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An investigation into Predator-prey systems

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Abstract

This paper looked at how to obtain quantitative information about the behaviour of Predator-Prey models using analytical methods, we look at how to solve the Lotka-Volterra model analytically, analysed the stability and behaviour of the critical points of a bounded Lotka-Volterra model and the Holling-Tanner model and how to look for Hopf bifurcation and limit cycles in the Holling-Tanner model. We have also compared a variety of numerical methods used to solve the predator-prey models. It has also used these results to validate our findings from our analytical analysis.

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Chapter 1

Introduction

1 Population dynamics

Population dynamics is a field of science that studies both long and short term changes to a species population. It has important implications to conservatism as well as resource management. The Predator-prey models which we will be considering throughout this paper can be adapted to be applied to a wide array of topics, Volterra for example developed the Lotka-Volterra predator-prey system whilst studying chemical reactions. We will first discuss single species models to introduce the basic concepts of population dynamics before moving on to systems of species. Single species models are unrealistic outside of laboratory conditions as real life scenarios will include interactions between multiple different species.

Discrete vs Continuous time

Population growth can be described by either using a discrete time model or a continuous time one.

- Continuous time models use a differential equation to model a continuing overlap of generations. The most basic continuous model gives the growth of a population as the number of births proportional to the current population minus the number of deaths. Let $N(t)$ denote a population this basic model is given by

$$\frac{dN}{dt} = bN - mN, \tag{1.1}$$

where b and m denote the rate of birth and mortality rate, respectively.

We can integrate the differential equation (1.1) to get

$$N(t) = N_0 e^{(b-m)t}, \tag{1.2}$$

where $N(0) = N_0$ is the initial population.

Equation (1.2) is known as the Malthusian model. By analysing the Malthusian model we can see that if $m > b$ then the population will become extinct, but if $b > m$ then the population will grow exponentially.. This unrestricted exponentially growth is of course unrealistic so to counteract it a *carrying capacity* is often added to the model. A carrying capacity is a term which restricts the potential growth of a population. The carrying capacity represents the maximum sustainable population of a species. It is possible for a population to exceed the carrying capacity possibly by migration, but due to a lack of resources the population will

decrease towards the carrying capacity. Verhulst's model developed in 1836 introduced a self-limiting process, where the population is reduced by a term proportional to the population. The Verhulst model is given by

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), \quad (1.3)$$

where r is a parameter relating to the growth rate and K is the carrying capacity. This model is also known as the logistic growth model; the rate of growth decreases as t increases, until N reaches the carrying capacity K at which point the rate of growth becomes 0. We can show this by solving (1.3) analytically. Indeed the equation (1.3) can be rewritten as

$$\frac{dN}{dt} - rN = -\frac{rN^2}{K},$$

from which we get

$$\frac{1}{N^2} \frac{dN}{dt} - \frac{r}{N} = -\frac{r}{K}. \quad (1.4)$$

By introducing the variable z given by

$$z = \frac{1}{N},$$

we have that

$$\frac{dz}{dt} = \frac{-1}{N^2} \frac{dN}{dt}.$$

Thus (1.4) becomes

$$-\frac{dz}{dt} - \frac{r}{z} = -\frac{r}{K},$$

or

$$\frac{dz}{dt} + \frac{r}{z} = \frac{r}{K}.$$

We can solve the last equation by using the integrating factor method, let the integrating factor be given by

$$e^{\int r dt} = e^{rt}. \quad (1.5)$$

By using (1.5) we obtain

$$e^{rt} \frac{dz}{dt} + \frac{r}{z} e^{rt} = \frac{r}{K} e^{rt},$$

i.e.,

$$\frac{d}{dt} (e^{rt} z) = \frac{r}{K} e^{rt}.$$

By integrating both sides of the equation we obtain

$$e^{rt} z = \frac{1}{K} e^{rt} + C,$$

hence

$$z(t) = \frac{1}{K} + C e^{-rt}.$$

We can now change the variable back to $N(t)$ to get

$$\frac{1}{N} = \frac{1}{K} + C e^{-rt} = \frac{1 + CK e^{-rt}}{K},$$

so

$$N = \frac{K}{1 + CKe^{-rt}} \quad (1.6)$$

By applying the initial condition $N(0) = N_0$ we have that

$$C = \frac{K - N_0}{N_0K}.$$

We can substitute this into our solution (1.6) to obtain the solution of the Verhulst model as

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}} \quad (1.7)$$

We can see that $\lim_{t \rightarrow \infty} N(t) = K$.

- Discrete time models measure the population of a species per generation. It measures population in steps, the population of each subsequent generation is based on the population of the previous one. A generic discrete model is

$$N_{t+1} = N_t F(N_t).$$

There are many arguments in favour for each type of model. As data in real life is collected at points this makes it easier to obtain a discrete model by fitting it to the collected data. However for discrete time models the population at a specific time step can only be found if the population of previous time steps is known, where with continuous time the population at a specific time can easily be calculated. This makes continuous time models more suitable for mathematical analysis. A continuous time model can be seen as a discrete model with an infinitely small time step. Because of this it is possible to convert a continuous model into a discrete one using the process called discretisation. The type of models we will be discussing throughout are all continuous with respect to time.

1.1 Interacting Populations

When we consider the population dynamics of more than one species we must take into account how the two species interact with each other. Types of interacting populations include:

- If each population inhibits the other we have a competitive interaction. It can be inter-specific if the competition is between different species, or intra-specific if the competition is between the same species. Competition can be caused by a limited supply of a resource required by both species, territory disputes or if the actions of one species has a negative impact on another. If we have two species a competitive relationship can be denoted by $[-, -]$ where $-$ denotes a negative effect on the other species.
- If the two species interact but has neither a positive or negative effect on the other population we have neutralism, this can be denoted by $[0, 0]$ where 0 denotes no effect.
- If one population lives off the waste products of the first, but does not directly affect the population of the first species, we have a scavenging relationship. This is denoted by $[+, 0]$, where $+$ denotes a positive impact.

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- If the two populations have a mutually beneficial relationship we have symbiosis. This can be denoted by $[+, +]$
 - If the second species consumes the first as sustenance we have a predator-prey relationship, this can be denoted by $[+, -]$. It is this kind of relationship that we will be focusing on.

In this section we shall briefly discuss several different models for two interacting species with the focus entirely on systems which are classified as predator-prey models. The interaction between two or more species is classed as a predator-prey situation if the growth rate of one species is negative as the other is positive.

- **Lotka-Volterra model:**

We shall start with the simplest of the predator-prey models, which is known as the Lotka-Volterra model. It was independently developed by Volterra in 1926 [19] and by Lotka in 1925 [13]. Volterra formulated the method as a means to explain oscillatory population levels of types of fish being caught in the Adriatic sea. Whereas Lotka derived the same system of ordinary differential equations by studying a hypothetical chemical reaction, which he claimed could exhibit periodic behaviour in the concentration levels of the chemicals. For this system we shall denote the population of the prey species by $N(t)$ and that of the predator species by $P(t)$. The Lotka-Volterra system is defined as

$$\begin{aligned}\frac{dN}{dt} &= N(a - bP), \\ \frac{dP}{dt} &= P(cN - d).\end{aligned}\tag{1.8}$$

Here a, b, c and d are all arbitrary positive constants that describe the following interactions between the two species:

- a is the per-capita birth rate of the prey species.
- b is the mortality rate per-capita of the prey species due to predation.
- c is the per-capita reproduction rate for each prey captured.
- d is the per-capita mortality of the predator species.

When we construct the Lotka-Volterra model we are required to make the following assumptions:

1. In the absence of predation ($P = 0$) the prey population will grow unboundedly in the manner described by the Malthusian model (1.1) with the death rate parameter $m = 0$. We can prove this assumption by considering our system (1.8) when $P = 0$. In such a scenario we will be left with the single equation

$$\frac{dN}{dt} = aN.\tag{1.9}$$

We can then integrate (1.9) to get

$$N(t) = Ce^{at},\tag{1.10}$$

where C is an arbitrary constant.

If we denote our initial population as $N(0) = N_0$ we can solve the equation (1.10) at $t = 0$ to obtain $C = N_0$ thus by substituting this value into (1.10) we obtain the Malthusian model (1.1).

2. In the absence of prey ($N = 0$) the population of the predator species will show exponential decay, this is the $-dP$ term in predation equation of system (1.8).
3. The number of encounters between the two populations is proportional to their product. Each encounter will negatively effect the growth of the prey population and positively effect the population of the predator species. These effects are represented by the term $-bPN$ in the prey equation and by cNP in the predator equation of system (1.8).

As system (1.8) is such a simple model it makes it useful as a starting point from which more realistic models can be developed. It is also useful for representing a generic model for two interacting species. However, to achieve this simplicity we had to make the above assumptions. These assumptions make the model unrealistic when considering real life biological factors. For example the assumption that the prey species will grow exponentially in the absence of predation. This is unrealistic as there will be other limits to the growth of the population, such as the availability of the resources needed for their own sustenance. Another unrealistic assumption is that the predators are able to consume an infinite quantity of prey. This model also does not factor for any environmental complexity. A further disadvantage of the Lotka Volterra model is that it has a centre system, this means that the solutions of the equation will orbit around the singular point, this makes the system structurally unstable as any small perturbations can result in a drastic change of orbit. Centre systems, singular points and stability will be discussed in greater detail in later chapters.

The other models discussed throughout this paper all use the Lotka-Volterra model as their basis, however they have been modified to display more realistic behaviour.

- **The Lotka-Volterra model with bounded prey population:**

One of the key issues of the Lotka-Volterra model is that in the absence of predation the prey population will experience exponential growth. To prevent this we can modify the system by introducing some form of the logistic term $-N^2$ to the prey population equation; this will introduce the factor of interspecies competition for available resources thereby creating a maximum carrying capacity for the prey population. One such example of a new bounded system of equations is:

$$\frac{dN}{dt} = aN \left(1 - \frac{N}{K} - b \frac{P}{K} \right), \tag{1.11}$$

$$\frac{dP}{dt} = P(cN - d),$$

where K is a positive constant relating to the carry capacity of the prey population.

This system makes the following assumptions:

- In the absence of predation ($P = 0$) the prey population will have logistic growth similar to that of the Verhulst model (1.3), and will grow towards a carrying capacity dependent on the value of K .

- The rate of predation is proportional to the encounter rate between the two populations.
- The birth rate for the predators is proportional to the number of encounters between the two species.

This alteration has the further effect of eliminating the centre of the Lotka-Volterra system, which made that model structurally unstable, it also causes the population oscillations to decay.

- **The Leslie and Gower model**

The Leslie-Gower model is a variation of the bounded Lotka-Volterra model. It is described by the following system

$$\begin{aligned}\frac{dN}{dt} &= aN\left(1 - \frac{N}{K}\right) - (mN)P, \\ \frac{dP}{dt} &= P\left(c - d\frac{P}{N}\right),\end{aligned}\tag{1.12}$$

where m is the maximum rate of predation. The predator system now takes into account the relative sizes of the two species. The larger the term P/N becomes, the less prey is available to each predator, therefore limiting the availability of the predator's resources. The term mP from the prey equation is known as a Holling type 1 functional response.

Definition 1.1 (Holling Functional Responses) *Holling derived three types of increasingly complex functional responses, which are often incorporated into a large variety of predator-prey systems.*

- **Type 1:** *This is the most basic form of the functional responses it takes the form*

$$mN.$$

It is derived from the assumption that the probability of a predator encountering prey is dependent on the prey density.

- **Type 2:** *This type functional response adds a parameter relating to the efficiency of the predators ability to process food it takes the form of*

$$\frac{mN}{A + N},\tag{1.13}$$

where A represents a constant proportional to the efficiency of the predation.

- **Type 3:** *This type of functional response now incorporates the learning process of the predator population. It postulates that at higher predator populations there will be a greater probability of previous encounters between the two species, thus leading to more efficient predation, it is defined as*

$$\frac{mN^k}{A + N^k}$$

for some $k > 1$.

Although we defined three types of Holling functional responses above, we will only be considering models with the first two types.

- **The Gause Model**

The Gause model is a generalisation of the Lotka-Volterra model. The system suggested by Gause (1934) [8] introduces a new term $p(N)$ into the Lotka Volterra system

$$\begin{aligned}\frac{dN}{dt} &= aN - Pp(N), \\ \frac{dP}{dt} &= P(cp(N) - d),\end{aligned}$$

where the term $p(N)$ represents the rate of predation per predator. It is generally assumed that $p(0) = 0$ and that $p'(N) > 0$ for all $N > 0$.

We can generalise the Gause model by introducing a density-dependent prey growth in the absence of predation.

$$\begin{aligned}\frac{dN}{dt} &= Ng(N) - Pp(N), \\ \frac{dP}{dt} &= P(h(N) - d).\end{aligned}\tag{1.14}$$

Now instead of the constants a, b and c , the system has three generalised terms $g(N)$, $p(N)$ and $h(N)$ dependent on the density of the prey population. These terms can be replaced to suit the needs of the model (for more detail see [6]).

- **The Rosenzweig-McArthur model**

The Rosenzweig-McArthur model [15] takes the generalised Gause model (1.14) and sets the generalised terms as

$$\begin{aligned}p(N) &= \frac{mN}{A + N}, \\ g(N) &= r\left(1 - \frac{N}{K}\right), \\ h(N) &= \frac{mN}{A + N},\end{aligned}$$

where A, K and m are positive constants.

As we can see from (1.13), $h(N)$ is the Holling type 2 functional response. We can substitute these terms into our generalised Gause model to obtain

$$\begin{aligned}\frac{dN}{dt} &= aN\left(1 - \frac{N}{K}\right) - \frac{mN}{A + N}P, \\ \frac{dP}{dt} &= P\left(\frac{mN}{A + N} - d\right).\end{aligned}\tag{1.15}$$

- **The Holling-Tanner model:**

The Holling-Tanner model was suggested by Tanner [18] and it is similar to the Rosenzweig

and McArthur model (1.15). More precisely, the prey equation remains the same but the predator equation is modified to:

$$\frac{dP}{dt} = cP\left(1 - \frac{dP}{N}\right).$$

Here the carrying capacity is proportional to the prey population. The most important feature of this model is that it now includes interspecies competition for prey amongst the predators.

Chapter 2

Analysing Quantitative Behaviour of Predator-Prey Models

As the predator-prey models introduced in the previous chapter are non-linear, it is often the case that they are unsolvable analytically. In this section we will solve the Lotka-Volterra model analytically as it is one of the few cases of a non-linear system which we can obtain a solution. We will consider how we can use analytical methods to extract information about the qualitative behavior of more complicated systems. For this we will be focusing exclusively on the bounded Lotka-Volterra and the Holling and Tanner models. Firstly, we will introduce the concepts of the methods we will be applying to our models.

1 Phase Plane Analysis:

Many natural phenomena can be described by the following system of ordinary differential equations

$$\begin{aligned}\frac{dx}{dt} &= f(x, y), \\ \frac{dy}{dt} &= g(x, y).\end{aligned}\tag{2.1}$$

This is known as an *autonomous system* as the independent variable t does not appear explicitly. In order to see how the solutions of this system behave it is often necessary to perform phase plane analysis.

Phase Planes and Phase Portraits of a System of Equations:

It is much easier to determine the quantitative behaviour, of the system if we have a form of visual representation of the phase plane.

Definition 1.1 (Phase Planes) *A phase plane is a two dimensional plane on which we can construct a phase portrait (see below for definition) of the characteristics of a system of differential equations with two state variables (a variable which describes the mathematical state of a dynamical system i.e. a set of relationships amongst two or more measurable quantities). The axes of the phase plane are defined by these two state variables.*

We assume throughout that our functions are continuously differentiable in some region D . Then the xy -plane will represent the phase plane. The quantitative behaviour of the system is derived from its trajectories.

Definition 1.2 (Trajectories) *A trajectory is the path that the solution to the system follows, and they are given by the solutions to*

$$\frac{dy}{dx} = \frac{y'}{x'} = \frac{f(x, y)}{g(x, y)}. \quad (2.2)$$

Once we know the trajectories of the system, we can use them to construct a phase portrait to give us the visual representation of the quantitative behaviour of it.

Definition 1.3 (Phase Portraits) *A phase portrait is the visual representation of the characteristics shown on the phase plane, namely they show the trajectories of the dynamical system.*

In the case where the equation (2.2) is analytically solvable, then its solution can be written implicitly as $H(x, y) = C$. The phase portrait is constructed by plotting the curves of one state variable against the other for various initial conditions (x_0, y_0) . If the initial condition is a critical point, then there is no trajectory and the point is denoted by a dot.

Definition 1.4 (Critical Points) *Critical points (sometimes known as singular points, equilibrium points or steady states) are points where the trajectory of the equation is stationary, therefore they are the points at which the first order differential equations of the system are equal to zero. To denote the coordinates of a critical point we use (x^*, y^*)*

For our system (2.1) the critical points occur when

$$\frac{dx}{dt} = \frac{dy}{dt} = 0$$

A critical point may be one of three forms:

1. **Maximum:** A maximum is an extremum of a function that represents the largest value of a function over a neighbourhood. If the value of the point is the greatest value of the function over the whole domain, then it is said to be a *global maximum*. If the value of the function is the maximum relative to its surrounding values but not necessarily the greatest value of the function over the whole domain, it is said to be a *local maximum*.
2. **Minimum:** A minimum represents the opposite end of the extremum, it is the smallest value of a function. Like the maximum it can be either a *global minimum* or a *local minimum*, depending on whether it is the smallest value over the whole domain of the function or just relative to its surrounding points.
3. **Saddle Point:** A saddle point is a stationary point which is not an extrema of the function. In other words the value of the differential calculated at a small perturbation to either side of the critical point will have the same sign.

To determine which of these forms a critical point takes further analysis is required. To conduct further analysis we will need to construct the *Hessian matrix* of the system (2.1) and evaluate it at the critical point. The Hessian matrix is comprised of the second order partial derivatives of the

system. To simplify the following analysis of the matrix we will call the elements a, b and c as seen below.

$$\begin{pmatrix} \partial^2 H / \partial x^2 & \partial^2 H / \partial x \partial y \\ \partial^2 H / \partial y \partial x & \partial^2 H / \partial y^2 \end{pmatrix} = \begin{pmatrix} a & b \\ b & c \end{pmatrix}.$$

To determine the form of the critical point we can calculate the determinant (det) of the matrix.

$$\det = ac - b^2$$

1. If $\det > 0$ and $a > 0$, then the Hessian matrix is positive definite and the critical point is a minimum.
2. If $\det > 0$ and $a < 0$, then the Hessian matrix is negative definite and the critical point is a maximum.
3. If $\det < 0$, then the critical point is a saddle point.
4. If $\det = 0$, then the test is inconclusive and the critical point could be either of the three forms.

The sketch of the critical points and the trajectory curves show the qualitative behaviour of the solutions of a system.

Stability Analysis of non-linear systems-linearisation

We consider the system (2.1) around the critical point (x^*, y^*) . In order to study the stability of the critical point (x^*, y^*) , we linearise the system (2.1) around it. For this purpose we consider small perturbations δx and δy around the critical point and denote the point $x = x^* + \delta x$ and $y = y^* + \delta y$. By using a Taylor expansion about this point we have,

$$f(x, y) \approx f(x^*, y^*) + f_x(x^*, y^*)\delta x + f_y(x^*, y^*)\delta y.$$

Since $f(x^*, y^*)$ is a critical point, $f(x^*, y^*) = 0$. Therefore

$$f(x, y) \approx f_x(x^*, y^*)\delta x + f_y(x^*, y^*)\delta y.$$

Repeating the process for $g(x, y)$, we can see that we have a linear system of equations defined by

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} \begin{pmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{pmatrix} \begin{pmatrix} \delta x \\ \delta y \end{pmatrix} = J \begin{pmatrix} \delta x \\ \delta y \end{pmatrix},$$

where J is the *Jacobian matrix* at our critical point. When the above linear system has two independent eigenvectors \mathbf{v}_1 and \mathbf{v}_2 the solutions have the form of

$$\begin{pmatrix} \delta x \\ \delta y \end{pmatrix} = c_1 \mathbf{v}_1 e^{\lambda_1 t} + c_2 \mathbf{v}_2 e^{\lambda_2 t},$$

where $c_{1,2}$ are arbitrary constants, $\lambda_{1,2}$ are the eigenvalues of J and $\mathbf{v}_{1,2}$ are the corresponding

eigenvectors.

To calculate the eigenvectors of J we solve the equation

$$\det|J - \lambda I| = \begin{vmatrix} \frac{\partial f}{\partial x}(x^*, y^*) - \lambda & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) - \lambda \end{vmatrix} = 0.$$

Case 1:

- If λ_1 and λ_2 are real, distinct and have the same sign the critical point is called a *node* singularity and the trajectories travel in the same direction along \mathbf{v}_1 and \mathbf{v}_2 . If the eigenvalues are less than zero then it is a stable node and the trajectories head in the direction of the equilibrium point. If the eigenvalues are positive it is an unstable node and the trajectories head in the direction away from the equilibrium point.

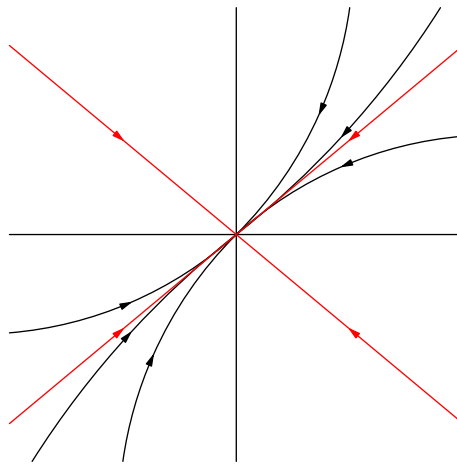


Figure 2.1: Example of a stable node (eigenvectors are in red).

- If the eigenvalues are real and distinct but have different signs then it is a *saddle point singularity*. The trajectories travel in different directions along \mathbf{v}_1 and \mathbf{v}_2 . This kind of singularity is always unstable except for strictly along the eigenvector corresponding to the negative eigenvalue.

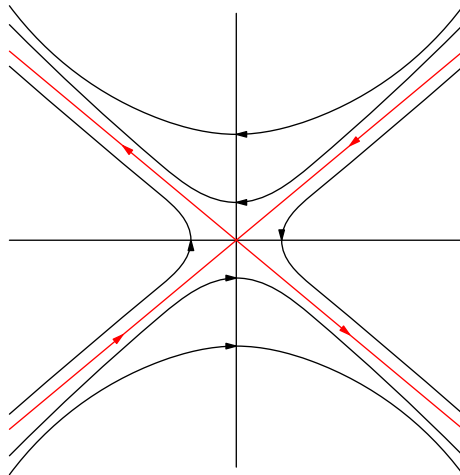


Figure 2.2: Example of a saddle point.

Case 2:

- Suppose that the eigenvalues are complex, namely $\lambda_1, \lambda_2 = \alpha \pm i\beta$ with $\alpha \neq 0$ and $\beta > 0$. In this case the singularity is called a *spiral singularity*. If $\alpha < 0$ the critical point is stable and the trajectories will converge towards it with a spiral motion. If $\alpha > 0$ the trajectories will spiral away from the critical point.

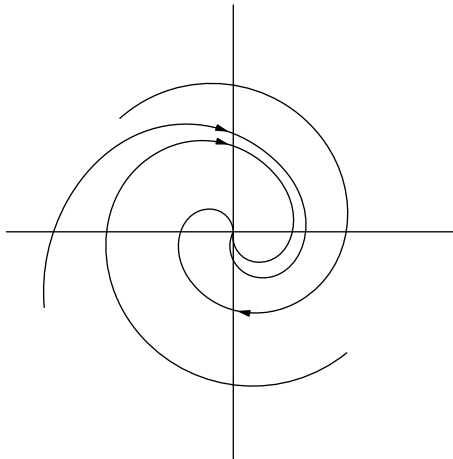


Figure 2.3: Example of a stable spiral.

- In the case when the eigenvalues are purely imaginary, the critical point is called a *centre singularity* and the solutions orbit the equilibrium point in a closed phase trajectory. These are not said to be stable in the usual sense as a small perturbation may knock the solution from its current orbit on to a new orbit, but they can be said to be neutrally stable.

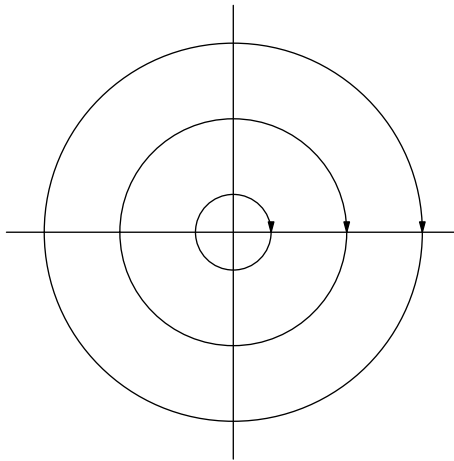


Figure 2.4: Example of a centre.

Case 3:

- If $\lambda_1 = \lambda_2 = \lambda$ then there are two possible scenarios.
 1. There are two independent eigenvectors and the solution are of the form

$$\begin{pmatrix} x \\ y \end{pmatrix} = c_1 \mathbf{v}_1 e^{\lambda t} + c_2 \mathbf{v}_2 e^{\lambda t}.$$

Here every trajectory travels in a straight line through the critical point. This is known as either a *star node* or a *proper node*. Star nodes are stable if the eigenvalue is a negative value and unstable if it is a positive one.

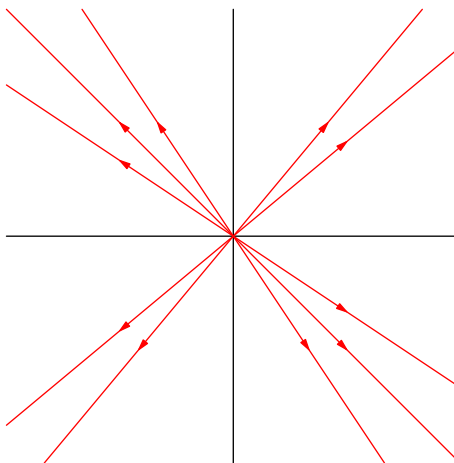


Figure 2.5: Example of an unstable star node.

2. The other case is if the solutions contain the term $te^{\lambda t}$, and the eigenvalue only has a single eigenvector along which the solutions tend to the critical point. This is known as an *improper node* (it is also sometimes known as node type *II*). Similarly its stability is dependent on the sign of the eigenvalue.

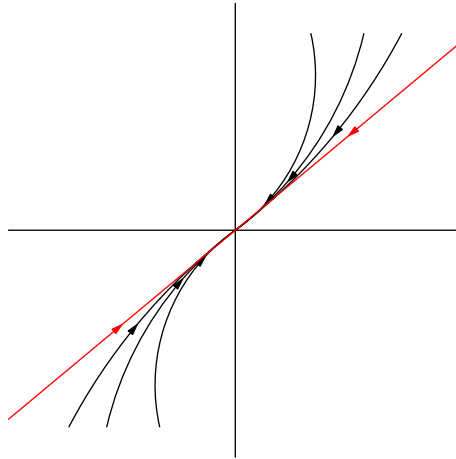


Figure 2.6: Example of a stable improper node.

Stability of Critical points

For equation (2.2), we can see that there will be a unique curve which passes through any point $(x(t), y(t))$, as

$$\frac{dy}{dx}(x(t), y(t)) = \frac{f(x(t), y(t))}{g(x(t), y(t))},$$

except for when $(x(t), y(t)) = (x^*, y^*)$ at which the equation blows up or becomes degenerate.

The stability of the solution alludes to how the solution behaves if we make a small perturbation to the initial condition. In basic terms a solution is said to be stable if a small perturbation to the initial condition leads to a small change to the solution, and unstable if the small perturbation results in a large change in the solution.

- If a solution which starts near an critical point stays forever near that point it is said to be *Lyapunov stable*.
- If the trajectories converge towards the critical point as $t \rightarrow \infty$, it is said to be *asymptotically stable* or attracting.
- If the solution is Lyapunov stable but not asymptotically stable it is said to be *neutrally stable*.
- A point which is not stable is called unstable. In this case the trajectories diverge from the critical point.

An important concept to consider when looking at stability is whether it is locally stable or whether the stability is global. Local stability is when we consider the stability with any small deviation from the critical point, whereas with global stability we consider the entire the region. A system is said to be *globally asymptotically stable* if for every trajectory $(x(t), y(t))$ converges towards (x^*, y^*) as $t \rightarrow \infty$. A system is said to be locally asymptotically stable near or at (x^*, y^*) if there exists a constant δ such that

$$\|(x(0), y(0)) - (x^*, y^*)\| \leq \delta \Rightarrow (x(t), y(t)) \rightarrow (x^*, y^*) \text{ as } t \rightarrow \infty$$

During this studu we will consider two ways of proving global stability, we will apply both of these methods to the Holling and Tanner model.

- **Lyapunov's Second Method Isolated points**

In the previous paragraph we discussed the stability of locally linear systems. However, no conclusion can be made in case that the critical point is center. In this paragraph we will explore another approach, the so-called Lyapunov's second method. We can determine global asymptotic stability of our system (2.1) without having to calculate the trajectories by considering a positive definite C^1 function $V(x, y)$. Where $V(x, y)$ is defined in an open region D of an *isolated critical point* (x^*, y^*) of the system this is known as the Lyapunov function for said system.

Definition 1.5 (Isolated Critical Point) *A critical point is said to be isolated if it is the only critical point in some small neighbourhood of the point.*

Definition 1.6 (Positive (Negative) Definition and Semi-Definition) *Let $V(x, y)$ be defined on some domain D containing the critical point (x^*, y^*) . Then $V(x, y)$ is called positive definite on D if $V(0, 0) = 0$ and $V(x, y) > 0$ for all other points in D . Similarly it is said to be negative definite on D if $V(0, 0) = 0$ and $V(x, y) < 0$ for all other points in D . If the inequalities $>$ and $<$ are replaced by \leq and \geq , then V is said to be positive semi-definite and negative semi-definite, respectively.*

Let the gradient of $V(x, y)$ be given by

$$\nabla V(x, y) = \left[\frac{\partial V(x, y)}{\partial x}, \frac{\partial V(x, y)}{\partial y} \right],$$

then the time derivative $\dot{V}(x, y)$ can be written as

$$\dot{V}(x, y) = \frac{\partial V(x, y)}{\partial x} f(x, y) + \frac{\partial V(x, y)}{\partial y} g(x, y).$$

We can use the Lyapunov function and its time derivative to analyse the stability of the system (2.1) with the following two theorems defined by Boyce and DiPrima [1].

Theorem 1.1 *Suppose that an autonomous system (2.1) has an isolated critical point (x^*, y^*) . If there exists a positive definite C^1 function V for which the time derivative \dot{V} is positive definite on some domain D containing (x^*, y^*) , then (x^*, y^*) is an asymptotically stable. If \dot{V} is negative semidefinite then the (x^*, y^*) is a stable critical point.*

Theorem 1.2 *Let (x^*, y^*) be an isolated critical point of the autonomous system (2.1). Let V be a function that is continuous and has continuous first partial derivatives. Suppose that $V(x^*, y^*) = 0$ and that in every neighborhood of (x^*, y^*) there is at least one point at which V is positive (negative). If there exists a domain D containing (x^*, y^*) such that the time derivative $\dot{V}(x, y)$ is positive definite (negative definite) on D , then (x^*, y^*) is an unstable critical point.*

By the first theorem we can see that if $\dot{V}(x, y) < 0$ for all (x, y) in D of the critical point of the system then $V(x, y)$ is called a *global Lyapunov function* and the system is globally asymptotically stable. This is known as LaSalle's invariance principle [?., LA]

- **Dulac Criterion** The Dulac criterion can be used to rule out the existence of a limit cycle in the region of a plane D .

Definition 1.7 (Limit Cycles) A *Limit Cycle* is a closed orbit in the phase plane that attracts trajectories. If all trajectories that start near the closed orbit converge towards the orbit then the limit cycle is asymptotically stable. If the trajectories spiral away from the closed orbit it is said to be unstable.

Lemma 1.3 Let D be a simply connected region of the phase plane, i.e. every closed loop within D can be shrunk to a point without leaving D . If there exists a continuously differentiable function known as the Dulac function $H(x, y)$ such that the total differential

$$\frac{d}{dx}[H(x, y)f(x, y)] + \frac{d}{dy}[H(x, y)g(x, y)] \quad (2.3)$$

has the same sign ($\neq 0$) anywhere in a simply connected region of the plane, then the system has no periodic solutions entirely within the region.

Definition 1.8 (Boundness) A function is said to be bounded if there exists some real constant M such that $|f(x)| \leq M$.

Note that this is an important concept since in an unbounded system like the Lotka Volterra model (1.8) the prey population will grow without limits in the absence of predation. This is an obviously unrealistic representation as the population will be limited by other factors, such as lack of territory, or limits to its nutrient supply. Also boundness is an important concept when it comes to analysing the Lyapunov function (see below).

Proof This can be proved by using Green's theorem which states that if we have simple closed curve C and a region D bounded by C and two functions $k(x, y)$ and $l(x, y)$ on an open region containing D then the relationship between the line integral around C and the double integral over D is

$$\oint_C (k(x, y)dx + l(x, y)dy) = \int \int_D \left(\frac{dk}{dx} - \frac{dl}{dy} \right) dx dy. \quad (2.4)$$

From our Dulac criterion we know that

$$\int \int_D \left(\frac{d}{dx}[H(x, y)f(x, y)] + \frac{d}{dy}[H(x, y)g(x, y)] \right) dx dy \neq 0.$$

So without loss of generality let $H(x, y)$ be such that

$$\int \int_D \left(\frac{d}{dx}[H(x, y)f(x, y)] + \frac{d}{dy}[H(x, y)g(x, y)] \right) dx dy > 0.$$

By applying Green's theorem (2.4) we get

$$\begin{aligned} 0 &< \int \int_D \left(\frac{d}{dx}[H(x, y)f(x, y)] + \frac{d}{dy}[H(x, y)g(x, y)] \right) dx dy \\ &= \int \int_D \left(\frac{d}{dx}[H(x, y)f(x, y)] - \frac{d}{dy}[-H(x, y)g(x, y)] \right) dx dy \\ &= \oint_C (-H(x, y)g(x, y)dx + H(x, y)f(x, y)dy) \end{aligned}$$

$$= \oint_C H(x, y)(-g(x, y)dx + f(x, y)dy). \quad (2.5)$$

If we rearrange our system (2.1) we get that

$$\begin{aligned} dx &= f(x, y)dt, \\ dy &= g(x, y)dt. \end{aligned}$$

Substituting these values into (2.5) we obtain that

$$0 < \oint_C H(x, y)(-f(x, y)g(x, y)dt + f(x, y)g(x, y)dt) = 0,$$

which is a contradiction, therefore we can conclude that there are no closed orbits in C . ■

We can use this result to prove global asymptotic stability by using Poincaré-Bendixson's theorem [1].

Theorem 1.4 (Poincaré-Bendixson) *Let the functions f and g from our system (2.1) have continuous first order partial derivatives in a domain D of the xy -plane. Let D_1 bounded sub-domain in D , and let R be the region that consists of D_1 and its boundary. Suppose that the critical points of system (2.1) do not lie in R . If there exists a constant t_0 such that $x = \sigma(t), y = \psi(t)$ is a solution of the system (2.1) that exists and stays in R for all $t \geq t_0$, then $x = \sigma(t), y = \psi(t)$ is either: a closed trajectory (periodic solutions) or spirals. In either case, the system (2.1) has a periodic solution in \mathbb{R}*

Therefore by the Poincaré-Bendixson theorem if we can prove that no limit cycles exist in the region and if the system is bounded. Then any orbit in the region tends to the critical point as $t \rightarrow \infty$ giving us globally stability.

Both of these methods suffer from the same problem which is the difficulty of finding a suitable function, so for the purposes of this paper we will use functions defined by Hsu et. al. [11]. When we analyse the Holling-Tanner model we will be looking for Hopf Bifurcation.

Definition 1.9 (Hopf Bifurcation) *Hopf Bifurcation occurs when a critical point changes stability. It can take one of two forms, it can either be supercritical where the limit cycles generated are stable or sub-critical when they are unstable. A Hopf bifurcation occurs when the three following conditions are met:*

- $f(x, y) = 0,$
- $g(x, y) = 0,$
- $\frac{df}{dx}(x, y) + \frac{dg}{dy}(x, y) = 0.$

Notice that Hopf bifurcation only occurs at critical points and where the trace of the Jacobian matrix $\text{Tr}(J) = 0$.

2 Solving the Lotka-Volterra model:

To solve the Lotka-Volterra model we must first simplify the parameters. To do this we non-dimensionalise the system through a change of variables. If we introduce the terms:

$$u = \frac{N}{c_1}, \quad v = \frac{P}{c_2}, \quad \tau = \frac{t}{c_3}.$$

We can differentiate then obtain the differential equations

$$\begin{aligned} \frac{dN}{dt} &= c_1 \frac{du}{dt} = c_1 \frac{du}{d\tau} \frac{d\tau}{dt} = \frac{c_1}{c_3} \frac{du}{d\tau}, \\ \frac{dP}{dt} &= c_2 \frac{dv}{dt} = c_2 \frac{dv}{d\tau} \frac{d\tau}{dt} = \frac{c_2}{c_3} \frac{dv}{d\tau}. \end{aligned} \tag{2.6}$$

We can substitute (2.6) into the Lotka-Volterra system (1.8) to obtain:

$$\frac{c_1}{c_3} \frac{du}{d\tau} = a(c_1 u) - b(c_1 u)(c_2 v),$$

$$\frac{c_2}{c_3} \frac{dv}{d\tau} = c(c_1 u)(c_2 v) - d(c_2 v).$$

Rearranging these equations we get:

$$\frac{du}{d\tau} = (c_3 a)u - (c_2 c_3 b)uv,$$

$$\frac{dv}{d\tau} = (c_1 c_3 c)vu - (dc_3)v.$$

The last equation may be simplified by selecting $c_1 = d/c$, $c_2 = a/b$, $c_3 = 1/a$. We also introduce a new coefficient $\alpha = d/a$ which gives the ratio between the increasing and decreasing factors of the predator and the prey. By introducing the new variables u, v and τ defined as

$$u(\tau) = \frac{cN(t)}{d}, \quad v(\tau) = \frac{bP(t)}{a}, \quad \tau = at, \quad \alpha = \frac{d}{a},$$

the system (2.6) can be rewritten as follows

$$\frac{du}{d\tau} = u(1 - v), \tag{2.7}$$

$$\frac{dv}{d\tau} = \alpha v(u - 1),$$

which is a system which contains only one parameter.

By eliminating τ we obtain the trajectory equation in the u, v phase plane:

$$\frac{dv}{du} = \alpha \frac{v(u - 1)}{u(1 - v)}. \tag{2.8}$$

As (2.8) is a separable first order equation we can integrate it exactly. We first rearrange the equation to get:

$$\frac{(1-v)}{v}dv = \alpha \frac{(u-1)}{u}du.$$

By integrating both sides of this equation we get

$$\ln v - v = \alpha u - \alpha \ln u + C.$$

Thus, the equation (2.8) has the solutions $H(u, v) = C$, where $H(u, v)$ is given by

$$H(u, v) = \alpha u + v - \ln |u^\alpha v|. \quad (2.9)$$

Now we can find the critical points of equation (2.9) by differentiating H with respect to u and v and by calculating

$$\frac{\partial H}{\partial u} = \frac{\partial H}{\partial v} = 0.$$

From this we get

$$\frac{\partial H}{\partial u} = \alpha - \frac{\alpha}{u} = 0, \quad (2.10)$$

$$\frac{\partial H}{\partial v} = 1 - \frac{1}{v} = 0.$$

We can see from (2.10) that the system has a critical point at $v = u = 1$. We can determine the nature of this critical point by analysing the Hessian matrix.

$$\begin{pmatrix} \frac{\partial^2 H}{\partial u^2} & \frac{\partial^2 H}{\partial u \partial v} \\ \frac{\partial^2 H}{\partial v \partial u} & \frac{\partial^2 H}{\partial v^2} \end{pmatrix} = \begin{pmatrix} \alpha/u^2 & 0 \\ 0 & 1/v^2 \end{pmatrix}.$$

The determinate D of this matrix is

$$D = \frac{\alpha}{u^2 v^2}.$$

We can see that $\alpha = d/a > 0$ as d and a are both positive constants, this also makes $D > 0$. So the matrix is positive definite and the critical point is a local minimum. We can see by substituting the values of u and v at the critical point into the equation for H that $H_{min} = H(1, 1) = 1 + \alpha$. From equation (2.9) we can see that $H = C$ which is a constant, so for values of $H > H_{min}$ the solutions orbit in a closed trajectory as seen in figure 2.8. These trajectories form a collection of periodic orbits i.e an orbit which repeats itself in time. This means that u and v will have periodic solutions in τ , as is illustrated below by figure 2.7. The value of H is determined by the initial conditions $u(0)$ and $v(0)$ which also determines the phase trajectory.

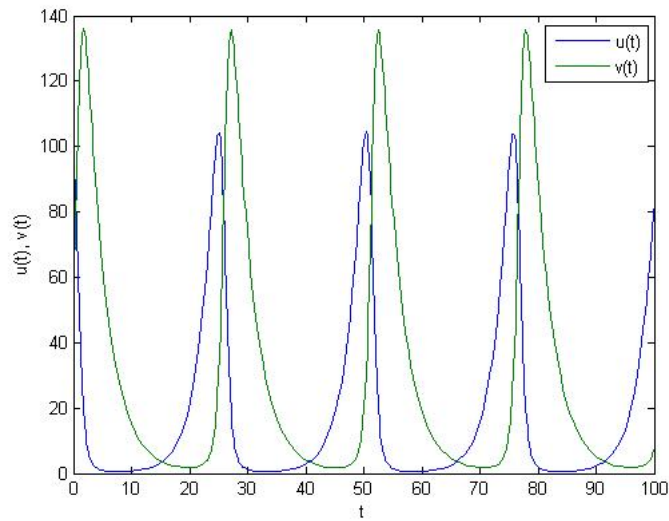


Figure 2.7: Example of periodic solutions for the Lotka-Volterra system with $a = 0.4$, $b = 0.013$, $c = 0.3$ and $d = 0.015$, with $u(0) = 50$ and $v(0) = 100$.

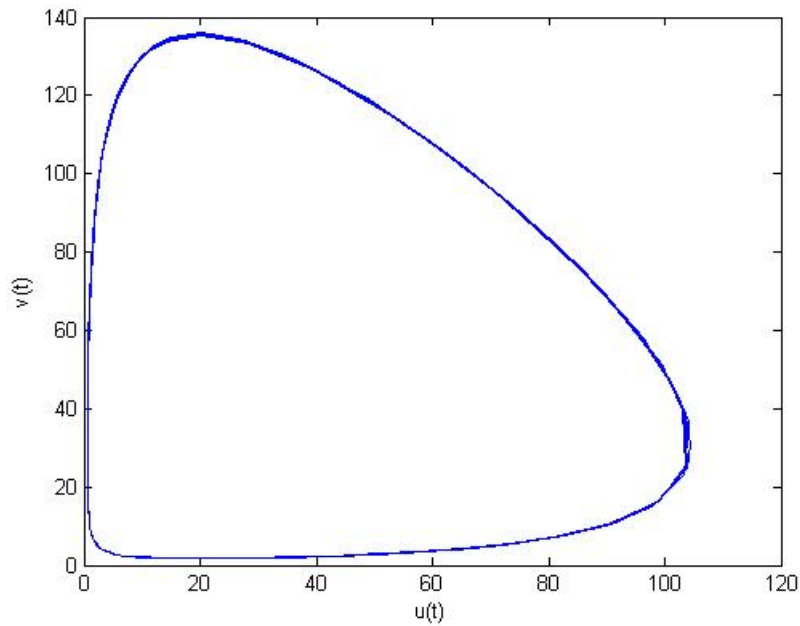


Figure 2.8: Example of the phase plane trajectory for the system with $a = 0.4$, $b = 0.013$, $c = 0.3$ and $d = 0.015$. $u(0) = 100$ and $v(0) = 50$, therefore $H = 75.85445834$.

These closed orbits are a major flaw of the Lotka-Volterra system, as they result in a system with solutions that are not structurally stable. This means any small perturbation will move the solution onto another trajectory resulting in vastly different solutions. These are called conservative systems and they are of limited use when it comes to modeling real populations.

Determining the stability of the critical points

We consider our non-dimensionalized system

$$\frac{du}{d\tau} = u(1 - v),$$

$$\frac{dv}{d\tau} = \alpha v(u - 1).$$

It can be easily seen that this system has critical points at $(u^*, v^*) = (0, 0)$ and $(u^*, v^*) = (1, 1)$. We first consider the critical point $(u^*, v^*) = (0, 0)$ and let x and y be small perturbations about $(0, 0)$, we get that $u = x$ and $v = y$. Now we substitute these new terms into our system we get

$$\frac{d(u^* + x)}{d\tau} = x(1 - y),$$

$$\frac{d(v^* + y)}{d\tau} = \alpha y(x - 1).$$

We then expand the right hand side of the above equations using Taylor expansions and by keeping only the linear terms to get

$$\begin{pmatrix} dx/d\tau \\ dy/d\tau \end{pmatrix} \approx \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = J \begin{pmatrix} x \\ y \end{pmatrix}.$$

We can determine the type of the steady state by calculating the eigenvalues of the matrix J . We have

$$\det |J - \lambda I| = \begin{vmatrix} 1 - \lambda & 0 \\ 0 & -\alpha - \lambda \end{vmatrix} = 0.$$

From this we can easily see that J has eigenvalues at $\lambda_1 = 1$ and $\lambda_2 = -\alpha$. The solution of this system is given by

$$\begin{pmatrix} x(\tau) \\ y(\tau) \end{pmatrix} = \mathbf{j}e^{\tau} + \mathbf{k}e^{-\alpha\tau},$$

where \mathbf{j} and \mathbf{k} are two independent eigenvectors, corresponding to λ_1 and λ_2 , respectively.

As shown in the previous chapter, since $\lambda_1 > 0$ and $\lambda_2 < 0$ the critical point $(0, 0)$ is a saddle point. This is because there are different directions along the eigenvectors, therefore the solution approaches the origin along one eigenvector and moves away from it along the other. Being a saddle point this means it is unstable, we can see this as $\lambda_1 > 0$ resulting in $x(\tau)$ and $y(\tau)$ growing exponentially.

Now we consider the other critical point $(u^*, v^*) = (1, 1)$. Working in an analogous way we introduce $u = 1 + x$ and $v = 1 + y$. We then substitute these terms into our system to get:

$$\frac{d(u^* + x)}{d\tau} = (x + 1)(1 - y - 1) = -y(x + 1),$$

$$\frac{d(v^* + y)}{d\tau} = \alpha(y + 1)(x + 1 - 1) = \alpha x(y + 1).$$

Using the same process as above we obtain the system:

$$\begin{pmatrix} dx/d\tau \\ dy/d\tau \end{pmatrix} \approx \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = J \begin{pmatrix} x \\ y \end{pmatrix}.$$

We can now calculate the eigenvalues of J :

$$\det |J - \lambda I| = \begin{vmatrix} -\lambda & -1 \\ \alpha & -\lambda \end{vmatrix} = 0,$$

i.e.

$$\lambda^2 + \alpha = 0,$$

from which we obtain that $\lambda_{1,2} = \pm i\sqrt{\alpha}$. As the eigenvalues are purely imaginary the critical point is a centre singularity. The solution to this system is given by:

$$\begin{pmatrix} x(\tau) \\ y(\tau) \end{pmatrix} = \mathbf{l}e^{i\sqrt{\alpha}\tau} + \mathbf{m}e^{-i\sqrt{\alpha}\tau},$$

where \mathbf{l} and \mathbf{m} are eigenvectors, corresponding to λ_1 and λ_2 , respectively.

Therefore around the critical point the solutions are periodic with a period of $\tau = 2\pi/\sqrt{\alpha}$. If we then dimensionalise this we get the period $T = 2\pi(a/d)^{1/2}$. This means that the period is proportional to the square root of the ratio of the linear growth rate of the prey to the death rate of the predators. This results are shown by [14]

3 Analytical solution of other predator prey models

Now that we have the basics of analytically solving predator-prey models we can start to look at solving the more complicated realistic systems.

3.1 Analytically solving the bounded Lotka-Volterra system

We will start by looking at the Lotka-Volterra with a bounded prey population (see system (1.11))

$$\frac{dN}{dt} = aN \left(1 - \frac{N}{K} - b \frac{P}{K} \right),$$

$$\frac{dP}{dt} = P(cN - d).$$

We first non-dimensionalise the system, by setting

$$N = c_1 u, \quad P = c_2 v, \quad \tau = c_3 t.$$

Therefore our system becomes

$$c_1 c_3 \frac{du}{d\tau} = a c_1 u \left(1 - \frac{c_1 u}{K} - \frac{b c_2 v}{K} \right),$$

$$c_2 c_3 \frac{dv}{d\tau} = c_2 v (c c_1 u - d).$$

Dividing both sides of the first and second equation by c_1c_3 and c_2c_3 respectively, we get

$$\frac{du}{d\tau} = \frac{a}{c_3}u \left(1 - \frac{c_1u}{K} - \frac{bc_2v}{K}\right),$$

$$\frac{dv}{d\tau} = \frac{v}{c_3}(cc_1u - d).$$

We can simplify the above system by choosing the parameters c_1, c_2 and c_3 as follows

$$c_1 = K, \quad c_2 = \frac{K}{b}, \quad c_3 = a.$$

This gives us the three dimensionless variables

$$u = \frac{N}{K}, \quad v = \frac{bP}{K}, \quad \tau = at.$$

Thereby we arrive at the following system of equations

$$\frac{du}{d\tau} = u(1 - u - v)$$

$$\frac{dv}{d\tau} = v\left(\frac{cK}{a}u - \frac{d}{a}\right)$$

By setting

$$\delta = \frac{d}{a}, \quad \beta = \frac{cK}{a},$$

the system can be written as follows

$$\frac{du}{d\tau} = u(1 - u - v),$$

$$\frac{dv}{d\tau} = v(\beta u - \delta).$$

(2.11)

We will next find the critical points of system (2.11), which are the solutions of the homogeneous system

$$0 = u(1 - u - v),$$

$$0 = v(\beta u - \delta).$$

The first equation is satisfied when either $u = 0$, or $1 - u - v = 0$. If $u = 0$, then the second equation gives $v = 0$. If $u = 1 - v$, the second equation gives $v = 1 - \frac{\beta}{\delta}$, then from the first equation it follows that $u = \beta\delta$. The other option is when $v = 0$, then $u = 1$. Thus, our system has three possible critical points.

$$(u^*, v^*) = (0, 0), \quad (u^*, v^*) = (1, 0), \quad (u^*, v^*) = \left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right).$$

Since our critical points corresponds to populations we assume that $u^* > 0$ and $v^* > 0$. Thus, the critical point $(u^*, v^*) = \left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right)$ is in the first quadrant if $\delta \leq \beta$. For our system we get the Jacobian matrix

$$J(u, v) = \begin{pmatrix} 1 - 2u - v & -u \\ \beta v & \beta u - \delta \end{pmatrix}.$$

We first consider the case of $(u^*, v^*) = (0, 0)$. We have that

$$J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & -\delta \end{pmatrix},$$

with eigenvalues $\lambda_1 = 1$ and $\lambda_2 = -\delta$. Since $\lambda_1 > 0$ and $\lambda_2 < 0$ this critical point is a saddle point. Now for the critical point $(u^*, v^*) = (1, 0)$ the corresponding Jacobian matrix is given by

$$J(1, 0) = \begin{pmatrix} -1 & -1 \\ 0 & \beta - \delta \end{pmatrix}.$$

The eigenvalues of this matrix are $\lambda_1 = -1$ and $\lambda_2 = \beta - \delta$, therefore the behavior of the critical point depends on the values of the constants β and δ . As stated before for the critical point $(u^*, v^*) = \left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right)$ to exist we need $\beta \geq \delta$, otherwise the v value will be negative. Therefore, if we have three critical points then $\lambda_1 < 0$ and $\lambda_2 > 0$ and the singular point is a saddle point. If $(u^*, v^*) = \left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right)$ is not biologically possible then both eigenvalues will be negative and it will be a stable node.

We consider the case $\beta \geq \delta$, then the Jacobian matrix for the critical point $(u^*, v^*) = \left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right)$ is

$$J\left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right) = \begin{pmatrix} 1 - \frac{2\delta}{\beta} - \left(1 - \frac{\delta}{\beta}\right) & -\frac{\delta}{\beta} \\ \beta\left(1 - \frac{\delta}{\beta}\right) & -\delta + \frac{\beta\delta}{\beta} \end{pmatrix} = \begin{pmatrix} -\frac{\delta}{\beta} & -\frac{\delta}{\beta} \\ \beta - \delta & 0 \end{pmatrix}.$$

The eigenvalues of this matrix are the solutions of the following equation.

$$\det\left(J\left(\frac{\delta}{\beta}, 1 - \frac{\delta}{\beta}\right) - \lambda I\right) = \begin{vmatrix} -\frac{\delta}{\beta} - \lambda & -\frac{\delta}{\beta} \\ \beta - \delta & -\lambda \end{vmatrix} = \lambda^2 + \frac{\delta}{\beta}\lambda + \frac{\delta}{\beta}(\beta - \delta) = 0. \tag{2.12}$$

Therefore, by using the quadratic formula we obtain

$$\begin{cases} \lambda_1 = \frac{-\frac{\delta}{\beta} + \sqrt{\left(\frac{\delta}{\beta}\right)^2 - 4\frac{\delta}{\beta}(\beta - \delta)}}{2}, \\ \lambda_2 = \frac{-\frac{\delta}{\beta} - \sqrt{\left(\frac{\delta}{\beta}\right)^2 - 4\frac{\delta}{\beta}(\beta - \delta)}}{2}. \end{cases}$$

Another way of looking at this is to consider the quadratic formula as

$$\lambda_{1,2} = \frac{\text{Tr}(J) \pm \sqrt{(\text{Tr}(J))^2 - 4(\det(J))}}{2},$$

Where $\text{Tr}(J)$ is the trace of our matrix (2.12) and $\det(J)$ is its determinant. Note that $\text{Tr}(J) = \frac{-\delta}{\beta} < 0$ and $\det(J) = \frac{\delta}{\beta}(\beta - \delta) > 0$. This gives us two possible scenarios: if $4(\det(J)) > \text{Tr}(J)^2$, then the eigenvalues are complex and as $\alpha = \text{Tr}(J) < 0$ the critical point is a stable spiral. If this is not the case then both eigenvalues will be negative and it will be a stable node.

3.2 Analysis of Holling Tanner model

We consider the system of equations suggested by Holling-Tanner, which is defined as

$$\begin{aligned} \frac{dN}{dt} &= aN\left(1 - \frac{N}{K}\right) - \frac{mN}{A+N}P, \\ \frac{dP}{dt} &= cP\left(1 - \frac{dP}{N}\right). \end{aligned} \tag{2.13}$$

We now non-dimensionalise our system. We let

$$N = Ku, \quad P = \frac{aKv}{m}, \quad \tau = at,$$

and then substitute the new variables into the system (2.13) to get

$$\begin{aligned} aK \frac{du}{d\tau} &= aKu\left(1 - \frac{Ku}{K}\right) - \frac{mKu}{A+Ku} \frac{aKv}{m}, \\ \frac{a^2K}{m} \frac{dv}{d\tau} &= \frac{acK}{m} v\left(1 - \frac{adKv}{mKu}\right). \end{aligned}$$

We can simplify these equations to get

$$\begin{aligned} \frac{du}{d\tau} &= u(1 - u) - \frac{Kuv}{(A + Ku)}, \\ \frac{dv}{d\tau} &= v\left(\frac{c}{r} - \frac{cdv}{mu}\right). \end{aligned}$$

We then introduce the parameters

$$r_1 = \frac{c}{a}, \quad b_1 = \frac{cd}{m}, \quad a_1 = \frac{A}{K}.$$

to obtain the non-dimensionalised system

$$\begin{aligned} \frac{du}{d\tau} &= u(1-u) - \frac{u}{a_1+u}v, \\ \frac{dv}{d\tau} &= v\left(r_1 - b_1\frac{v}{u}\right). \end{aligned} \tag{2.14}$$

We can generalise this non-dimensionalised system by writing it in the form

$$\begin{aligned} \frac{du}{d\tau} &= uf(u) - g(u)v, \\ \frac{dv}{d\tau} &= v\left(r_1 - b_1\frac{v}{u}\right). \end{aligned} \tag{2.15}$$

Now, by using different functions for $f(u)$ and $g(u)$ we can obtain non-dimensionalised systems for the class of predator-prey system. If $f(u) = 1 - u$ and $g(u) = u$ then we get the non-dimensionalised form for the Leslie-Gower model (1.12). For the Holling-Tanner model we set $f(u) = 1 - u$ and $g(u) = \frac{u}{a_1 + u}$. In general if $f(u) = 1 - u$ then we can set $g(u)$ as any of the Holling type functional responses to create a plausible model. We can use this to obtain some general analysis for any of the models with a Holling type functional response. We can see that for such models the following conditions are satisfied

- $f(1) = 0$ and $f'(u) < 0$ for all $u > 0$.
- $g(0) = 0$ and $g'(u) > 0$ for all $u > 0$.

Note that $(u^*, v^*) = (1, 0)$ is a critical point for Holling systems. To find the non-trivial critical (u^*, v^*) points for our generalized system we can equate (2.15) to 0, namely

$$\begin{aligned} 0 &= u^*f(u^*) - g(u^*)v^*, \\ 0 &= v^*\left(r_1 - b_1\frac{v^*}{u^*}\right). \end{aligned}$$

By assuming $u^*, v^* > 0$ we conclude that the critical point satisfies

$$v^* = \frac{u^*f(u^*)}{g(u^*)} = \frac{r_1}{b_1}u^*, \tag{2.16}$$

from which we obtain that $f(u^*) = \frac{r_1}{b_1}g(u^*)$. As $f(1) = 0$ with $f'(u) < 0$ and $g(0) = 0$ with $g'(u) > 0$, this implies that if we plot the graph of $g(u)$ and $\frac{r_1}{b_1}p(u)$ then we obtain an intersection u^* satisfying $0 < u^* < 1$. We can use these results to show that our class of predator-prey models with a Holling function type response are positive and bounded. The Jacobian matrix at the point

(u^*, v^*) is given by

$$J(u^*, v^*) = \begin{pmatrix} f(u^*) - u^* f'(u^*) - g'(u^*)v^* & -g(u^*) \\ b_1 \left(\frac{v^*}{u^*}\right)^2 & r_1 - \frac{2b_1 v^*}{u^*} \end{pmatrix}.$$

By introducing the prey isocline derived from (2.16) $h(u) = \frac{uf(u)}{g(u)}$, and by using the relation $v^* = \frac{r_1}{b_1}u^*$, we can rewrite our Jacobian matrix as

$$J(u^*, v^*) = \begin{pmatrix} u^* f'(u^*) + f(u^*) - \frac{u^* f(u^*) g'(u^*)}{g(u^*)} & -g(u^*) \\ b_1 \left(\frac{r_1^2 u^*}{b_1^2 u^*}\right) & r_1 - 2b_1 \left(\frac{r_1 u^*}{b_1 u^*}\right) \end{pmatrix}$$

Since

$$h'(u) = \frac{g(u)(uf'(u) + f(u)) - uf(u)g'(u)}{(g(u))^2},$$

we can rewrite this as

$$J(u^*, v^*) = \begin{pmatrix} g(u^*)h'(u^*) & -g(u^*) \\ \frac{r_1^2}{b_1} & -r_1 \end{pmatrix}. \quad (2.17)$$

There eigenvalues of the Jacobian matrix can be found by solving the equation

$$0 = \begin{pmatrix} g(u^*)h'(u^*) - \lambda & -g(u^*) \\ \frac{r_1^2}{b_1} & -r_1 - \lambda \end{pmatrix} = \lambda^2 + \lambda(r_1 - g(u^*)h'(u^*)) + r_1 g(u^*) \left(\frac{r_1}{b_1} - h'(u^*)\right).$$

By assuming that

$$r_1 - g(u^*)h'(u^*) > 0, \quad (2.18)$$

and

$$\frac{r_1}{b_1} - h'(u^*) > 0. \quad (2.19)$$

The eigenvalues are complex with a negative real part and therefore the singular point is a stable spiral if $(r_1 - g(u^*)h'(u^*))^2 - 4r_1g(u^*)\left(\frac{r_1}{b_1} - h'(u^*)\right) > 0$ we will have a stable spiral. In the situation where (2.18) and (2.19) are satisfied but $(r_1 - g(u^*)h'(u^*))^2 - 4r_1g(u^*)\left(\frac{r_1}{b_1} - h'(u^*)\right) < 0$ both of the eigenvalues are negative. We can thus conclude that the singular point is a stable node. We can see that the conditions (2.18) and (2.19) are satisfied if the prey isocline is non increasing at the critical point. Therefore, if $h'(u^*) \leq 0$ then the critical point is locally asymptotically stable.

3.3 Global Stability

We can look for global stability by using a Lyapunov function.

Proposition 3.1 *If the prey isocline is non-increasing for $u \in [0, 1]$, then the critical point (u^*, v^*) is globally asymptotically stable.*

Proof Let V be the Lyapunov function defined by

$$V(u, v) = \int_{u^*}^u \frac{\epsilon - u^*}{\epsilon g(\epsilon)} d\epsilon + c \int_{v^*}^v \frac{\nu - v^*}{\nu} d\nu, \quad (2.20)$$

where $c > 0$ is to be determined.

Apply the fundamental theorem of calculus to get

$$\nabla V = \left(\frac{u - u^*}{ug(u)}, c \frac{v - v^*}{v} \right).$$

Since $v^* = \frac{r_1}{b_1} u^*$, we can rewrite system (2.15) as

$$\frac{du}{d\tau} = uf(u) - g(u)(v + v^* - v^*), \quad (2.21)$$

$$\frac{dv}{d\tau} = v \left(\frac{b_1 v^*}{u^*} - \frac{b_1 v}{u} \right) = vb_1 \left(\frac{uv^* - u^*v}{uu^*} \right) = vb_1 \left(\frac{v^*(u - u^*) - u^*(v - v^*)}{uu^*} \right).$$

Using ∇V and the system (2.21) we obtain the time derivative of V computed along the solution of our system as

$$\dot{V} = \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - \frac{(u - u^*)(v - v^*)}{u} + cb_1(v - v^*) \left(\frac{v^*(u - u^*) - u^*(v - v^*)}{uu^*} \right).$$

Now by letting $c = \frac{u^*}{b_1 v^*}$ we obtain

$$\begin{aligned} \dot{V} &= \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - \frac{(u - u^*)(v - v^*)}{u} + cb_1(v - v^*) \left(\frac{v^*(u - u^*) - u^*(v - v^*)}{uu^*} \right) \\ &= \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - \frac{(u - u^*)(v - v^*)}{u} + \frac{b_1(v - v^*)u^*}{b_1 v^*} \left(\frac{v^*(u - u^*) - u^*(v - v^*)}{uu^*} \right) \\ &= \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - \frac{(u - u^*)(v - v^*)}{u} + \frac{(v - v^*)}{v^*} \left(\frac{v^*(u - u^*) - u^*(v - v^*)}{u} \right) \\ &= \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - \frac{(u - u^*)(v - v^*)}{u} + \frac{(u - u^*)(v - v^*)}{u} - \frac{(v - v^*)^2 u^*}{b_1 u v^*} \\ &= \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - cb_1 \frac{(v - v^*)^2}{u} \end{aligned}$$

If the condition

$$(u - u^*) \left(\frac{uf(u)}{g(u)} - v^* \right) < 0, \quad (2.22)$$

is satisfied for $0 < u < 1$ and $u \neq u^*$, then we have

$$\dot{V} = \frac{u - u^*}{u} \left(\frac{uf(u)}{g(u)} - v^* \right) - cb_1 \frac{(v - v^*)^2}{u} < 0.$$

Hence \dot{V} is negative definite which proves that the system is globally stable. ■

3.4 Stability of Holling-Tanner Model

Calculating the Critical Points

We can analyse the critical points by looking at our non-dimensionalised Holling-Tanner system (2.14). In this form you can see that as u appears in the denominator it cannot be equal to 0. Therefore we have two possible critical points. One is the trivial solution $(u^*, v^*) = (1, 0)$ and the other is the non-trivial solution. Indeed, the critical points are the solution of the system $\frac{du}{d\tau} = \frac{dv}{d\tau} = 0$. From $\frac{dv}{d\tau} = 0$, we get

$$0 = v \left(r_1 - b_1 \frac{v}{u} \right) = r_1 - b_1 \frac{v}{u},$$

therefore

$$u = \frac{b_1}{r_1} v.$$

Now in view of the last equation, $\frac{du}{d\tau} = 0$ gives

$$0 = u(1 - u) - \frac{r_1 u^2}{b_1(a_1 + u)}.$$

Since $u \neq 0$ we can divide both sides of the equation by u to obtain

$$(1 - u) = \frac{r_1 u}{b_1(a_1 + u)}.$$

This can be rewritten as

$$(1 - u)(a_1 + u) - \frac{r_1}{b_1} u = 0,$$

from which we can obtain the quadratic equation

$$u^2 + \left(a_1 + \frac{r_1}{b_1} - 1 \right) u - a_1 = 0.$$

We can thus conclude that the non-trivial critical point (u^*, v^*) satisfies

$$\begin{cases} u^2 + \left(a_1 + \frac{r_1}{b_1} - 1 \right) u - a_1 = 0, \\ u = \frac{b_1}{r_1} v. \end{cases} \quad (2.23)$$

Analysing the Stability of the Critical Points

First we will study the stability of the trivial critical point $(u^*, v^*) = (1, 0)$. The Jacobian matrix at the point (u^*, v^*) is given by

$$J(u^*, v^*) = \begin{pmatrix} 1 - 2u^* - \frac{v^*}{a_1 + u^*} + \frac{u^*v^*}{(a_1 + u^*)^2} & \frac{-u^*}{a_1 + u^*} \\ \frac{b_1(v^*)^2}{(u^*)^2} & r_1 - \frac{2b_1(v^2)^*}{(u^2)^*} \end{pmatrix}.$$

Therefore,

$$J(1, 0) = \begin{pmatrix} -1 & \frac{-1}{a_1 + 1} \\ 0 & r_1 \end{pmatrix}.$$

The eigenvalues of this matrix are $\lambda_1 = -1$ and $\lambda_2 = r_1$, as we have a negative eigenvalue and a positive one, we can conclude that the trivial solution is a saddle point.

We can now use (2.18) and (2.19) to check the local asymptotic stability of the Holling-Tanner model. In this case we have

$$g(u) = \frac{u}{a_1 + u}, \quad f(u) = (1 - u).$$

This gives us the prey isocline

$$h(u) = v^* = \frac{uf(u)}{g(u)} = \frac{u(1-u)(a_1+u)}{u} = (1-u)(a_1+u),$$

which we differentiate to get

$$h'(u) = -2u - a_1 + 1.$$

If we substitute $h'(u)$ into (2.19) we obtain that

$$0 < \frac{r_1}{b_1} - ((1 - a_1) - 2u^*) = \frac{v^*}{u^*} - ((1 - a_1) - 2u^*).$$

Since $v^* = h(u^*)$ this can be rewritten as

$$\begin{aligned} \frac{(1 - u^*)(a_1 + u^*)}{u^*} - ((1 - a_1) - 2u^*) &= \frac{1}{u^*}[(1 - u^*)(a_1 + u^*) - u^*((1 - a_1) - 2u^*)] \\ &= \frac{1}{u^*}(a_1 + u^* + u^*a_1 - (u^*)^2 - u^* - a_1u^* + 2(u^*)^2) = \frac{1}{u^*}((u^*)^2 + a_1) = R(u^*) > 0. \end{aligned}$$

We can see that as by definition $a_1 > 0$ and $u^* > 0$ then $R(u^*)$ will always be satisfied. Similarly, by substituting $g(u)$ and $h'(u)$ into condition (2.18) we get the second condition for local stability

$$0 < r_1 - \frac{u^*(-2u^* + (1 - a_1))}{a_1 + u^*} = \frac{r_1(a_1 + u^*) + 2(u^*)^2 - (1 - a_1)u^*}{a_1 + u^*}, \quad (2.24)$$

i.e,

$$0 < 2(u^*)^2 + (a_1 + r_1 - 1)u^* + a_1r_1 = Q(u^*). \quad (2.25)$$

Since $R(u) > 0$ for all $u > 0$ we can see that our critical point is locally asymptotically stable if $Q(u^*) > 0$. A sufficient condition for the last inequality to be satisfied is

$$a_1 + r_1 \geq 1. \quad (2.26)$$

In the situation when $a_1 + r_1 < 1$ we can prove that $Q(u) > 0$ for all u if we can show that the discriminant is negative, as in that scenario the equation will have no real roots. We will require for

$$a_1 + r_1 < 1 \text{ and } (1 - a_1 - r_1)^2 - 8a_1r_1 \leq 0, \quad (2.27)$$

for our condition to be satisfied. For our critical point to be unstable we require that

$$a_1 + r_1 < 1 \text{ and } (1 - a_1 - r_1)^2 - 8a_1r_1 > 0.$$

We can factorize $Q(u)$ to get

$$Q(u) = 2(u - \alpha_1)(u - \alpha_2),$$

where

$$\begin{aligned} \alpha_1 &= \frac{1}{4} \left[1 - a_1 - r_1 - \sqrt{(1 - a_1 - r_1)^2 - 8a_1r_1} \right], \\ \alpha_2 &= \frac{1}{4} \left[1 - a_1 - r_1 + \sqrt{(1 - a_1 - r_1)^2 - 8a_1r_1} \right], \end{aligned} \quad (2.28)$$

$$0 < \alpha_1 < \alpha_2 < 1.$$

From here we can rewrite our stability conditions (2.26) and (2.27) to get that $Q(u) > 0$ if

$$0 < u^* < \alpha_1,$$

or

$$\alpha_2 < u^* < 1,$$

then the critical point is stable. Therefore for our critical point to be unstable we require that

$$\alpha_1 < u^* < \alpha_2.$$

If we now take the condition for global stability (2.22) when we apply the terms for the Holling-Tanner model we get

$$(u - u^*)((1 - u)(u + a_1) - v^*) < 0.$$

As you can see that this condition is dependent on the prey isocline for the Holling-Tanner model $h(u)(1 - u)(u + a_1)$. As

$$\frac{dh}{du} = -2u - a + 1,$$

this is monotone decreasing provided $a \geq 1$, hence in this case the critical point is globally asymptotically stable.

It is difficult to obtain any more information for non-trivial solutions as we have three parameters. However we can look for certain types of behaviours.

3.5 Hopf Bifurcation in Holling Tanner model

For our Holling Tanner model to have Hopf Bifurcation we need the trace of the Jacobian matrix linearised around the steady state to be equal to zero. If we take the Jacobian matrix (2.17), and substitute in our values for the Holling Tanner model we get

$$J(u^*, v^*) = \begin{pmatrix} \frac{(-2u^* - a_1 + 1)u^*}{a_1 + u^*} & \frac{-u^*}{a_1 + u^*} \\ \frac{r_1^2}{b_1} & -r_1 \end{pmatrix}$$

Therefore, if $\text{Tr}(J) = 0$, then

$$0 = \frac{(-2u - a_1 + 1)u}{u + a_1} - r_1,$$

$$r_1 = \frac{(-2u - a_1 + 1)u}{u + a_1}.$$

We can see that Hopf bifurcation is dependent on the growth rate parameter r_1 . We can rearrange this to get

$$0 = \frac{(2u + a_1 - 1)u}{u + a_1} + r_1 = 2u^2 + a_1u - u + r_1a_1 + r_1u = 2u^2 + (a_1 + r_1 - 1)u + r_1a_1,$$

then by applying the quadratic formula we get obtain the values for u where Hopf bifurcation occurs

$$u = \frac{1}{4} \left(1 - a_1 - r_1 \pm \sqrt{(a_1 + r_1 - 1)^2 - 8a_1r_1} \right).$$

We can see from here that if the determinant

$$(a_1 + r_1 - 1)^2 - 8a_1r_1 > 0$$

we get two bifurcation points, but if the determinant is negative then there exists no points of bifurcation. Therefore to get Hopf bifurcation we require that

$$0 < (1 - a_1 - r_1)^2 - 8a_1r_1 = a^2 + 2ar_1 - 2a_1 + r_1^2 - 2r_1 + 1 - 8a_1r_1 = r_1^2 + (-6a_1 - 2)r_1 + (a_1^2 - 2a_1 + 1).$$

So by applying the quadratic formula and considering only the positive result we get

$$r_1 < 1 + 3a_1 - 2\sqrt{2a_1 + 2a_1^2}.$$

Therefore Hopf bifurcation can only occur in the region defined by

$$\begin{aligned} 0 < r_1 < 1 + 3a_1 - 2\sqrt{2a_1 + 2a_1^2}, \\ 0 < a_1 < 1. \end{aligned} \tag{2.29}$$

This region is illustrated by the blue shaded area shown below 2.9, this result was also shown by Braza (2003) [2].

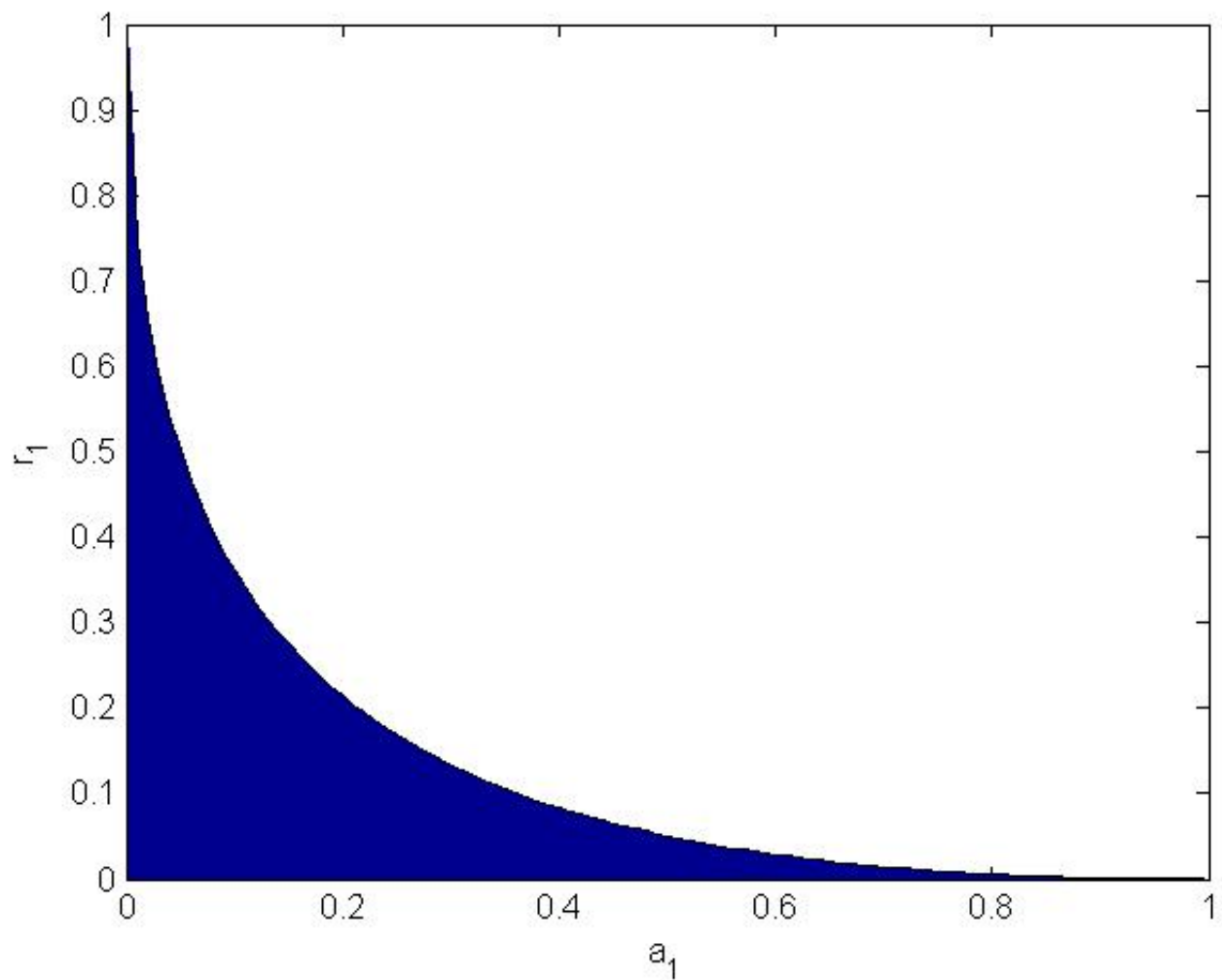


Figure 2.9: Region where Hopf bifurcation can occur. Inside the blue region we get two bifurcation points, outside it we get none.

Limit cycles

To look for Limit cycles in our Holling Tanner system we can transform our model into a Liénard system. Liénard systems are a class of differential equations which can be used to show the existence of stable limit cycles. Let G and F be defined by

$$G(u) = \int_0^u g(\epsilon) d\epsilon,$$

$$F(u) = \int_0^u f(\epsilon) d\epsilon,$$

then the Liénard system is described as

$$\frac{du}{dt} = v - F(u),$$

$$\frac{dv}{dt} = -g(u).$$

Then, the non-dimensionalised Holling-Tanner model we can be transformed into a Liénard system by rewriting it as

$$\frac{du}{d\tau} = f_0(u) - f_1(u)v, \tag{2.30}$$

$$\frac{dv}{d\tau} = g_0(u) + g_1(u)v + g_2(u)v^2,$$

where

$$f_0(u) = u(1 - u), \quad f_1(u) = \frac{u}{a_1 + u}, \quad g_0(u) = 0, \quad g_1(u) = r_1, \quad g_2(u) = -\frac{b_1}{u}. \tag{2.31}$$

Systems of the form (2.30) can be transformed into a Liénard system (see [20]) However, A.Gasull et.al [7] use the following lemma of Zegeing and Kooij [21], to transform the system into a simplified Liénard system.

Lemma 3.2 *Let $f_0(u), f_1(u), g_0(u), g_1(u), g_2(u)$ be a continuously differentiable function on the open interval (s_1, s_2) with $s_1 < 0 < s_2$ and $f_1(0) \neq 0$. Let $v = \psi(u)$ be a given orbit of the system (2.30) where $\psi(0) \neq 0$. Then the system can be transformed into the equivalent Liénard system:*

$$\frac{dx}{dt} = \phi v - \int_0^u \bar{f}(\tau) d\tau, \tag{2.32}$$

$$\frac{dy}{dt} = -\bar{g}(u),$$

where

$$\bar{g}(u) = [f_1(u)(g_1(u)\psi(u) + f_1(u)\psi'(u)) + g_2(u)f_0(u)]/f_1^2(u)\omega(u),$$

$$\bar{f}(u) = [f_0'(u)f_1(u) - f_1'(u)f_0(u) - f_1^2(u)\psi'(u) + g_2(u)f_0(u) - f_1(u)g_2(u)\psi(u)]/f_1^2(u)\omega(u), \tag{2.33}$$

$$\phi(u) = e^v + \gamma, \quad \gamma = [-f_0(0) + f_1(0)\psi(0)]/f_1(0)\omega(0),$$

where $\omega(u)$ satisfies

$$\frac{\omega'(u)}{\omega(u)} = -\frac{g_2(u)}{f_1(u)}.$$

See [21] for proof. Therefore, if we know a solution to $v = \psi(u)$ of our system (2.30) then we can use this simplified Liénard system. We have seen for the (2.15) that $v \equiv 0$ is a solution we can apply the transformation from (2.32)

$$v = \omega(u)e^z, \quad \frac{dt}{d\tau} = -\frac{1}{f_1(u)\omega(u)},$$

as $\omega(u)$ satisfies

$$\frac{\omega'(u)}{\omega(u)} = -\frac{g_2(u)}{f_1(u)},$$

when we substitute in the relevant terms from (2.31) we get

$$\frac{\omega'(u)}{\omega(u)} = \frac{b_1(a_1 + u)}{u^2}.$$

Therefore

$$\omega(u) = \exp\left(\int \frac{b_1 a_1}{u^2} du + \int \frac{b_1}{u} du\right) = \exp\left(\frac{-b_1 a_1}{u} + r_1 \ln u\right) = \exp\left(\frac{-b_1 a_1}{u}\right) \exp(\ln u^{r_1}),$$

so

$$\omega(u) = u^{b_1} \exp\left(-\frac{a_1 b_1}{u}\right).$$

By substituting (2.31) into (2.33) we get:

$$\phi(v) = e^z,$$

$$\begin{aligned} \bar{f}(u) &= \left(\frac{u - 2u^2}{a_1 + u} - \frac{a_1 u(1 - u)}{(a_1 + u)^2} - \left(\frac{u}{a_1 + u}\right)^2 \cdot 0 - \frac{b_1}{u} u(1 - u)\right) / \left(\frac{u}{r_1 + u}\right)^2 u^{b_1} \exp\left(\frac{-a_1 b_1}{u}\right) \\ &= \left(\frac{u - 2u^2}{a_1 + u} - \frac{a_1 u(1 - u)}{(a_1 + u)^2} - b_1(1 - u)\right) / \left(\frac{u}{a_1 + u}\right)^2 u^{b_1} \exp\left(\frac{-a_1 b_1}{u}\right) \\ &= f(u) u^{-2-b_1} \exp\left(\frac{a_1 b_1}{u}\right), \end{aligned}$$

where

$$f(u) = (1 - a_1)u^2 - 2u^3 - b_1(1 - u)(a_1 + u)^2.$$

Moreover, we have

$$\begin{aligned} \bar{g}(u) &= \left(\frac{ur_1}{a_1 + u} + b_1(1 - u)\right) / \left(\frac{u}{a_1 + u}\right)^2 u^{b_1} \exp\left(\frac{-a_1 b_1}{u}\right) \\ &= g(u) u^{-2-b_1} \exp\left(\frac{a_1 b_1}{u}\right), \end{aligned}$$

where

$$g(u) = (r_1 u - b_1(1 - u)(a_1 + u))(a_1 + u).$$

We now map our equilibrium point (u^*, v^*) from model (2.14) onto the equilibrium point for the system (2.32), where z^* satisfies

$$v^* = w(u^*)e^{z^*}.$$

The stability is determined by the sign of $-\bar{f}(u^*)$ which is equivalent to the sign of $-f(u^*)$. If we rearrange $g(u^*) = 0$ to solve b_1 we get

$$0 = r_1 u^* - b_1(1 - u^*)(a_1 + u^*),$$

hence

$$b = \frac{r_1 u^*}{(1 - u^*)(a_1 + u^*)}.$$

We can substitute this into $f(u)$ to get:

$$\begin{aligned} f(u^*) &= (1 - a_1)u^{*2} - 2u^{*3} - \frac{r_1(1 - u^*)(a_1 + u^*)^2}{(1 - u^*)(a_1 + u^*)} \\ &= u^*((1 - a_1)u^* - 2u^{*2} - r_1(a_1 + u^*)) \\ &= u^*(-2u^{*2} + (1 - a_1 - r_1)u^* - a_1 r_1) = -u^*Q(u^*), \end{aligned}$$

which defines the function

$$Q(u) = 2u^2 + (a_1 + r_1 - 1)u + a_1 r_1 \quad (2.34)$$

As you can see this is the same as the function (2.25) we derived when looking at the local stability of the critical points. Therefore if $Q(u) \geq 0$, then as the solution to our system is positive and bounded we can prove that there exists no limit cycles in the region by looking at the Dulac criterion. If we take the Dulac function defined by Hsu et. al. [10]

$$H(u, v) = \left(\frac{u}{(a_1 + u)} \right)^{-1} v^{-2}.$$

We can take

$$\frac{d(fH)}{du} = \frac{d}{du} \left[\frac{\left((a_1 + u)u - \frac{uv}{(a_1 + u)} \right)}{uv^2} \right] = \frac{1 - a_1 - 2u}{v^2},$$

$$\frac{d(gH)}{dv} = \frac{d}{dv} \left[\frac{\left((a_1 + u) \left(r_1 - \frac{b_1 v}{u} \right) \right)}{uv} \right] = -\frac{r_1(a_1 + u)}{uv^2}.$$

Hence

$$\frac{d(fH)}{du} + \frac{d(gH)}{dv} = -\frac{r_1}{uv^2} - \frac{(b_1 - a_1 + 1 - 2u)}{v^2} = \frac{H(u, v)}{a_1 + u}(-Q(u)),$$

therefore if $Q(u) \geq 0$ then there will be no non-trivial periodic solutions and the equilibrium will be globally asymptotically stable in the first quadrant. So if $r_1 \geq 1$ our system will not have limit cycles.

To look for limit cycles then, we require $Q(u)$ to have two positive roots $0 < \alpha_1 < \alpha_2 < 1$ as was shown by (2.28). By rearranging the inequality from (3.4) we obtain

$$0 < (1 - a_1 - r_1)^2 - 8a_1r_1 = a^2 + 2ar_1 - 2a_1 + r_1^2 - 2r_1 + 1 - 8a_1r_1 = r_1^2 + (-6a_1 - 2)r_1 + (a_1^2 - 2a_1 + 1).$$

As we can see this is the same condition required for Hopf bifurcation, and our limit cycles can only occur within the same region illustrated by the blue shaded area shown by figure 2.9. This result is to be expected as the limit cycle is generated by the Hopf bifurcation.

Chapter 3

Numerical analysis

Since it is not possible to solve many of the versions of the Lotka Volterra model analytically, it is necessary to use numerical schemes to approximate solutions to the problem. In this section we will first introduce several numerical methods for first order differential equations. Then, we will apply those methods to the Predator-Prey models discussed in the previous chapter. In addition, the numerical results will be compared with the analytical results proved previously. We will also use numerical method ode45 routine of MATLAB to investigate if the Holling-Tanner model displays the type of behaviour predicted for certain parameters.

1 Basics of numerical analysis

One-step and multi-step methods

There are two types of numerical analysis one-step methods and multi-step ones. One step methods express each iteration only in the terms of the previous one in other words y_{i+1} is expressed in terms of y_i all other past information is disregarded. Whereas multi-step methods retain the information from previous steps. Some methods such as the Runge Kutta method (see below for details) take an intermediate step by evaluating the function between y_{i+1} and y_i but then disregard previous information before calculating the next iteration.

Error analysis

To determine the accuracy of the results obtained by the approximations it is important to perform an error analysis. The global truncation error is defined as

$$e_i = |y(x_i) - y_i|,$$

where $y(x_i)$ is the analytical solution and y_i is the approximated solution.

The global error gives us the difference between the approximated solution and the analytical one. The local truncation error T_i gives us a measure of the error caused by one iteration. It is shown by Süli [17] to be calculated by the following equation

$$T_n = \frac{y(x_{n+i}) - y(x_i)}{h} - \Phi(x_i, y(x_i); i),$$

where $\Phi(x_i, y(x_i); i)$ is a continuous function of its variables.

Order of accuracy

The order of accuracy tells us how quickly the approximate solution converges to the exact solution as the step size tends towards 0. A numerical method is said to have an order of accuracy of p where p is the largest positive integer such that there exists for any sufficiently smooth curve a constants C and h_0 such that

$$|T_i| \leq Ch^p \quad \text{for } 0 < h < h_0$$

where h is the step size, T_i is the truncation error.

Experimental Order of Convergence

We will also look at the experimental order of convergence (EOC) defined as follows: for a given finite sequence of successive experiments i which correspond to time-steps h_i , the EOC of the corresponding sequences of errors is defined by

$$E.O.C = \log_2 \frac{|y(x_i) - y(x_{i/2})|}{|y(x_{i/2}) - y(x_{i/4})|}. \quad (3.1)$$

This method was developed by Olaf Runborg [16] and it is useful in the situation where it is not possible to calculate exact solutions. The E.O.C is the numerical measure of the rate of convergence as $h_n \rightarrow 0$, it is equal to the order of accuracy of the method. For the purposes of this paper we will be using the second method (3.1), and we will be using the the value of N_i calculated at the end point.

2 Numerical Methods

In this section we will look at the different methods of numerical analysis. Here we will only focus on explicit and semi-implicit methods.

Explicit Euler method

The explicit Euler method is a

$$t_i = ih, \quad i = 0, 1, 2, \dots, N$$

Now for each subsequent iteration the Euler equation is the simplest numerical scheme to approximate solutions of first order ODEs. Before we proceed with the description of the numerical methods, we need some notation. For $N \in \mathbb{N}$ let $0 = t^0 < t^1 < \dots < t^N = T$ be a partition of $[[0, T]$. and denote by h_n the step-size $h_n := t^n - t^{n-1}$. If the partition is uniform, then $h_n = h = T/N$ and

$$y_{i+1} = y_i + hf(t_i, y_i).$$

There are several issues with the basic Euler method, as each approximation of i is based on the previous approximation it can lead to the approximate solution diverging away from the exact solution for large values of i .

Symplectic Euler method

The symplectic Euler method is a semi-implicit modification of the Euler method (see [10]), it is applied by treating one variable as implicit and the other as explicit. Therefore if we have a system defined as

$$\frac{dx}{dt} = a(x, y),$$

$$\frac{dy}{dt} = b(x, y),$$

then the symplectic Euler method can be written as either

$$\begin{aligned}x_{i+1} &= x_i + ha(x_i, y_{i+1}), \\y_{i+1} &= y_i + hb(x_i, y_{i+1}),\end{aligned}$$

or as

$$\begin{aligned}x_{i+1} &= x_i + ha(x_{i+1}, y_i), \\y_{i+1} &= y_i + hb(x_{i+1}, y_i).\end{aligned}\tag{3.2}$$

Runge-Kutta Methods

Runge-Kutta methods aim to improve the accuracy of the approximation by re-evaluating the function at points between the iterations of $(x_i, y(x_i))$ and $(x_{i+1}, y(x_{i+1}))$

4th Order Runge-Kutta method

The 4th order Runge-Kutta method is one of the most often used variations of the Runge-Kutta methods:

$$\left\{ \begin{aligned}k_1 &= f(x_i, y_i), \\k_2 &= f\left(x_i + \frac{1}{2}h, y_i + \frac{1}{2}hk_1\right), \\k_3 &= f\left(x_i + \frac{1}{2}h, y_i + \frac{1}{2}hk_2\right), \\k_4 &= f(x_i + h, y_i + hk_3). \\y_{i+1} &= y_i + \frac{1}{6}h(k_1 + 2k_2 + 2k_3 + k_4),\end{aligned} \right.$$

As the name suggest this method has an order of accuracy of 4, making it much more accurate than the basic Euler method, but due to the increased amount of calculations it has a greater computational cost.

Ode45

Ode45 is a matlab code which applies a modified mix between a 4th and 5th order Runge Kutta method

Definition 2.1 (Butcher Tableau) *A mnemonic device giving the coefficients (a_{ij}), weights (b_i) and nodes (c_i) for a particular Runge Kutta method. If we have s number of stages it takes the form shown below.*

0						
c_1	a_{21}					
c_2	a_{31}	a_{32}				
\vdots	\vdots					
c_s	a_{s1}	a_{s2}	\dots	$a_{s,s-1}$		
	b_1	\dots		b_s		

For ode45 we obtain the Butcher tableau shown below.

0								
$1/5$	$1/5$							
$3/10$	$3/40$	$9/40$						
$4/5$	$44/44$	$-56/15$	$32/9$					
$8/9$	$19372/6561$	$-25360/2187$	$64448/6561$	$-212/729$				
1	$9017/3168$	$-355/33 * 46732/5247$	$49/176$	$-5103/18656$				
1	$35/384$	0	$500/1113$	$125/192$	$-2187/6784$	$11/84$		
	$35/384$	0	$500/1113$	$125/192$	$-2187/6784$	$11/84$	0	
	$5179/576000$	0	$7571/16695$	$393/640$	$-92097//339200$	$187/2100$	$1/40$	

A particularly useful feature of ode45 is its use of adaptivity which sets the step size depending on the rate of change of the equation, the smaller the rate of change is the larger the step size is, this helps to maximize the efficiency of the method and to minimize the computational cost.

Differential Transformation Method

The differential transformation method (DTM) is a semi-numerical analytical method which approximates solutions using polynomials. We consider the initial value problem for the system of ODEs

$$\begin{aligned}
 x'_1(t) &= f_1(t, x_1, x_2, \dots, x_i), \\
 x'_2(t) &= f_2(t, x_1, x_2, \dots, x_i), \\
 &\vdots \\
 x'_i(t) &= f_i(t, x_1, x_2, \dots, x_i),
 \end{aligned}
 \tag{3.3}$$

which subjects to the initial conditions

$$x_i(t_0) = c_i, \quad i = 1, 2, \dots, n.$$

If we have the interval $[t_0, T]$ over which we find the solution to our initial value problem then when we apply the differential transformation method the K th-order solution can be expressed by the finite series

$$x_i(t) = \sum_{k=0}^K X_i(k)(t - t_0)^k, \quad t \in [t_0, T], i = 1, 2, \dots, n,$$

where

$$X_i(k) = \frac{1}{k!} \left[\frac{d^k X_i(t)}{dt^k} \right]_{t=t_0}, \quad i = 1, 2, \dots, n.$$

To implement the DTM we first apply the differential transform which will give us a recurrence relation, we then apply the inverse transformation to the solution of the recurrence relation will give us our solution. To help with the process of transforming the function we consult a table of operations.

Original function $x(t)$	Transformed function $X(k)$
$x(t) = u(t) \pm v(t)$	$X(k) = U(k) \pm V(k)$
$x(t) = cu(t)$	$X(k) = cU(k)$
$x(t) = u(t)v(t)$	$X(k) = \sum_{k_1=0}^k V(k_1)U(k - k_1)$
$f(t) = \frac{du(t)}{dt}$	$X(k) = (k + 1)U(k + 1)$
$x(t) = \frac{d^n u(t)}{dt^n}$	$x(k) = (k + 1)(k + 2)\dots(k + n)U(k + n)$
$x(t) = \int_{t_0}^t u(x)dx$	$X(k) = \frac{U(k - 1)}{k}, k \geq 1,$
$x(t) = t^n$	$X(k) = \delta(k - n) = \begin{cases} 1 & k = n \\ 0 & k \neq n \end{cases}$
$x(t) = \exp(\lambda t)$	$X(k) = \frac{\lambda^k}{k!}$

By using these operators we have the recurrence relation

$$(k + 1)X_i(k + 1) = F_i(k, X_1, X_2, \dots, X_n), \quad X_i(0) = c_i, \quad i = 1, 2, \dots, n,$$

where $F_i(k, X_1, X_2, \dots, X_n)$ is the differential transform of the function $f_i(t, x_1, x_2, \dots, x_n)$, for $i = 1, 2, \dots, n$.

The DTM is a useful tool for solving ordinary and partial differential equations as well as integrals. It provides the solution as a convergent series with easily computable components. However, there are disadvantages, the series solution given does not show the real behaviour of the problem it only approximates the solution over a small region, over a larger region it has a slow rate of convergence or may actually diverge. However a multi-step DTM which improves the accuracy and accelerates the convergence of the series solution over a large region. To apply the multi-step DTM we divide our interval $[t_0, T]$ into M sub-intervals $[t_{m-1}, t_m]$, $m = 1, 2, \dots, M$ with equal length step size $h = (T - t_0)/M$ by using the nodes $t_m = t_0 + mh$. We first apply the DTM to our initial value problem (3.3) over the interval $[t_0, t_1]$ to obtain the approximate solution

$$x_{i,1}(t) = \sum_{k=0}^K X_{i,1}(k)(t - t_0)^k, \quad t \in [t_0, t_1], \tag{3.4}$$

with the initial conditions $x_i(t_0) = c_i$. When $m \geq 2$ at each sub-interval we will use the initial condition $x_{i,m}(t_{m-1}) = x_{i,m-1}(t_{m-1})$ and again apply the DTM to our initial value problem (3.3),

over the interval $[t_{m-1}, t_m]$, this process is repeated to generate a sequence of approximate solutions $x_{i,m}(t)$, $m = 1, \dots, M$, $i = 1, \dots, n$ for the solutions of $x_i(t)$

$$x_{i,m}(t) = \sum_{k=0}^K X_{i,m}(k)(t - t_0)^k, \quad t \in [t_{m-1}, t_m].$$

This gives us the following solution

$$x_i(t) = \begin{cases} x_{i,1}, & [t_0, t_1], \\ x_{i,2}, & [t_1, t_2], \\ \vdots & \\ x_{i,M}, & [t_{M-1}, t_M], \end{cases}$$

where $i = 1, 2, \dots, n$.

This method of applying the multi-step DTM was shown by El-Zahar [4].

Application of DTM to the Lotka Volterra model

We apply the relevant transformations from our table to both sides of our basic Lotka Volterra equation

$$\frac{dN}{dt} = N(t)(a - bP(t)) = aN(t) - bP(t)N(t), \tag{3.5}$$

$$\frac{dP}{dt} = P(t)(cN(t) - d) = -dP(t) + cN(t)P(t),$$

with the initial conditions $N(0) = c_N$ and $P(0) = c_P$. We obtain the system

$$(k + 1)\dot{N}(k + 1) = a\dot{N}(k) - b \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k - k_1), \tag{3.6}$$

$$(k + 1)\dot{P}(k + 1) = -d\dot{P}(k) + c \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k - k_1),$$

which can be rearranged to

$$\dot{N}(k + 1) = \frac{1}{k + 1} \left(a\dot{N}(k) - b \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k - k_1) \right), \tag{3.7}$$

$$\dot{P}(k + 1) = \frac{1}{k + 1} \left(-d\dot{P}(k) + c \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k - k_1) \right),$$

where $\dot{P}(k)$ and $\dot{N}(k)$ are the transforms of $P(t)$ and $N(t)$ respectively. With the initial conditions of $\dot{N}(0) = c_N$ and $\dot{P}(0) = c_P$. The series solution for our system is then given by:

$$\begin{cases} N(t) = \sum_{j=0}^J \dot{N}(j)t^j, \\ P(t) = \sum_{j=0}^J \dot{P}(j)t^j. \end{cases}$$

If we expand this result over the multi-step DTM we get:

$$N(t) = \begin{cases} \sum_{j=0}^J \dot{N}_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J \dot{N}_2(j)(t - t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J \dot{N}_M(j)(t - t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.8)$$

$$P(t) = \begin{cases} \sum_{j=0}^J \dot{P}_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J \dot{P}_2(j)(t - t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J \dot{P}_M(j)(t - t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.9)$$

where for all $i = 1, 2, \dots, M$ $\dot{N}_i(j)$ and $\dot{P}_i(j)$ satisfy the below recurrence relations ,

$$\begin{cases} \dot{N}_i(k+1) = \frac{1}{k+1} (a\dot{N}_i(k) - b \sum_{l=0}^k \dot{N}_i(l)\dot{P}_i(k-l)), \\ \dot{P}_i(k+1) = \frac{1}{k+1} (-d\dot{P}_i(k) + c \sum_{l=0}^k \dot{N}_i(l)\dot{P}_i(k-l)), \end{cases} \quad (3.10)$$

such that $\dot{N}_i(0) = \dot{N}_{i-1}(0)$ and $\dot{P}_i(0) = \dot{P}_{i-1}(0)$. By using the initial points $\dot{N}_0 = c_N$ and $\dot{P}_0 = c_P$ and the recurrence relations we can obtain the multi step solution.

Application of DTM to the Lotka Volterra model with a bounded prey equation

If we apply the DTM to the Lotka Volterra model with a bounded prey equation (1.11) we get

$$\begin{aligned} \dot{N}(k+1) &= \frac{1}{k+1} (a\dot{N}(k) - \frac{a}{K} \sum_{k_1=0}^k \dot{N}(k_1)\dot{N}(k-k_1) - \frac{ab}{K} \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k-k_1)), \\ \dot{P}(k+1) &= \frac{1}{k+1} (-d\dot{P}(k) + c \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k-k_1)), \end{aligned} \quad (3.11)$$

We can expand this to a multi-step method in the same way as before,

$$N(t) = \begin{cases} \sum_{j=0}^J \dot{N}_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J \dot{N}_2(j)(t - t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J \dot{N}_M(j)(t - t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.12)$$

$$P(t) = \begin{cases} \sum_{j=0}^J \dot{P}_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J \dot{P}_2(j)(t - t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J \dot{P}_M(j)(t - t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.13)$$

where for all $i = 1, 2, \dots, M$ $\dot{N}_i(j)$ and $\dot{P}_i(j)$ satisfy the below recurrence relations ,

$$\begin{cases} \dot{N}(k+1) = \frac{1}{k+1} (a\dot{N}(k) - \frac{a}{K} \sum_{k_1=0}^k \dot{N}(k_1)\dot{N}(k-k_1) - \frac{ab}{K} \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k-k_1)), \\ \dot{P}(k+1) = \frac{1}{k+1} (-d\dot{P}(k) + c \sum_{k_1=0}^k \dot{N}(k_1)\dot{P}(k-k_1)), \end{cases} \quad (3.14)$$

Application of DTM to the Holling-Tanner model

To apply DTM to the Holling tanner model we will use the work of Gökdoğan and Merdan [9] as a basis, he applied the method to a modified Holling-Tanner model which altered the type two functional response to ratio dependent one. To transform our model we are required to introduce a new transformation. If

$$f'(t) = \frac{g(x(t), y(t))}{ax(t) + by(t) + c}, \quad (3.15)$$

then,

$$F(t+1) = \left[G(X(k), Y(k)) - a \sum_{l=1}^k (k - k_1 + 1) X(k_1) F(k - k_1 + 1) - b \sum_{k_1=1}^k (k - k_1 + 1) Y(k_1) F(k - k_1 + 1) \right] / (aX(0) + bY(0) + c)(k+1). \quad (3.16)$$

To simplify matters we will use our non-dimensionalised Holling Tanner model (2.14), which we will need to rewrite in the form of (3.15).

$$\frac{du}{d\tau} = \frac{(1-a)u^2 + au - u^3 - uv}{a+u}, \quad (3.17)$$

$$\frac{dv}{d\tau} = \frac{r_1 uv - bv^2}{u}. \quad (3.18)$$

If we first look at (3.17) we can see that $G(u, v) = -au^2 + au - u^3 + u^2 - uv$ so by applying our transform (3.16) and the other relevant transforms from our table we get,

$$U(k+1) = \left[U(k) + (1-a) \sum_{k_1=0}^k U(k_1)U(k-k_1) - \sum_{k_2=0}^k \sum_{k_1=0}^k U(k_1)U(k_2-k_1)U(k-k_2) \right. \\ \left. - \sum_{k_1=0}^k U(k_1)V(k-k_1) - \sum_{k_1=1}^k (k-k_1+1)U(k_1)U(k-k_1+1) \right] / (U(0) + a)(k+1).$$

If we do the same thing for our predator model (3.18) where $G(u, v) = r_1 uv - bv^2$ we get

$$V(k+1) = \frac{r_1 \sum_{k_1=0}^k U(k_1)V(k-k_1) - b \sum_{k_1=0}^k V(k)V(k-k_1) - \sum_{k_1=1}^k U(k_1)V(k-k_1+1)}{U(0)(k+1)}$$

Like before we can expand this result over the multi-step DTM we get:

$$u(t) = \begin{cases} \sum_{j=0}^J U_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J U_2(j)(t-t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J U_M(j)(t-t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.19)$$

$$v(t) = \begin{cases} \sum_{j=0}^J V_1(j)t^j, & t \in [0, t_1] \\ \sum_{j=0}^J V_2(j)(t-t_1)^j, & t \in [t_1, t_2] \\ \vdots \\ \sum_{j=0}^J V_M(j)(t-t_{M-1})^j, & t \in [t_{M-1}, t_M] \end{cases} \quad (3.20)$$

where for all $i = 1, 2, \dots, M$ $U_i(j)$ and $V_i(j)$ satisfy the below recurrence relations ,

$$\left\{ \begin{array}{l} U(k+1) = \left[U(k) + (1-a) \sum_{k_1=0}^k U(k_1)U(k-k_1) - \sum_{k_2=0}^k \sum_{k_1=0}^k U(k_1)U(k_2-k_1)U(k-k_2) \right. \\ \quad \left. - \sum_{k_1=0}^k U(k_1)V(k-k_1) - \sum_{k_1=1}^k (k-k_1+1)U(k_1)U(k-k_1+1) \right] / (U(0) + a)(k+1). \\ \\ V(k+1) = \frac{r_1 \sum_{k_1=0}^k U(k_1)V(k-k_1) - b \sum_{k_1=0}^k V(k)V(k-k_1) - \sum_{k_1=1}^k U(k_1)V(k-k_1+1)}{U(0)(k+1)} \end{array} \right. \quad (3.21)$$

such that $U_i(0) = U_{i-1}(0)$ and $V_i(0) = V_{i-1}(0)$. By using the initial points $U_0 = c_u$ and $V_0 = c_v$ and the recurrence relations we can obtain the multi step solution.

3 Application of numerical methods to the Lotka-Volterra model

In this section we will be applying several numerical methods to the Lotka-Volterra system (1.8). We will be using the initial conditions of $u_0 = 2$ and $v_0 = 2$ and the parameters used by Hairer et al. [10] $a = b = c = 1$ and $d = 2$ throughout, giving us a system

$$\begin{aligned}\frac{dN}{dt} &= N(1 - P), \\ \frac{dP}{dt} &= P(N - 2).\end{aligned}\tag{3.22}$$

As we know the parameters we don't need to non-dimensionalise our system for analysis. Our system has critical points when

$$0 = N(1 - P),$$

$$0 = P(N - 2),$$

therefore we have a non-trivial critical point at $(N^*, P^*) = (2, 1)$. We can analyse this critical point by looking at the Jacobian matrix

$$J = \begin{pmatrix} 1 - P & -N \\ P & N - 2 \end{pmatrix},$$

and calculating the eigenvalues at $(N^*, P^*) = (2, 1)$,

$$\det|J(2, 1) - \lambda I| = \begin{vmatrix} -\lambda & -2 \\ 1 & -\lambda \end{vmatrix} = 0,$$

therefore

$$\lambda^2 + 2 = 0.$$

This gives us the eigenvalues $\lambda_{1,2} = \pm\sqrt{2}$ therefore as expected from our analysis of the non-dimensionalised Lotka Volterra model we get a centre singularity. The trajectory equation for the system is given by

$$\frac{dP}{dN} = \frac{P(N - 2)}{N(1 - P)}.$$

We can separate the variables and integrate to obtain the solution

$$H = N + P - \ln|N^2 P|,$$

where H is defined by the initial conditions. As our initial conditions are $u_0 = 2$ and $v_0 = 2$ we get $H = 1.920558458$.

Application of Explicit Euler method to the Lotka-Volterra model

We apply the explicit Euler method to our Lotka-Volterra model (3.22) using

$$N(t_{i+1}) = N(t_i) + hN(t_i)(1 - P(t_i)),$$

$$P(t_{i+1}) = P(t_i) + hP(t_i)(N(t_i) - 2).$$

We implemented Explicit Euler in Matlab using the initial conditions $u_0 = 2$ and $v_0 = 2$. In 3.1, we can see the approximate solution given by Euler method for $h = 0.05$ and over a period of time of $t = 30$ and the exact solution.

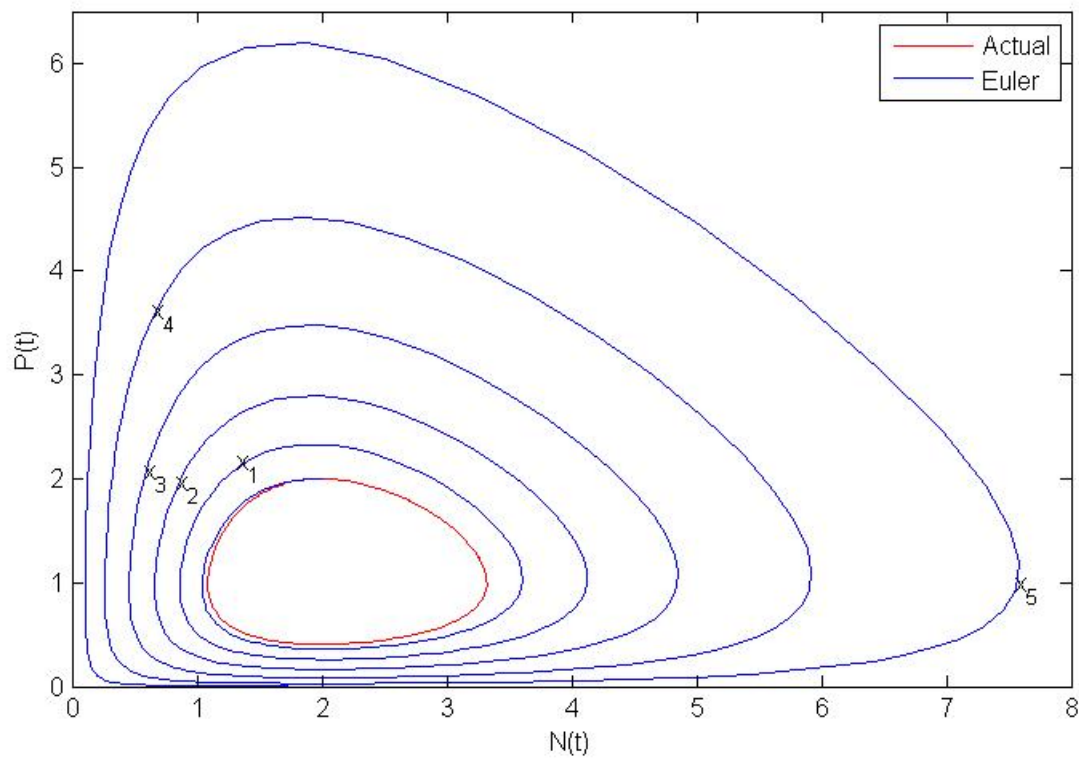


Figure 3.1: Phase plane for system (3.22) when applying the Euler method with $h = 0.05$ and initial conditions $u_0 = 2$ and $v_0 = 2$

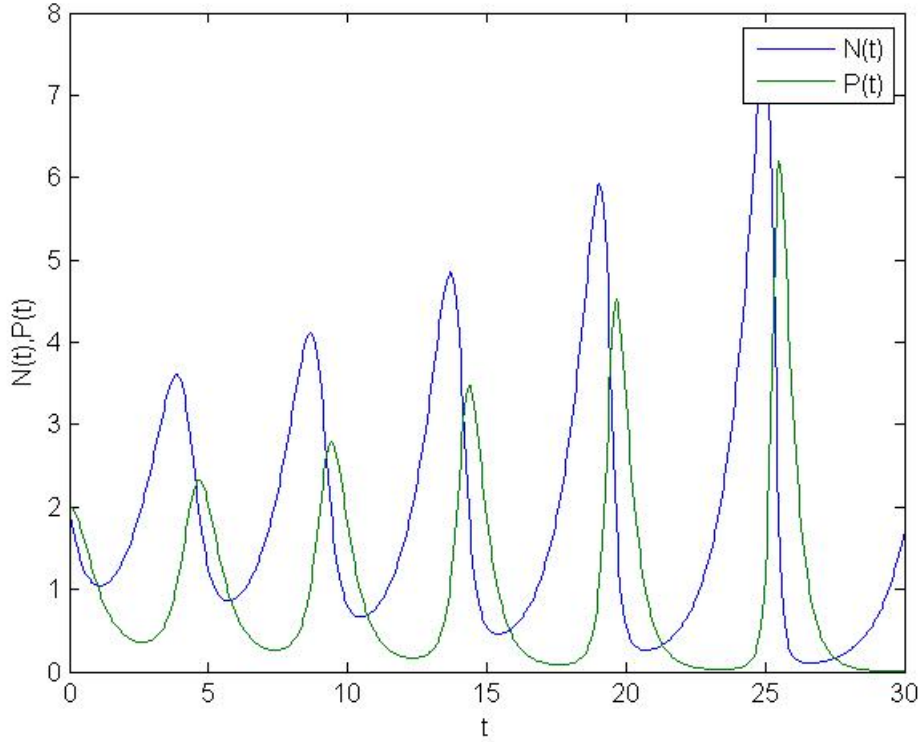


Figure 3.2: Oscillations in population sizes of N and P

As you can see from figure (3.2) when we apply the Euler method our solutions lack the closed trajectory which is expected from our analytically analysis and it diverges away from the singular point, giving us the increasing oscillations shown by figure 3.1 instead of consistent ones expected. We can reduce the amount of divergence by using smaller step sizes. We can calculate the E.O.C evaluated at the last time step $t = 30$ to obtain the results shown in table 3.1. The results show that it converges to one, which is expected as the explicit Euler method is a first order method.

Table 3.1: E.O.C for explicit Euler method

N_i	Step Size	E.O.C
1.70317240694349	0.0002	1.004524
1.7074507731644	0.0001	1.002272
1.70958325942551	0.00005	1.001139
1.71064782445216	0.000025	1.00057
1.71117968695766	0.0000125	1.000285
1.71144551314872	0.00000625	1.000143
1.7115783999715	0.000003125	
1.711644837	0.0000015625	

Application of the Symplectic Euler method

If we apply the Symplectic Euler method 3.2 where $N(t)$ is implicit and $P(t)$ is explicit we obtain the system

$$N(t_{i+1}) = N(t_i) + h[N(t_{i+1})(1 - P(t_i))],$$

$$P(t_{i+1}) = P(t_i) + h[P(t_i)(N(t_{i+1}) - 2)].$$

In order to implement this system we need to rearrange $N(t_{i+1})$ so

$$N(t_{i+1}) - hN(t_{i+1})(1 - P(t_i)) = N(t_i),$$

$$P(t_{i+1}) = P(t_i) + h[P(t_i)(N(t_{i+1}) - 2)],$$

therefore we get the system

$$N(t_{i+1}) = \frac{N(t_i)}{1 - h(1 - P(t_i))},$$

$$P(t_{i+1}) = P(t_i) + h[P(t_i)(N(t_{i+1}) - 2)].$$

Implementing this using matlab with the same step size as before we get

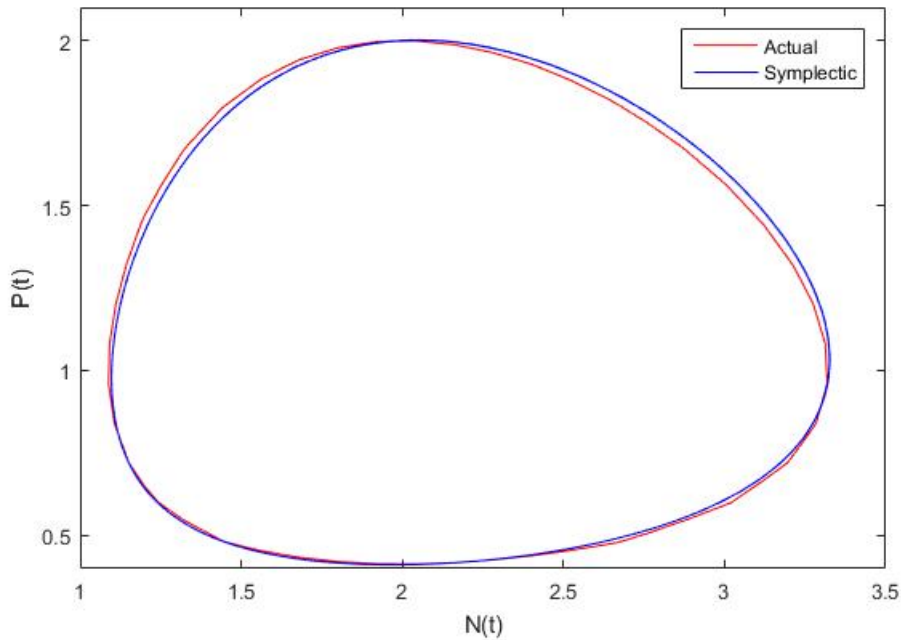


Figure 3.3: Phase plane for system (3.22) when applying the Symplectic Euler method with $h = 0.05$ and initial conditions $u_0 = 2$ and $v_0 = 2$

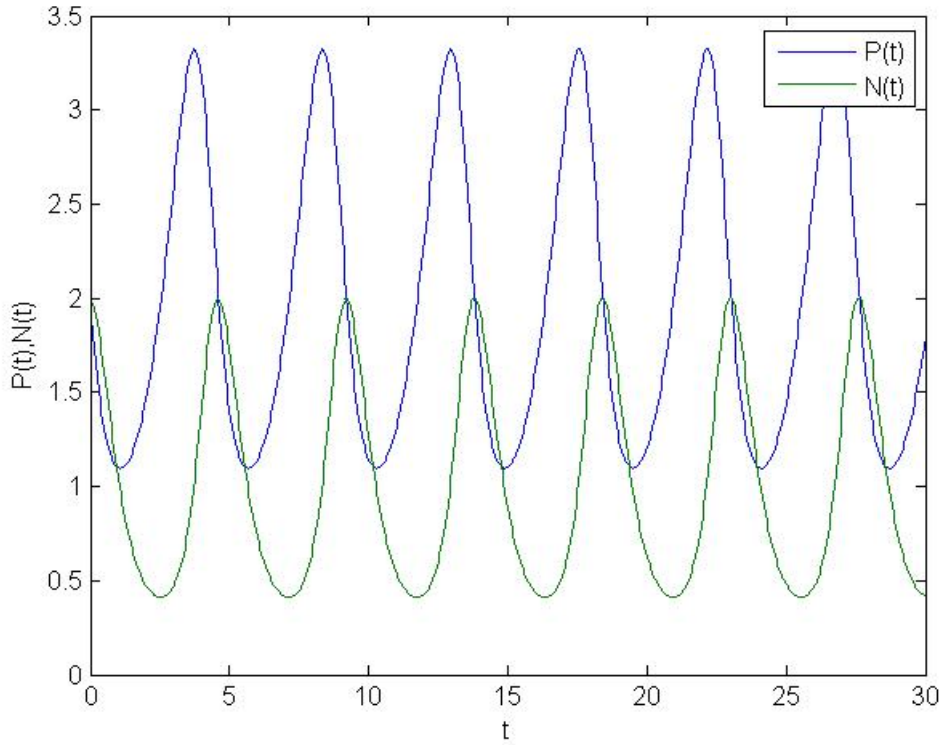


Figure 3.4: Oscillations in population sizes of N and P

From figure 3.3 we can see that the approximate solution calculated using the symplectic Euler method has a closed trajectory as expected from our analysis. Note that the closed trajectory of the approximate solution is very close to the one that the exact solution has. Figure 3.4 shows the population sizes repeating over time. By calculating the corresponding EOC at the last time step $t = 30$ we can see that the Symplectic Euler method is first order accurate, see table 3.2.

Table 3.2: E.O.C for symplectic Euler method

N_i	Step Size	E.O.C
2.2214678936924	0.2	1.444259406
1.91548874804142	0.1	1.226282
1.80304730129942	0.05	1.11375
1.75498786555181	0.025	1.057052
1.73278001443471	0.0125	1.028578
1.72210662751385	0.00625	1.014303
1.71687460626475	0.003125	1.007155
1.714284403	0.0015625	1.003579
1.712995709	0.00078125	
1.712352958	0.000390625	

Application of 4th order Runge Kutta method to the Lotka-Volterra model

If we implement the 4th order Runge Kutta method using matlab we obtain

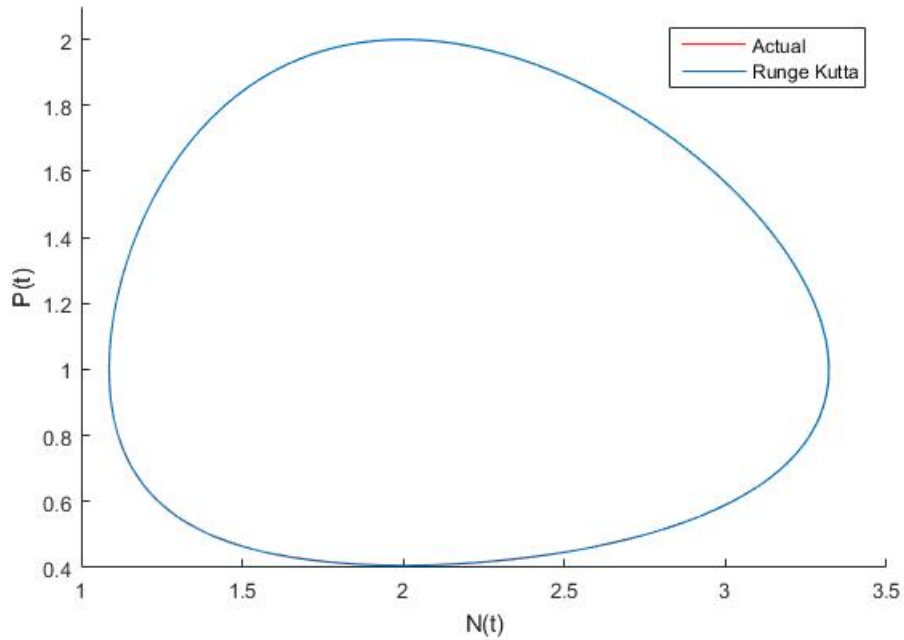


Figure 3.5: Phase plane for system (3.22) when applying the 4th order Runge Kutta method with $h = 0.05$ and initial conditions $u_0 = 2$ and $v_0 = 2$

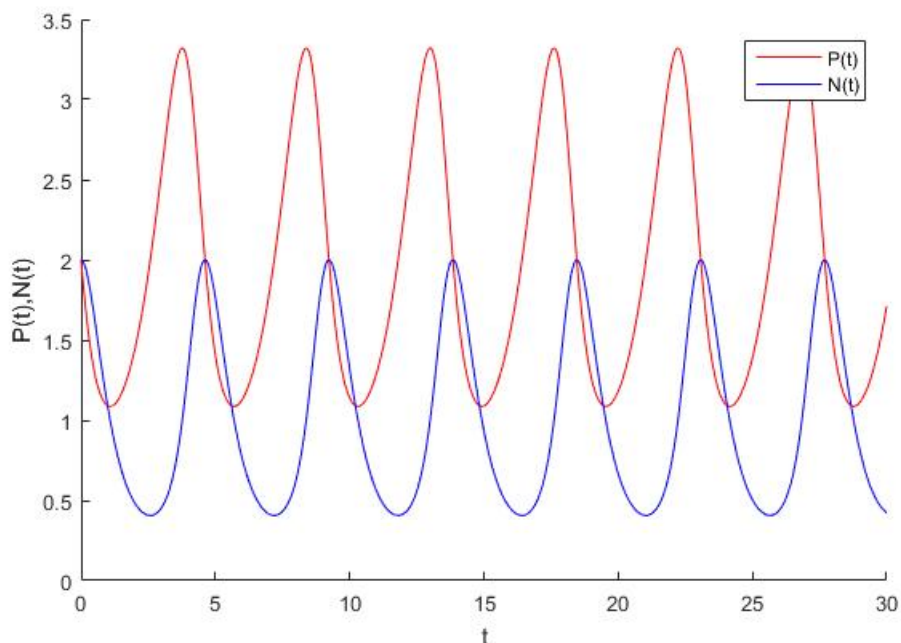


Figure 3.6: Oscillations in population sizes of N and P

Table 3.3: E.O.C for Runge Kutta

N_i	Step Size	E.O.C
1.71077297600439	0.2	3.588111
1.71163431095166	0.1	3.844004
1.71170593239339	0.05	3.930672
1.71171091989022	0.025	3.967187
1.7117112469541	0.0125	3.984011
1.7117112678659	0.00625	3.991586
1.7117112691874	0.003125	
1.7117112692705	0.0015625	

From figure 3.5 we can see that we have the expected closed trajectory, and figure 3.6 shows the population sizes repeating over time. When we calculate the E.O.C we can see that it converges to 4 as is expected for a fourth order method.

3.1 Comparison of results

Looking at our previous results we have used the E.O.C to validate that our matlab models are functioning correctly as they all converge to the expected outcomes. Out of the three methods the explicit Euler gives the least accurate approximations and we had to start from a much smaller step size as matlab could not calculate a solution for step sizes as large as 0.2. Both the Runge Kutta and the Symplectic Euler method displayed the expected behaviour of a continuous trajectory, but comparison of the results show that the Runge Kutta converges at a more rapid rate than the symplectic Euler, this is to be expected as it is of a higher order of accuracy.

4 Proof of analytical results for Holling-Tanner model

In this section we will apply ode45 to our Holling-Tanner model with various parameters to quantify the expected quantitative behaviour shown in the previous chapter. We first consider a Holling-Tanner model with a time interval of 200, initial values of $u(0) = 0.7$, $v(0) = 0.6$ and parameters $a = 0.3$, $r_1 = 0.1$ and $b = 0.05$ we obtain the below phase portrait.

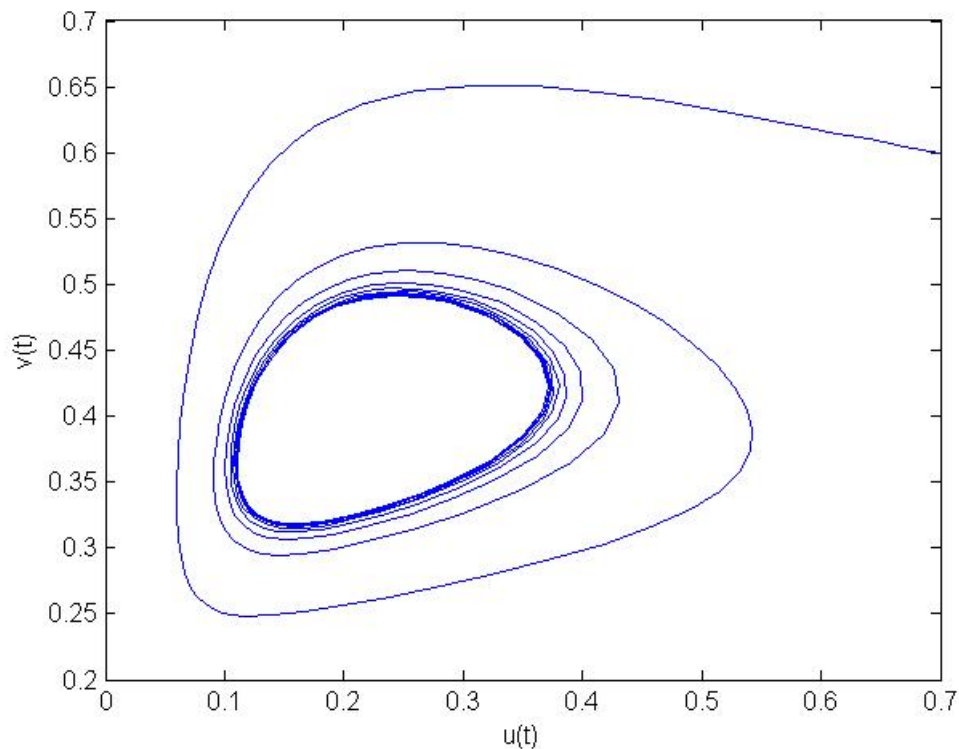


Figure 3.7: System (2.14) with $a = 0.3$, $r_1 = 0.1$, $b = 0.05$

We can see that we obtain a stable limit cycle around the non-trivial singular point $(u^*, v^*) = (0.2, 0.4)$. The existence of a limit cycle is the expected result as our parameters a and r_1 lie within the region shown by 2.9 i.e $0 < a < 1$ and $0 < r_1 < 1 + 3a - 2\sqrt{2a + 2a^2}$. If we consider the stability conditions from (2.27) that $a + r_1 = 0.4 < 1$ and $(1 - a - r_1)^2 - 8ar_1 \leq 0$ therefore this stability is expected. We can see from 3.8 that the populations oscillate between two stable limit cycles.

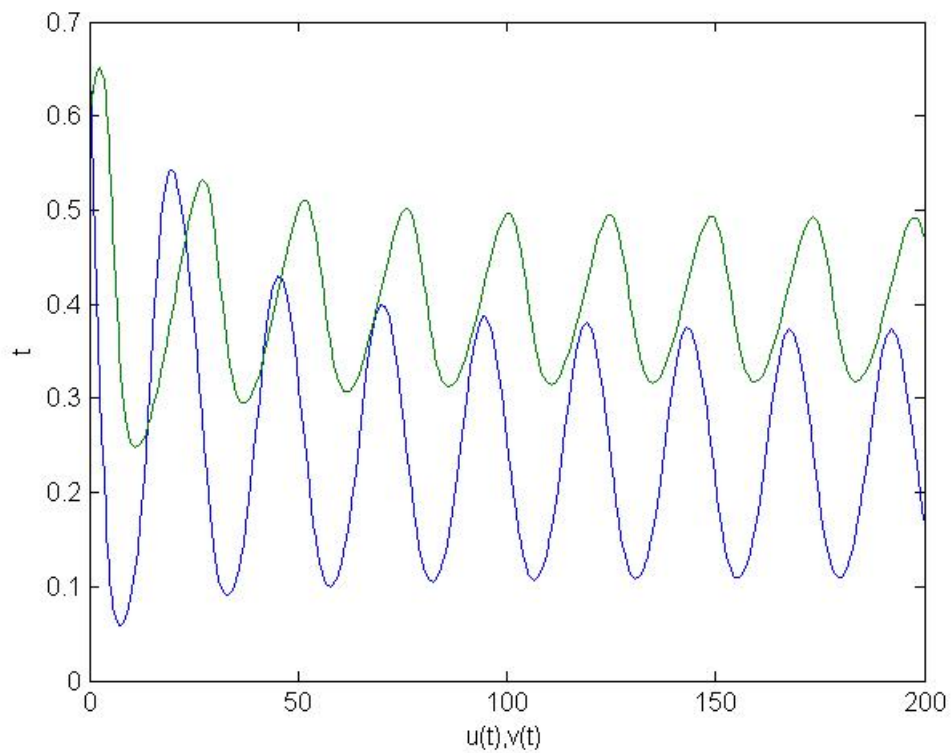


Figure 3.8: Stable limit cycles of system (2.14) with $a = 0.3$, $r_1 = 0.1$, $b = 0.05$

It doesn't matter what the initial conditions are the results will also spiral towards the limit cycle even if the initial conditions lie within the limit cycles, this is illustrated below with initial conditions of $u_0 = 0.25$ and $v_0 = 0.43$.

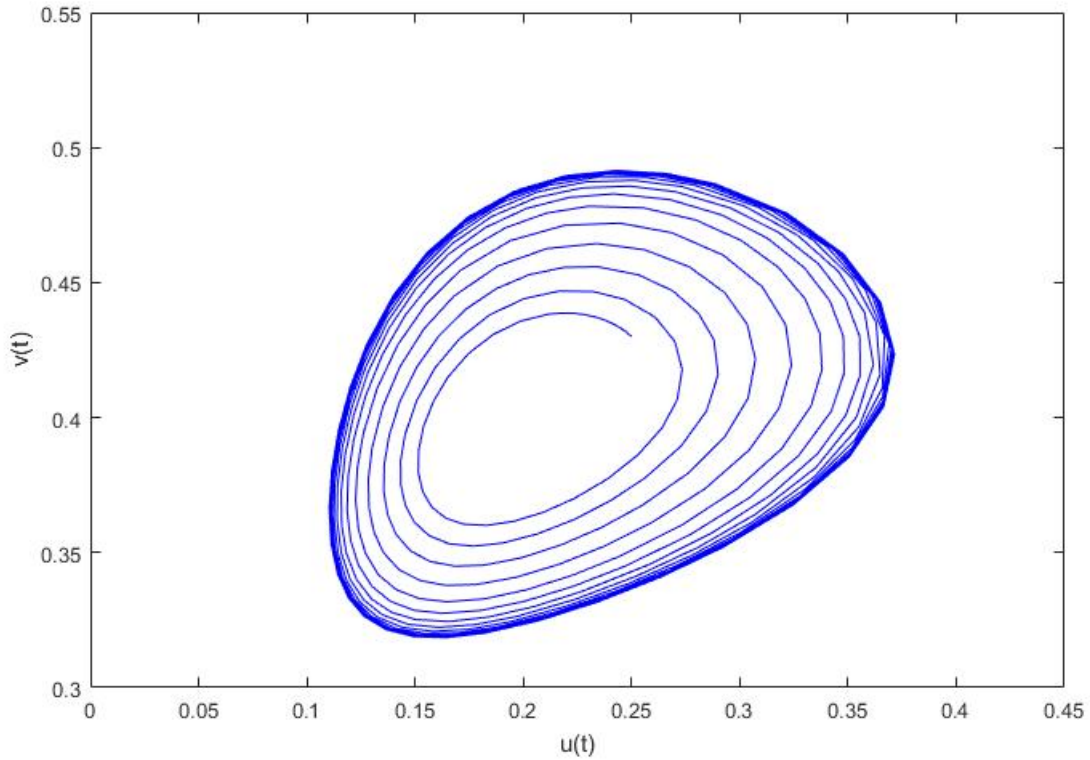


Figure 3.9: Stable limit cycles of system (2.14) with $a = 0.3$, $r_1 = 0.1$, $b = 0.05$ with $u_0 = 0.25$ and $v_0 = 0.43$

In another example if we keep our initial conditions but change our parameters to those used in an example by Gasull et. al [7] which are $a = 0.2$, $r_1 = 0.2$ and $b = 0.0682$ and our time interval to 2000. Here the r parameter lies outside the region required for limit cycles and by considering the stability conditions from (2.28) we can see that for our parameters $\alpha_1 = 0.1$ $0 < u^* < \alpha_1$ therefore we expect our solution to be asymptotically stable and that it will cycle towards the non-negative non-trivial singular point. $(u^*, v^*) = (0.0899872, 0.2638920821)$. These expected results are supported by the numerical analysis as is shown below.

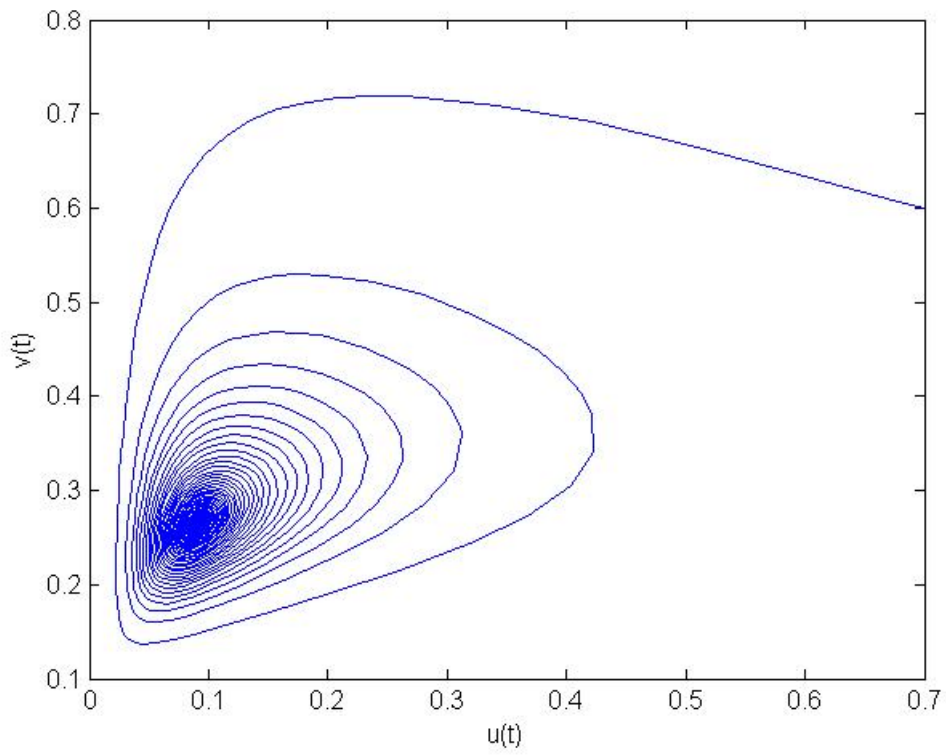


Figure 3.10: System (2.14)
with $a = 0.2$, $r_1 = 0.2$, $b = 0.0682$

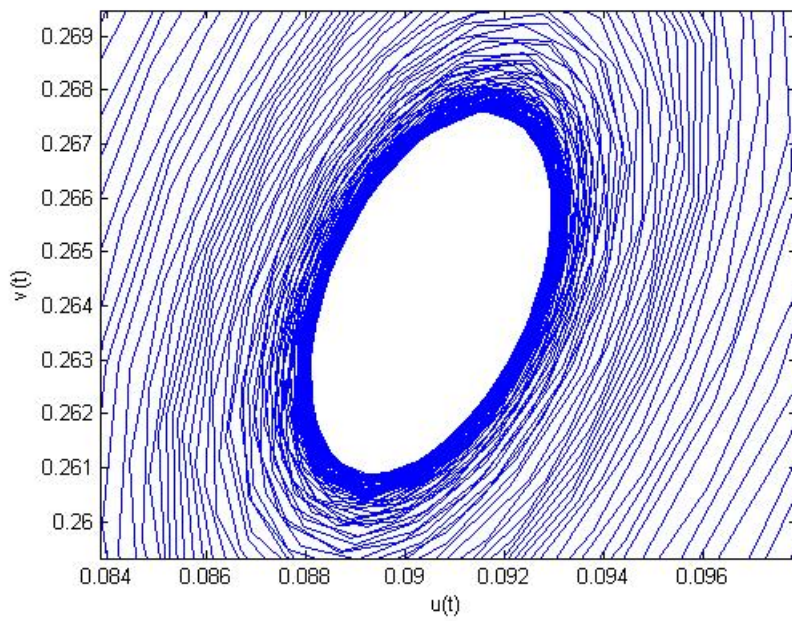


Figure 3.11: Close up of singular point of system (2.14) with $a = 0.2$, $r_1 = 0.2$, $b = 0.0682$

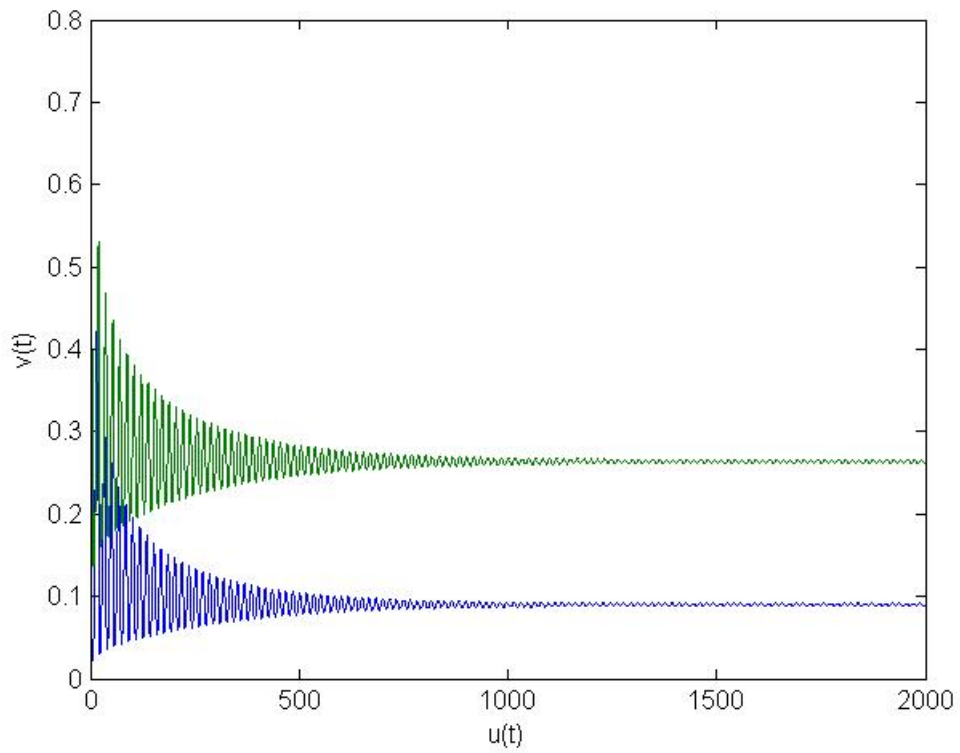


Figure 3.12: Plot showing populations converging towards singular point with $a = 0.2$, $r_1 = 0.2$, $b = 0.0682$

Throughout this paper we have demonstrated the difficulty of obtaining an exact analytical solution to predator-prey models. However this does not mean that it is impossible to obtain useful information from such models. We can still use analytical methods to determine quantitative behaviour which can determine long term trends in population. We can also use several numerical methods to obtain satisfactory approximations to our models.

Population dynamics is a vast topic and this dissertation focused on only a small facet of it. If we were to continue research in this subject in the future we would like to look at some of the other models mentioned in the types of predator-prey section, particularly a model including the more advanced Holling type 3 functional response. We can by using the terms $f(u) = 1 - u$ and $g(u) = \frac{mu^k}{A + u^k}$ modify system (2.15) to a model incorporating a Holling type 3 response as shown below

$$\frac{du}{d\tau} = u(1 - u) - \frac{mu^k v}{A + u^k},$$

$$\frac{dv}{d\tau} = v\left(r_1 - b_1 \frac{v}{u}\right).$$

There are a multitude of concepts related to predator-prey models which have yet to be mentioned. Two areas of particular interest to us is the concept of incorporating a prey refuge, an area where the prey where safe from predation. An example of a model modified to incorporate a refuge is proposed by F.Chen et. al. [3]: who modifying the Leslie-Gower model (1.12) by introducing the prey refuge rN , where $r \in [0, 1)$ is a constant. This leaves $(1 - r)N$ of the prey available to the predator. Therefore our system (1.12) becomes

$$\frac{dN}{dt} = aN\left(1 - \frac{N}{K}\right) - (m(1 - r)N)P,$$

$$\frac{dP}{dt} = P\left(c - d\frac{P}{(1 - r)N}\right),$$

The other concept of interest to us is when we have a system with more than two populations. Such models will allow us to examine a wide range of scenarios. A couple of examples of these scenarios include a system where one species is hunted by two independent predator populations. Another scenario is when we introduce a more complex food chain where one prey species and it's predator are both prey for an alpha predator. An example for a system with three populations proposed by Erica Chauvet et al [5] is given by

$$\frac{dx}{dt} = ax - bxy,$$

$$\frac{dy}{dt} = -cy + dxy - eyz,$$

$$\frac{dz}{dt} = -fz + gyz,$$

where $a, b, c, d, e, f, g > 0$.

Here a, b, c, d represent the same parameters as they did in our two populations systems and:

- e represents the effect of predation of species z on species y .
- f represents the death rate of species z in the absence of prey.
- g represents the birth rate for species z .

This system models the scenario where the predator from our Lotka Volterra model is preyed on by an alpha predator. Where the alpha predator has no interactions with the prey on the bottom of the food chain.

Numerical methods is another area we could more throughly research. Through our investigation we only analysed our Lotka-Volterra model by implementing four different methods, the explicit Euler, the symplectic Euler and 4th order Runge Kutta. Their are numerous different methods we could apply, of particular interest is implementing the differential transformation method (DTM) and the multistep DTM mentioned in the previous chapter.

Appendices

1 Matlab code

Code for graph of the region for Hopf bifurcation and limit cycles

```
1 a=0:0.01:1;
2 r1=1+3.*a-2.*sqrt(2.*a+2.*a.*a);
3
4 plot(a,r1)
5 area(a,r1)
6
7 xlabel('a_1');
8 ylabel('r_1');
```

Code for the phase plane for Limit cycles:

```
1 -
2 %enter parameters, intial conditions and size of time interval
3 a=input('enter parameter a:');
4 r1=input('enter parameter r1:');
5 b=input('enter parameter b:');
6 u0=input('enter initial prey population:');
7 v0=input('enter initial predator population:');
8 endtime=input('enter size of time interval:');
9
10
11 sys = @(t,x) [x(1)*(1-x(1))-x(1)*x(2)/(a+x(1));x(2)*(r1-b*x(2)/x(1))];
12 options = odeset('RelTol', 1e-4, 'NonNegative', [1 2]);
13 [t,u]=ode45(sys,[0 endtime],[u0 v0],options);
14 plot(t,u)
15 axis([0 1000 0 10])
16 xlabel('u(t)')
17 ylabel('v(t)')
18 hold off
```

Code for ode45 phase plane and example of stable cycles:

```
1 clear;
2 to = 0;
3 tf = 200;
4 uo = [100 50];
5 [t u] = ode45('lv2',[to tf],uo);
6 plot(u(:,1),u(:,2))
7 ylabel('v(t)')
8 xlabel('u(t)')

1 function lv2 =yprf(t,u)
2 lv2(1) = .4*u(1) - .013*u(1)*u(2);
3 lv2(2) = -.3*u(2) +.015*u(1)*u(2);
4 lv2 = [lv2(1) lv2(2)]';
```

Code for Euler equation:

```

1 t=[0:.0002:30];
2 x=zeros(size(t));
3 y=zeros(size(t));
4 x(1)=2;
5 y(1)=2;
6 xp=@(t,x,y) x-x*y;
7 yp=@(t,x,y) -2*y+x*y;
8 for k=1:length(t)-1
9 x(k+1)=x(k)+xp(t(k),x(k),y(k))*(t(k+1)-t(k));
10 y(k+1)=y(k)+yp(t(k),x(k),y(k))*(t(k+1)-t(k));
11 end
12 fh=@(N,P)(N+P-log(N^2*P)-1.920558458)
13 q=ezplot(fh);
14 set(q,'color',[1 0 0]);
15 hold on
16 plot(x,y)
17 ylabel('P(t)')
18 xlabel('N(t)')
19 legend('Actual','Symplectic');
20 axis([1,3.5,0.4,2.1])
21
22
23 df=length(x);
24 l99=x(df)

```

Code for Symplectic Euler equation:

```

1 format long
2 t=[0:.05:30];
3 x=zeros(size(t));
4 y=zeros(size(t));
5 x(1)=2;
6 y(1)=2;
7 for k=1:length(t)-1
8 x(k+1)=x(k)/(1-(t(k+1)-t(k))*(1-y(k)));
9 y(k+1)=y(k)+(y(k)*(x(k+1)-2))*(t(k+1)-t(k));
10 end
11
12 fh=@(N,P)(N+P-log(N^2*P)-1.920558458)
13 q=ezplot(fh,[0,30]);
14 set(q,'color',[1 0 0]);
15 hold on
16 plot(x,y)
17 ylabel('P(t)')
18 xlabel('N(t)')
19 legend('Actual','Symplectic');
20 axis([1,3.5,0.4,2.1])
21

```

```

22 df=length(x);
23 l99=x(df)
    Code for Runge Kutta method:
1
2
3
4 function rk4_systems(a, b, N, intial)
5 intial=[2 2];
6 b=30;
7 a=0;
8 m = size(intial,1);
9 if m == 1
10 intial = intial';
11 end
12 h = 0.05; %the step size
13 N=(b-a)/h
14 t(1) = a;
15 g(:,1) = intial; %initial conditions
16
17 for i = 1:N
18 k1 = h*f(t(i), g(:,i));
19 k2 = h*f(t(i)+h/2, g(:,i)+0.5*k1);
20 k3 = h*f(t(i)+h/2, g(:,i)+0.5*k2);
21 k4 = h*f(t(i)+h, g(:,i)+k3);
22 g(:,i+1) = g(:,i) + (k1 + 2*k2 + 2*k3 + k4)/6;
23 t(i+1) = t(i) + h;
24 end
25 hold on
26 fh=@(N,P)(N+P-log(N^2*P)-1.920558458);
27 q=ezplot(fh);
28 set(q,'color',[1 0 0])
29 hold on
30 axis([1,3.5,0.4,2.1])
31 plot(g(1,:),g(2,:))
32 xlabel('N(t)')
33 ylabel('P(t)')
34 legend('Actual','Runge Kutta');
35
36 df=length(g(1,:));
37 l99=g(1,df)
38 fprintf(1, 'l99 = %.20f\n', l99 )
39 function lv =f(t,g)
40 lv(1) =g(1)-g(1)*g(2);
41 lv(2) = g(1)*g(2)-2*g(2);
42
43 lv = [lv(1) lv(2)]';

```

Code for quantifying Holling-Tanner model:

```
1 —
2 %enter parameters, initial conditions and size of time interval
3 a=input('enter parameter a:');
4 r1=input('enter parameter r1:');
5 b=input('enter parameter b:');
6 u0=input('enter initial prey population:');
7 v0=input('enter initial predator population:');
8 endtime=input('enter size of time interval:');
9
10
11 sys = @(t,x) [x(1)*(1-x(1))-x(1)*x(2)/(a+x(1));x(2)*(r1-b*x(2)/x(1))];
12 options = odeset('RelTol', 1e-4, 'NonNegative', [1 2]);
13 [t,u]=ode45(sys,[0 endtime],[u0 v0],options);
14 plot(t,u)
15 axis([0 1000 0 10])
16 xlabel('u(t)')
17 ylabel('v(t)')
18 hold off
```

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