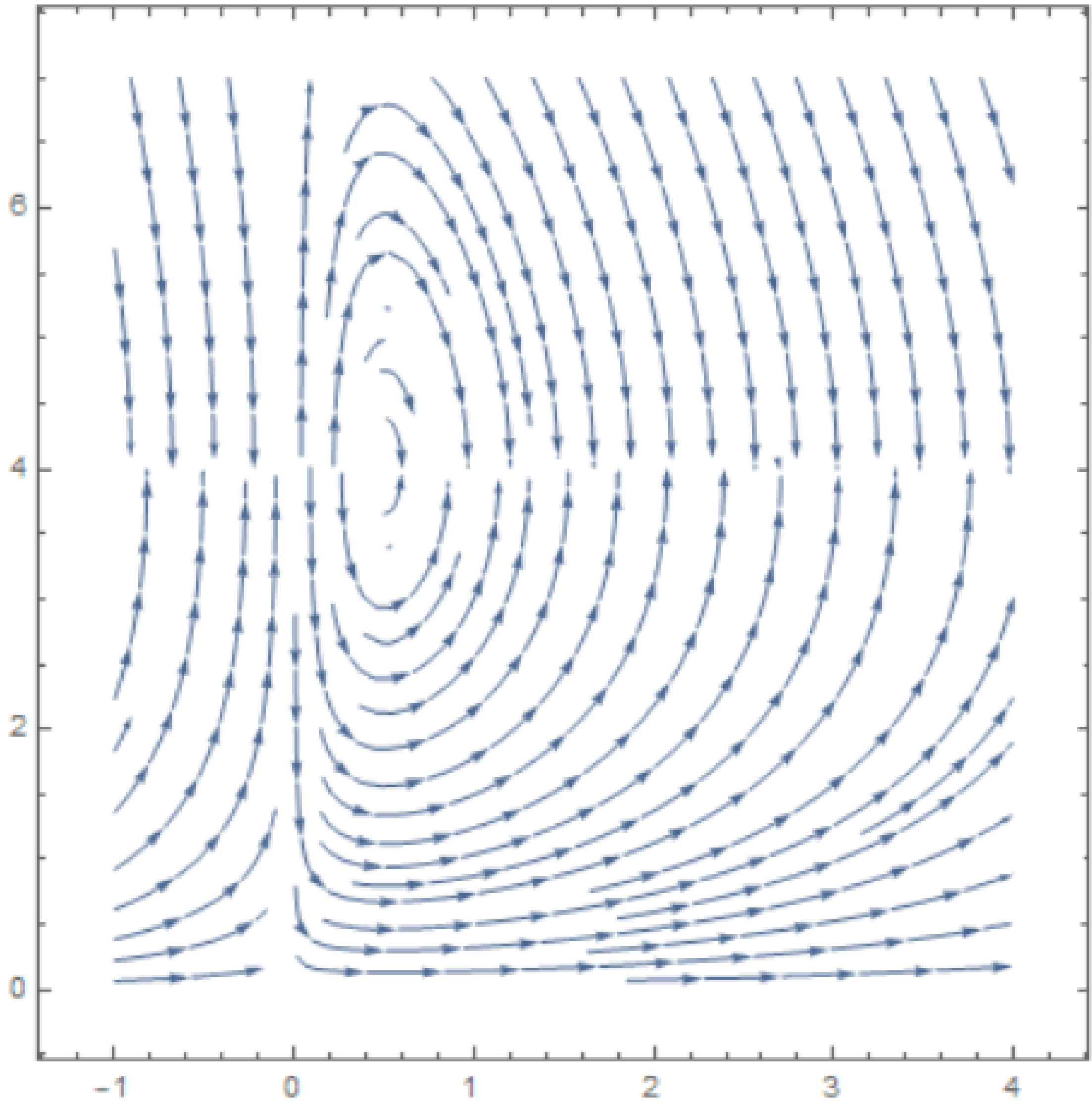

Figure 3.1: Direction field for system (3.1)

The critical points are therefore $(0, 0)$ and $(0.5, 4)$. The next step is finding a corresponding linear system for each critical point. We need to find the eigenvalues and eigenvectors of this linear system and classify each critical point as to type. The critical points stability are also going to be determined. To find the linear system, we need to examine the local behavior of solutions near each critical point. Let's start with the origin. Let's use the Jacobian matrix J for the system (3.1):

$$J = \begin{pmatrix} F_x(x,y) & F_y(x,y) \\ G_x(x,y) & G_y(x,y) \end{pmatrix} = \begin{pmatrix} 2-0.5y & -0.5x \\ y & -0.5+x \end{pmatrix} \tag{3.5}$$

For $(0, 0)$ we obtain the corresponding linear system

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 2 & 0 \\ 0 & -0.5 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \tag{3.6}$$

Finding the eigenvalues leads to:

$$\frac{d}{dt} = \begin{pmatrix} 2-r & 0 \\ 0 & -0.5-r \end{pmatrix} \tag{3.7}$$

This gives $(2-r)(-0.5-r) = 0 \rightarrow r_1 = 2$ and $r_2 = -0.5$. Then the eigenvectors are

$$\xi_1 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad \xi_2 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}. \tag{3.8}$$

The general solution is

$$\begin{pmatrix} x \\ y \end{pmatrix} = c_1\begin{pmatrix} 0 \\ 1 \end{pmatrix}e^{2t} + c_2\begin{pmatrix} 1 \\ 0 \end{pmatrix}e^{-0.5t}. \tag{3.9}$$

Since the eigenvalues are real and have opposite signs, the origin is a saddle point both of the linear system (3.6) and of the nonlinear system (3.1) and is unstable. As we can see from the figure (3.1), one trajectory enters the origin along the y-axis(not every point in y) and all other trajectories depart from the neighborhood of the origin.

Now let's find the linear system for the critical point $(0.5, 4)$. We use the Jacobian matrix again

$$J = \begin{pmatrix} F_x(x,y) & F_y(x,y) \\ G_x(x,y) & G_y(x,y) \end{pmatrix} = \begin{pmatrix} 2-0.5y & -0.5x \\ y & -0.5+x \end{pmatrix}. \tag{3.10}$$

For $(0.5, 4)$ we obtain the linear system

$$\frac{d}{dt}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} 0 & -0.25 \\ 4 & 0 \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix} \tag{3.11}$$

This leads to the eigenvalues $r_1 = i$ and $r_2 = -i$. This system gives

$$\frac{d}{dt}u = -0.25v, \quad \frac{d}{dt}v = 4u. \tag{3.12}$$

The eigenvectors then becomes

$$\xi_1 = \begin{pmatrix} i/4 \\ 1 \end{pmatrix}, \quad \xi_2 = \begin{pmatrix} -i/4 \\ 1 \end{pmatrix} \tag{3.13}$$

Since the eigenvalues are pure imaginary, the critical point $(0.5, 4)$ is a stable center for the linear system. But now we have a situation where the behaviour of the linear system may, or may not carry over to the nonlinear system. So the behaviour of the point $(0.5, 4)$ for the nonlinear system (3.1) can not be determined from this information. To find the trajectories for the linear system (3.11) we can divide the second of equations (3.12) by the first to obtain the differential equation

$$\frac{dv}{du} = \frac{dv/dt}{du/dt} = \frac{4u}{-0.25v} = -16u/v. \tag{3.14}$$

This can be written as $16udu + dvv = 0$ and this gives

$$8u^2 + 1/2v^2 = k \tag{3.15}$$

Here is k a nonnegative constant of intergration. The trajectories of the linear system (3.11) are ellipses centered at the critical point and is elongated in the vertical direction.

Let's return to the nonlinear system (3.1). Dividing the second of equations (3.1) by the first, we get

$$\frac{y(-0.5 + x)}{x(2 - 0.5y)} = \frac{dy}{dx}. \tag{3.16}$$

This becomes a separable equation and this leads to

$$2 \ln y - 0.5y + 0.5 \ln x - x = C. \tag{3.17}$$

This can be shown for a fixed C that the graph is a closed curve surrounding the critical point (0.5,4). The critical point is also a center for the nonlinear system (3.1) and the predator and prey populations exhibit a cyclic variation. Now we can draw some trajectories for the system (3.1) by using the solution (3.17). We see from the figure (3.2) that when t goes to infinity and $y = 0$ then x will go to infinity. This was expected from our previous calculations.

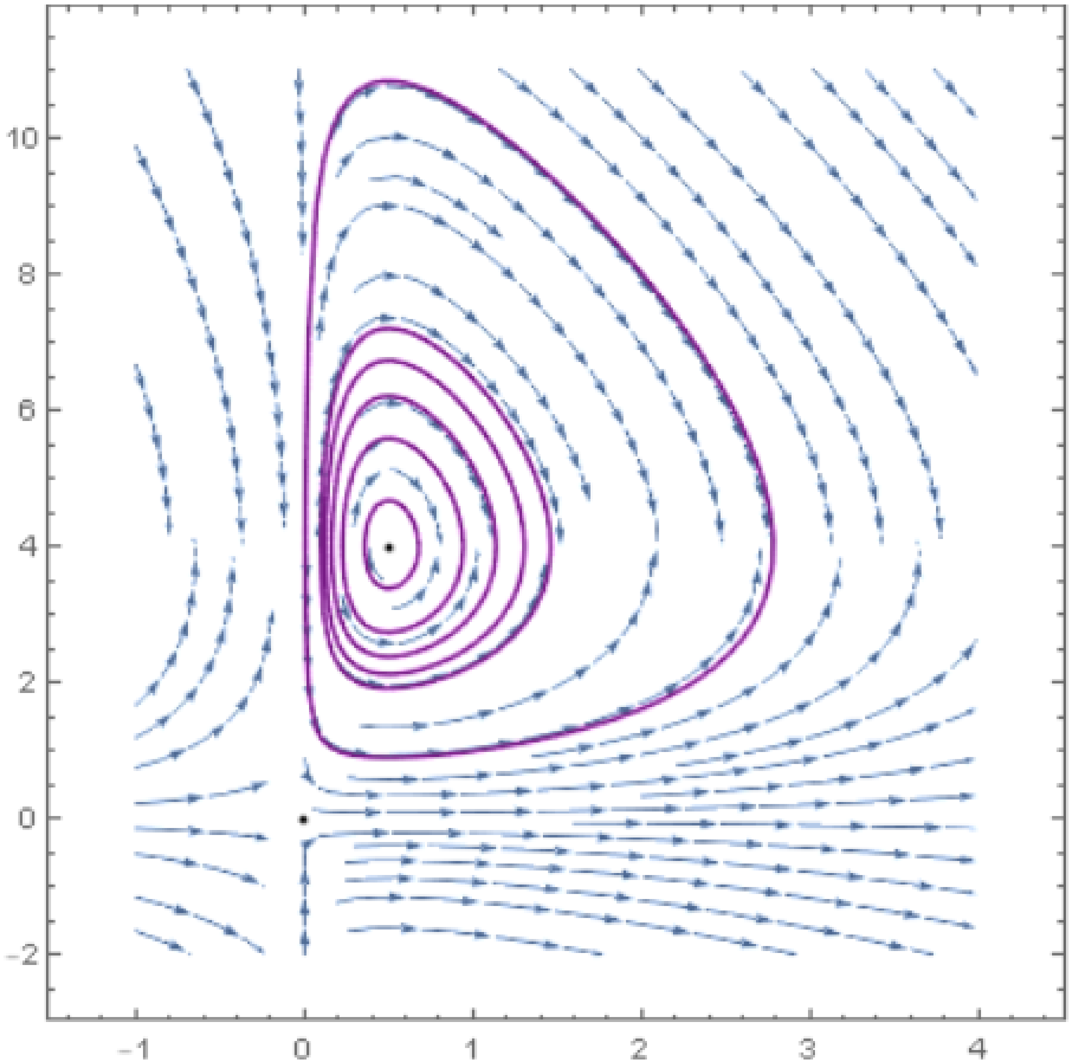

Figure 3.2: Trajectories for system (3.1)

When both $y > 0$ and $x > 0$ then some trajectories are almost elliptical in shape, but is elongated in the vertical direction. x and y are periodic function of t and they must be since the trajectories are closed curves. For other initial condition, the behaviour of the trajectories differ from ellipses. The oscillation of the predator lags behind of the prey. In the biggest trajectory in the figure (3.2), we begin with both of the prey and predator population as pretty small. We see from the figure that the prey first increase because there is little predation. After a while, the predator population increase because of a bigger food supply. This decreases the prey population as we see in the figure. With less abundant of prey, the predator population decrease again and the system returns to its original state. Then the trajectory begins to repeat itself.

3.2 The second example

The second example is characterized by these equations:

$$F = \frac{dx}{dt} = x(1 - 0.5y), \quad G = \frac{dy}{dt} = y(-0.25 + 0.5x) \tag{3.18}$$

By using the general equations given by (3.2). we see that $a = 2$ and $\alpha = 0.5$ for $\frac{dx}{dt}$. While $c = 0.25$ and $\gamma = 0.5$ for $\frac{dy}{dt}$. Now we draw a direction field for this system just like we did in the first example. The next step is trying to analyse how solutions seems to behave in this direction field. The origin looks like a saddle point. While the point $(0.5, 2)$ looks to be a center. However, just as in the first example, we can not determine this for certain by only looking at the direction field.

Let's find the critical points of the system. We see that the point (0,0) is a critical point. If $x = 0$ then y have to be zero. The next one we find by solving both of the parentheses of system (3.18). $1 - 0.5y = 0 \to y = 2$ and $-0.25 + 0.5x = 0 \to x = 0.5$. The critical points are $(0, 0)$ and $(0.5, 2)$. The next step is finding a corresponding linear system and finding the eigenvalues and eigenvectors of this linear system. After that we can classify the critical points as to type and its stability. We go by the same method as we did in the first example. Let's use the Jacobian matrix for the two critical points:

$$J = \begin{pmatrix} F_x(x,y) & F_y(x,y) \\ G_x(x,y) & G_y(x,y) \end{pmatrix} = \begin{pmatrix} 1 - 0.5y & -0.5x \\ 0.5y & -0.25 + 0.5x \end{pmatrix} \tag{3.19}$$

For the point (0,0) we obtain

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & -0.25 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \tag{3.20}$$

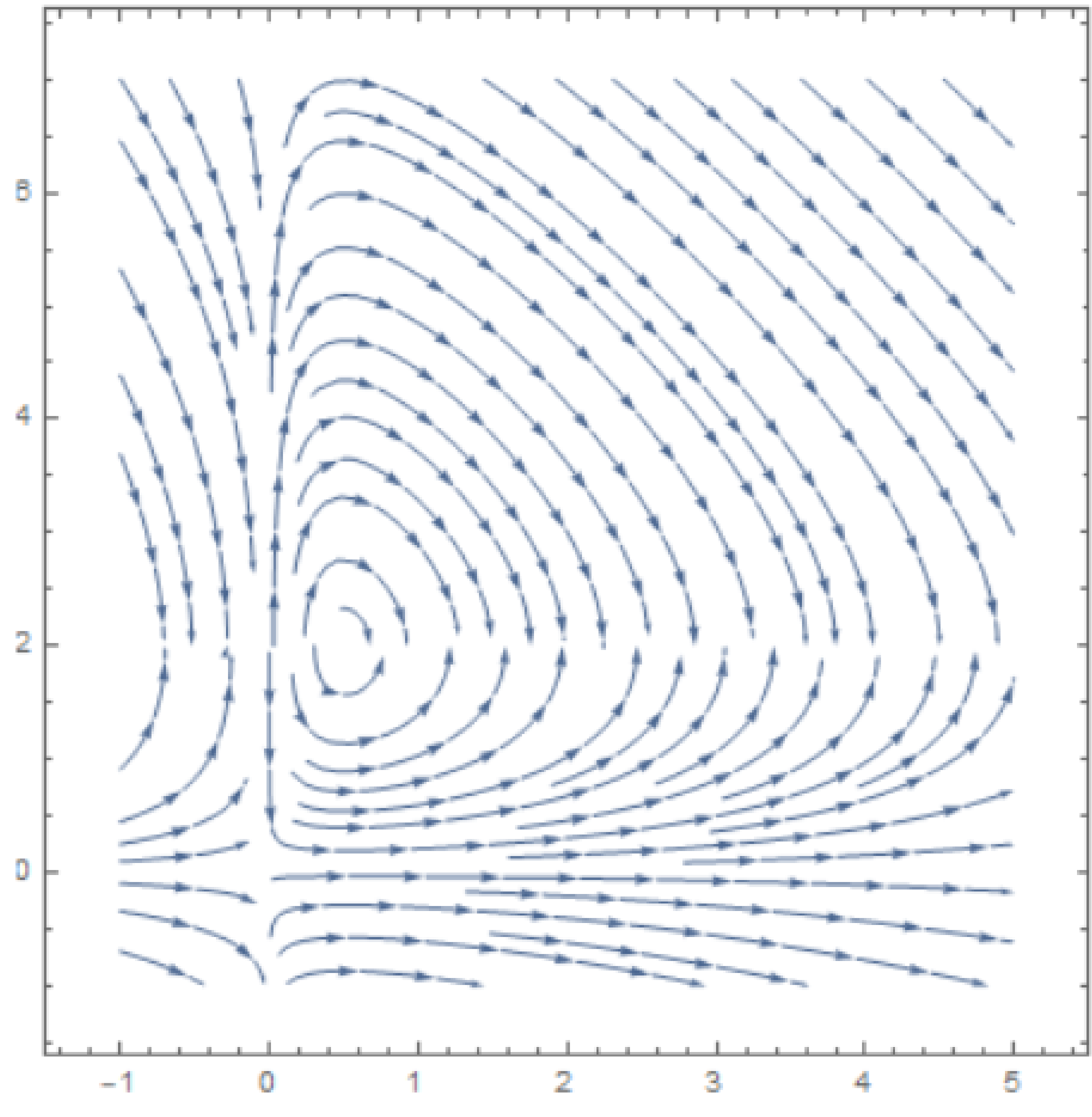

Figure 3.3: Direction field for system (3.18)

Finding the eigenvalues leads to

$$\frac{d}{dt} = \begin{pmatrix} 1-r & 0 \\ 0 & -0.25-r \end{pmatrix} \tag{3.21}$$

This leads to $(1-r)(-0.25-r)$ and eigenvalues are $r_1 = 1$ and $r_2 = -0.25$. The eigenvectors are:

$$\xi_1 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad \xi_2 = \begin{pmatrix} 1 \\ 0 \end{pmatrix} \tag{3.22}$$

The general solution for the origin is:

$$\begin{pmatrix} x \\ y \end{pmatrix} = c_1 \begin{pmatrix} 0 \\ 1 \end{pmatrix} e^t + c_2 \begin{pmatrix} 1 \\ 0 \end{pmatrix} e^{-0.25t} \tag{3.23}$$

Since the eigenvalues are real, unequal and have opposite signs the origin is a saddle point both for the linear system (3.20) and the nonlinear system (3.18). The point is unstable. For the point $(0.5, 2)$ we obtain the linear system:

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} 0 & -0.25 \\ 1 & 0 \end{pmatrix} \tag{3.24}$$

Finding the eigenvalues leads to $r^2 + 0.25 = 0$ which gives $r_1 = i/2$ and $r_2 = -i/2$.

$$u = -1/4v, \quad v' = u \tag{3.25}$$

The eigenvectors become

$$\xi_1 = \begin{pmatrix} -1 \\ 2i \end{pmatrix}, \quad \xi_2 = \begin{pmatrix} -i/2 \\ 1 \end{pmatrix} \tag{3.26}$$

Both of the eigenvalues are pure imaginary so the point is a center for the linear system (3.24). Since the eigenvalues are pure imaginary it is not certain that the behaviour of the linear system carry over to the nonlinear system (3.18). Let's find the trajectories of the linear system (3.24) by dividing the second equation by the first in system (3.25).

$$\frac{dv}{du} = \frac{dv/dt}{du/dt} = \frac{u}{-1/4v} \tag{3.27}$$

This can be written as $dv0.25v = -duu \rightarrow \quad dv0.25v + duu = 0$. This can be written as $1/8v^2 + 1/2u^2 = k$. Here is also k a nonnegative constant of integration. The trajectories of the linear system (3.24) are ellipses centered at the critical point. Now let's find the trajectories for the nonlinear system (3.18). Dividing the second of equations (3.18) by the first, we obtain:

$$\frac{-0.25y + 0.5xy}{x - 0.5xy} = \frac{dy}{dx} \tag{3.28}$$

This leads to

$$\ln y - 0.5y + 0.25 \ln x - 0.5x = C \tag{3.29}$$

Just like in the first example, this is a closed curve under a fixed C surrounding the critical point $(0.5, 2)$. The critical point is also a center for the nonlinear system (3.18). Now we can draw trajectories for the system (3.18) by using the equation (3.29). We see from the trajectories in figure (3.4) that we get a similar pattern as in the first example. When there is no predator, we see that the prey will grow indefinitely and will grow proportional to the current population. For some initial conditions, the trajectories represent small variations in x and y about the critical point and is almost elliptical in shape. This is apparent near the critical point $(0.5, 2)$.

For other initial conditions, the shape of the trajectories differ form an ellipse. An example is the biggest trajectory in figure (3.4). The oscillation of the predator population lags behind of the prey. In this trajectory, both the prey and predator population starts relatively small. The prey start growing first because of little predation. Then the predator population increase because there is an abundance of prey. This causes heavier predation and the prey starts to decrease. Finally, with a less food supply, the predator population also decreases and the system returns to its original state. And from here the trajectory starts to repeat itself.

3.3 The general system

The predator-prey equations showed very similar traits in both of the examples. Both of the examples had one critical point which was a saddle point in the origin and another one which was a center. The trajectories were also very much a like. The general system (3.2) can be analyzed in exactly the same as in the examples. The critical points of the system (3.2) are the solutions of

$$x(a - \alpha y) = 0, \quad y(-c + \gamma x) = 0, \tag{3.30}$$

that is the points $(0, 0)$ and $(\frac{c}{\gamma}, \frac{a}{\alpha})$. Let's first analyze the solutions of the corresponding linear system near each critical point. In the neighborhood of the origin, the corresponding linear system is

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \tag{3.31}$$

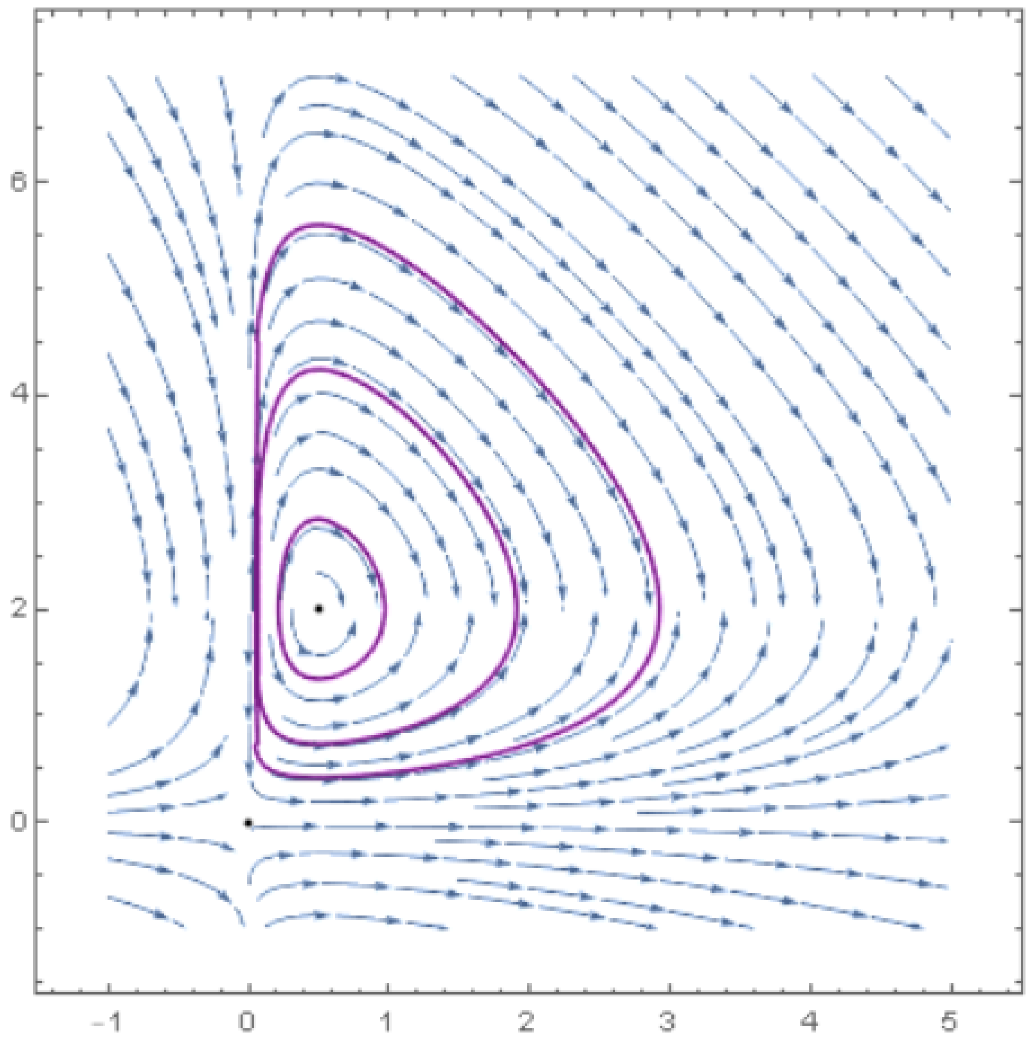

Figure 3.4: Some trajectories for the system (3.18)

The eigenvalues and eigenvectors are

$$r_1 = a, \quad \xi_1 = \begin{pmatrix}1\\0\end{pmatrix}; \quad r_2 = -c, \quad \xi_2 = \begin{pmatrix}0\\1\end{pmatrix} \tag{3.32}$$

and so the general system becomes

$$\begin{pmatrix}x\\y\end{pmatrix} = c_1\begin{pmatrix}1\\0\end{pmatrix}e^{at} + c_2\begin{pmatrix}0\\1\end{pmatrix}e^{-ct}. \tag{3.33}$$

Hence the origin is a saddle point and is unstable. This is true for the general system (3.2). All trajectories depart from the neighborhood of the critical point except along the positive y-axis. Along the positive y-axis trajectories "move" towards the critical point. The next critical point is $(\frac{c}{\gamma}, \frac{a}{\alpha})$. The Jacobian matrix is

$$J = \begin{pmatrix}a-\alpha y & -\alpha x\\ \gamma y & -c+\gamma x\end{pmatrix} \tag{3.34}$$

Evaluating J at this point, we obtain the approximate linear system

$$\frac{d}{dt}\begin{pmatrix}x\\y\end{pmatrix} = \begin{pmatrix}0 & -\frac{\alpha c}{\gamma}\\ \frac{\gamma a}{\alpha} & 0\end{pmatrix}\begin{pmatrix}u\\v\end{pmatrix}. \tag{3.35}$$

The eigenvalues of system (3.35) are $r = \pm\sqrt{ac}$, so the critical point is a stable center of the linear system. Just as in the examples, we can find the trajectories of the system (3.35) by dividing the second of equations by the first to obtain

$$\frac{dv}{du} = \frac{\frac{dv}{dt}}{\frac{du}{dt}} = -\frac{\frac{\gamma a}{\alpha}u}{\frac{\alpha c}{\gamma}v}, \tag{3.36}$$

or can be written as

$$\gamma^2 audu + \alpha^2 cvdv = 0. \tag{3.37}$$

This gives

$$\gamma^2 au^2 + \alpha^2 cv^2 = k, \tag{3.38}$$

where k is a nonnegative contant of integration. The trajectories are ellipses in the linear system (3.35), just as in the two examples.

Now looking at the nonlinear system (3.2), it can be reduced to the single equation

$$\frac{dy}{dx} = \frac{y(-c+\gamma x)}{x(a-\alpha y)} \tag{3.39}$$

The equation (3.39) is separable and has the solution

$$a\ln y - \alpha y + c\ln x - \gamma x = C, \tag{3.40}$$

where C is a constant of integration. It is possible to show that for a fixed C, the graph of equation (3.40) is a closed curve surrounding the critical point $(\frac{c}{\gamma}, \frac{a}{\alpha})$. Thus this critical point is also a center for the general nonlinear system (3.2).

We get the same critical points and general linear system for both the examples and the general system.

The cyclic variations of predator and prey as predicted by equations (3.2) has been observed in nature. One example is based on the records of the Hudson's Bay Company of Canada. This shows the abundance of lynx and snowshoe hare, as indicated by the number of pelts turned in over the period 1845-1935. The records shows a distinct periodic variation with a period of 9 to 10 years. The peaks of abundance are followed by very rapid declines and the peaks of abundance of the lynx and hare are out of phase, with that of the hare preceding that of the lynx by a year or more.

Chapter 4

Conclusion

When Lotka wanted to bring mathematics into biology and Volterra wanted to explain the observations of D'Ancona (see Introduction), they ultimately developed a very important mathematical model. The product of their research and study resulted into the predator-prey equations which is still being taught to this day. As mentioned before, it is a rather simple model, but it gave the basis for more complicated equations which describes situations more precisely. It was one of the first mathematical models applied to ecology and the model proved to be a useful teaching tool and a starting point for more complex analysis.

As we saw in the examples, the behaviour of the predator-prey model's solutions as time passes by were depended on the initial conditions. When there was no predator, we saw that the prey would grow at a rate proportional to its current population. If there were no prey, then the predator would die out. And one of the critical points were the origin which was an unstable saddle point. For other initial conditions, some trajectories were almost elliptical in shape and this was apparent near the second critical point. These trajectories were periodic functions of time, and they must be since the trajectories were closed curves. For other initial conditions, the oscillations in x and y were more pronounced and the pattern of the trajectories were different from an ellipse. The trajectories near the second critical point were cyclic where the predator lagged behind that of the prey. The predator also lagged behind that of the prey when the trajectories were different from an ellipse.

Criticisms of this model which I could not go into detail in this thesis became apparent in the study of this model. One of these is the critical point $(\frac{c}{\gamma}, \frac{a}{\alpha})$, since this point is a center, small perturbations of the predator-prey equations may lead to solutions that are not periodic. This has led to many attempts to replace the predator-prey equations by other systems that are less receptive to the effects of small perturbations. Another criticism is that in the absence of the predator, the prey will grow without bound. This can be fixed by allowing for the natural inhibiting effect that an increasing population has on the growth rate of that population. If $y = 0$ in equations (3.2), the first of equations can be modified so that it reduces to a logistic equation for x.

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