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## Chaos to Permanence-Through Control Theory

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# CHAOS TO PERMANENCE-THROUGH CONTROL THEORY

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A Dissertation  
Presented to  
the Graduate School of  
Clemson University

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In Partial Fulfillment  
of the Requirements for the Degree  
Doctor of Philosophy  
Mathematical Sciences

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by  
Sherli Koshy Chenthittayil  
May 2017

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Accepted by:  
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Dr. Matthew Macauley

# Abstract

Work by Cushing et al. [18] and Kot et al. [60] demonstrate that chaotic behavior does occur in biological systems. We demonstrate that chaotic behavior can enable the survival/thriving of the species involved in a system. We adopt the concepts of persistence/permanence as measures of survival/thriving of the species [35]. We utilize present chaotic behavior and a control algorithm based on [66, 72] to push a non-permanent system into permanence. The algorithm uses the chaotic orbits present in the system to obtain the desired state. We apply the algorithm to a Lotka-Volterra type two-prey, one-predator model from [30], a ratio-dependent one-prey, two-predator model from [35] and a simple prey-specialist predator-generalist predator (for ex: plant-insect pest-spider) interaction model [67] and demonstrate its effectiveness in taking advantage of chaotic behavior to achieve a desirable state for all species involved.

# Dedication

This thesis is dedicated to my sister, Sheena. My older sister has been my inspiration for as long as I can remember. She introduced me to great writers like Jane Austen, Agatha Christie, J.K. Rowling and tons of other things. She cajoled and pushed me to get out of my comfort zone in India and come to the States to pursue my doctorate. She showed interest in my research even though I know she hates math. She patiently listened to me practice for my conferences and also helped with my resumes. She has taught me to stand on my own two feet and for that I am immensely grateful. Thank you for always being there sister.

# Acknowledgments

I would like to first acknowledge God Almighty for his grace and kindness. I would also like to thank my parents, brother, sister-in-law and niece for their unwavering love and support. Next I am really grateful to my advisor Dr. Elena Dimitrova for helping me understand chaos theory, permanence and the list goes on. Thank you for keeping me on track and your staunch belief in me.

A special thank you to Dr. Oleg Yordanov for helping me to better explain my theories and for helping me understand chaotic systems better. I would like to thank Dr. Lea Jenkins for all her help with my MATLAB and LaTeX coding questions. Next, I am thankful to Dr. Brian Dean and Dr. Matthew Macaulay for their insights and support.

Finally a thank you to my friends, who helped me through all the crazy times.

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# Chapter 1

## Introduction

Extinction or survival of the species are important points to consider for any ecological system. Mathematical biologists are also concerned about this very question when they develop models based on an ecological system. Stability notions have been introduced and studied in different manners: “cooperativity” by Schuster et al. [43], “permanent coexistence” by Hutson and Vickers [69], “permanence and viability” by Aubin and Sigmund [5]. *Permanence* simply means the species remain at a safe threshold from extinction.

Certain ecologists have also been worried when chaotic behavior occurs in the system (such behavior does occur as shown in [18, 60]). They prefer to see either periodic or stable behavior. However, chaos need not be harmful to the system and can be used as a control as we will demonstrate. There is in fact an evolutionary advantage of using chaos as a control [19]. Very small changes in the initial conditions of a chaotic system can greatly alter the system’s trajectory. Thus, we won’t need to change the system completely to obtain our desired outcome.

In the literature, chaos and permanence have always been studied as separate entities. A few papers deal with both, but they derive conditions for permanence independently of any chaotic behavior and only observe chaos in their numerical simulations without tying it to permanence. In this thesis, we study *chaos and permanence in tandem* and use the properties of a chaotic trajectory to push a system which is non-permanent to become permanent.

Chapter 2 gives a description of dynamical systems and the different kinds of such systems. It then goes to give a definition of chaos in terms of Lyapunov exponents and defines such exponents. A method to calculate Lyapunov exponents [6] is also provided.

The next chapter (Chapter 3) gives a summary of some biologically relevant systems, namely the Lotka-Volterra model [35], ratio-dependent models [2], predator-prey models that have the Leslie-Gower type functional response [52] and Crowley-Martin type functional response [15]. These are only a few of the many different types of biologically relevant models that have been proposed throughout the literature. Further references to other models can be found in chapter 3.

We are using the concepts of permanence/persistence to describe the thriving/survival of the species. Chapter 4 presents some background information on how these concepts were developed. The chapter then goes on to give three methods to prove permanence: one for Lotka-Volterra equations and two for systems with boundary rest points. Examples of the applications of these methods are also provided. In each system, together with permanence, chaos is also observed.

There are situations where chaotic behavior and non-permanence are observed. In such a scenario, we use control theory to use the chaotic orbits to obtain permanence. An overview of some control theory methods and a chaotic control algorithm [66] is provided in Chapter 5.

In Chapter 6, we utilize present chaotic behavior and a control algorithm based on [66, 72] to push a non-permanent system into permanence. The algorithm uses the chaotic orbits present in the system to obtain the desired state. We apply the algorithm to a Lotka-Volterra type two-prey, one-predator model from [30], a ratio-dependent one-prey, two-predator model from [35] and a simple prey-specialist predator-generalist predator (for ex: plant-insect pest-spider) interaction model [67] and demonstrate its effectiveness in taking advantage of chaotic behavior to achieve a desirable state for all species involved.

In the Conclusions chapter, possible future work is given.

# Chapter 2

## Chaos in dynamical Systems

This chapter gives a brief description of dynamical systems, the different types of dynamical systems, types of behavior of one-dimensional, two-dimensional and higher dimensional continuous dynamical systems. Chaos will be indicated by a positive Lyapunov exponent. The definition of Lyapunov exponents and a method to find such exponents [6] is also provided.

### 2.1 Introduction to dynamical systems

A **dynamical system** consists of a set of possible states, together with a rule determining the present state based on the previous state [7]. For example consider a simple dynamical system given by  $x_{t+1} = ax_t$ . Here the variable  $t$  stands for time and  $x_t$  may denote the population at time  $t$  or a price of a commodity at a time  $t$ . The real number  $a$  is a parameter of the system, which determines the population growth rate or the price hike, respectively.

A **deterministic dynamical system** is one in which the present state is determined **uniquely** from the past states. In our previous examples, the present population/price is completely determined by the previous one.

### Types of Dynamical Systems

If the rule is applied at discrete times, the system is called a *discrete-time dynamical system*. Our examples above represent discrete systems.

*Continuous-time Dynamical Systems* are the limiting case of discrete system with smaller and smaller updating times. In this case, the governing rule will become a set of differential equations. Instead of expressing the current state as a function of the previous state, the differential equation expresses the **rate of change** of the current state as a function of the previous state [7].

We will be considering **continuous dynamical systems with ordinary differential equations**.

An ordinary differential equation is one in which the solutions are functions of an independent variable. In our case the independent variable will be time denoted by  $t$ . Such equations come in two types:

An *autonomous differential equation* is one in which  $t$  does not appear explicitly. An example for this would be the equation of pendulum given by:

$$\frac{dx}{dt} = -\sin x,$$

where  $x$  denotes the displacement angle from the position at rest ( $x_0$ ).

A *non-autonomous differential equation* is one where  $t$  explicitly appears. The equation of the forced damped pendulum

$$\ddot{x} = -c\dot{x} - \sin x + \rho \sin t$$

is an example of such an equation. Here  $x$  again denotes the displacement angle from the position at rest;  $-c\dot{x}$  denotes the friction at the pivot where  $c$  is the friction constant; and  $\rho \sin t$  is a periodic term which is an external force providing energy to the pendulum [7].

Any non-autonomous system can be transformed into an autonomous system by introducing a new variable  $y$  and setting it to be equal to  $t$ . So for the above example the autonomous version would be

$$\ddot{x} = -c\dot{x} - \sin x + \rho \sin y$$

$$\dot{y} = 1$$

We shall be dealing with **autonomous continuous dynamical systems with ordinary differential equations unless stated otherwise**.

## 2.2 Types of behavior in continuous dynamical systems

We shall denote  $x' = f(x)$ , where  $x \in \mathbb{R}^n$  as an autonomous continuous dynamical system of ordinary differential equations. Also we will assume  $f$  is a continuous vector-valued function with continuous derivatives in  $\mathbb{R}^n$ , i.e.  $f \in C^k(M, \mathbb{R}^n)$ ,  $k \geq 1$ ,

where  $M$  is an open subset of  $\mathbb{R}^n$  [65].

A **fixed point** is given by the zeroes of the function  $f$ , the right hand side of the system. In other words, they are obtained by solving  $f(x) = 0$ .

The fixed points are also called **equilibria, rest, or critical points**. If a dynamical system is tuned to a fixed point, its rate of change becomes zero and therefore the system stays in this state forever.

### 2.2.1 One dimension: fixed points

We consider first a continuous one-dimensional system  $x' = f(x)$ , where  $x, f(x) \in \mathbb{R}$ . We can have a fixed point or the other possibilities at a point are  $f(x) > 0$  or  $f(x) < 0$ .

**Lemma 2.2.1.** *No periodic behavior is possible (except for fixed points) in one-dimensional continuous systems [59].*

*Proof.* Consider a state  $x_1$  which we allegedly visit at times  $s$  and  $t$ , with  $s < t$ .

This is possible if  $x_1$  is a fixed point, but otherwise we have  $f(x_1)$  either positive or negative.

If  $f(x_1)$  is positive, then at least in a short run, the system moves to a state  $x_2 > x_1$ . Since  $f$  is continuous, we may assume that  $f$  is positive over the entire interval  $[x_1, x_2]$ . So in order to return to  $x_1$ , since we are in one dimension, the solution curve must “walk” back through a region with  $f(x) > 0$  which repels it. Therefore, we are at  $x_2$ ,  $x(t)$  still increasing and cannot come back to  $x_1$ . Similarly for  $f(x_1) < 0$ .  $\square$



To summarize, the one-dimensional systems either “explode” or tend to a fixed point. That is, the fixed point is either *attracting* or *repelling* in nature.

## 2.2.2 Two dimensions:

### Poincaré-Bendixson theorem

Now we consider two-dimensional (2D) autonomous systems. A solution curve to the system  $x' = f(x)$ , where  $x \in \mathbb{R}^2$  and  $f$  is a vector valued function of two scalar variables, is called a **trajectory (or orbit)** of the system. As in the case of one-dimensional systems, if we start at a fixed point, we are stuck there.

Two-dimensional dynamical systems demonstrate another behavior, namely periodic. The periodic solutions are possible owing to the fact that a trajectory could leave a point through a repelling direction and return to the point along the attracting direction. A dynamical system exhibits **periodic behavior** when it returns to a previously visited state. We can write this as  $x(t) = x(t + T)$  for some  $T > 0$ . The smallest positive number  $T$  for such behavior is called the **period** of the curve. Solution curves which exhibit periodic behavior are called **periodic orbits or closed orbits**.

For example, for the system

$$\begin{bmatrix} x_1' \\ x_2' \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

the trajectories are periodic with period  $2\pi$  which is seen in Fig. 2.2.1 (generated using MAPLE).

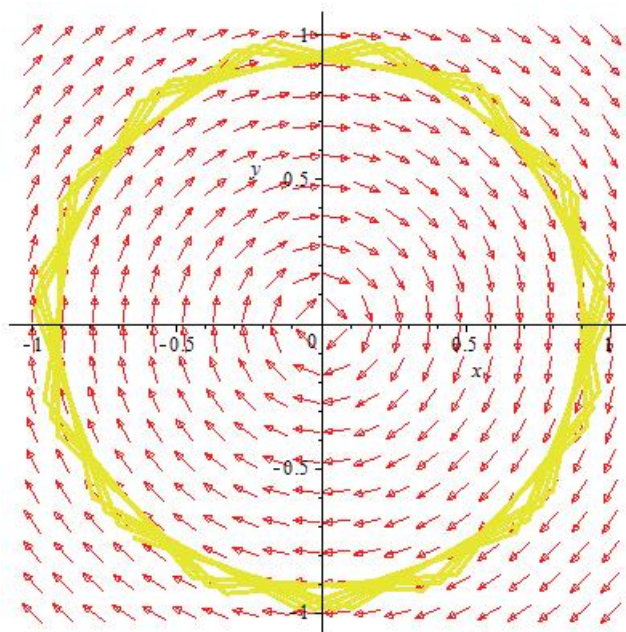


Figure 2.2.1: Periodic orbit

Certain trajectories may not exhibit periodic behavior but may approach a periodic orbit. To be more specific, let  $x_1(t)$  and  $x_2(t)$  be two different trajectories of a system  $x' = f(x)$ . We say that trajectory  $x_1$  approaches trajectory  $x_2$  provided  $|x_1(t) - x_2(t + c)| \rightarrow 0$  (where  $c$  is a constant and  $|\cdot|$  denotes the Euclidean distance) as  $t \rightarrow \infty$ .

Two trajectories of a dynamical system, however, cannot cross under certain conditions [59]. Consider the point of intersection if two trajectories actually did intersect. The trajectory of the system starting at that point of intersection is completely determined and therefore must proceed along a unique path. Otherwise it violates the theorem of uniqueness.

### Definitions

- **$\omega$ –limit (forward limit set):** Let  $\dot{x} = f(x)$  be an autonomous ODE where  $x \in \mathbb{R}^2$  and let  $x(t)$  be a solution defined for all  $t \geq 0$  with initial condition

$x(0) = \mathbf{x}$ . The  $\omega$ -limit of  $\mathbf{x}$  is the set of all accumulation points of  $x(t)$ , for  $t \rightarrow +\infty$ :

$$\omega(\mathbf{x}) = \{y \in \mathbb{R}^2 : x(t_k) \rightarrow y \text{ for some sequence } t_k \rightarrow +\infty\}.$$

- **$\alpha$ - limit (backward limit set):** The definition is similar as above except  $t_k \rightarrow -\infty$  [35].

The definitions of the forward and backward limit set are valid for  $\mathbb{R}^n, n \geq 2$  as well.

One of the famous theorems in dynamical systems, the Poincaré-Bendixson Theorem [65] is stated below:

**Theorem 2.2.2.** *Let  $M$  be an open subset of  $\mathbb{R}^2$  and  $f \in C^1(M, \mathbb{R}^2)$ . Fix  $x \in M$  and suppose the  $\omega$ -limit set ( $\alpha$ -limit set) is compact, connected and contains only finitely many fixed points. Then one of the following cases holds:*

- $\omega(x) (\alpha(x))$  is an equilibrium, or
- $\omega(x) (\alpha(x))$  is a periodic orbit, or
- $\omega(x) (\alpha(x))$  consists of (finitely many) fixed points  $x_j$  and non-closed orbits  $\gamma(y)$  such that  $\omega(y) (\alpha(y)) \in x_j$ .

In other words, according to the Poincaré-Bendixson Theorem, two-dimensional systems will either converge to a fixed point, diverge to infinity or approach a periodic orbit.

Heuristically, an aperiodic trajectory can approach a rest point or diverge to infinity. If however, a trajectory is converging to a periodic orbit, it cannot diverge

from its limit since this would require crossing itself.

### 2.2.3 Higher dimensions and chaos

In dimensions greater than 2, we see another interesting behavior other than rest points or periodic orbits. These orbits are called chaotic orbits defined below. In three or higher dimensions, an aperiodic trajectory could escape the manifold which bounds it to a periodic orbit through a repelling direction, along an extra dimension transversal to the manifold and returns via attracting path.

**A chaotic orbit** is one that experiences an unstable behavior, but that is not itself fixed or periodic. By unstable behavior, we mean at any point in such an orbit, there are points on the orbit arbitrarily near that will move away from the point during further iteration. In terms of solutions, it means they are very sensitive to small perturbations in the initial conditions and almost all of the orbits do not appear to be either periodic or converge to equilibrium solutions [7].

A dynamical system  $(X, f)$  has **sensitive dependence** on initial conditions on a subset  $X' \subset X$  if there is  $\epsilon > 0$ , such that for every  $x \in X'$  and  $\delta > 0$  there are  $y \in X$  and  $n \in \mathbb{N}$  for which  $d(x, y) < \delta$  and  $d(f^n(x), f^n(y)) > \epsilon$  [13].

Sensitive dependence on initial conditions is usually associated with positive *Lyapunov exponents*. Let  $f$  be a differentiable map of an open subset  $U \subset \mathbb{R}^m$  into itself, and let  $df(x)$  denote the derivative of  $f$  at  $x$ . For  $x \in U$  and a non-zero vector  $v \in \mathbb{R}^m$  define the *Lyapunov exponent* [13]  $\chi(x, v)$  by

$$\chi(x, v) = \limsup_{n \rightarrow \infty} \frac{1}{n} \log \|df^n(x)v\|.$$

If  $f$  has uniformly bounded first derivatives, then  $\chi$  is well defined for every  $x \in U$  and every non-zero vector  $v$ .

The Lyapunov exponent measures the exponential growth rate of tangent vectors along orbits.

Another formal definition of a chaotic attractor is given below.

Let  $F_t(v_0)$  be a solution of  $\dot{v} = f(v)$ , where  $v_0 \in \mathbb{R}^n$ . We say that the orbit  $F_t(v_0)$  is **chaotic** [7] if the following conditions hold:

1.  $F_t(v_0), t \geq 0$ , is bounded.
2.  $F_t(v_0)$  has at least one positive Lyapunov exponent; and
3. The  $\omega$ -limit set is not periodic and does not consist solely of equilibrium points, or solely of equilibrium points and connecting arcs (as in the conclusion of the Poincaré-Bendixson Theorem).

**Check for bounded orbits:** An orbit is bounded if the divergence at the initial condition is negative.

In the book [7], the concept of Lyapunov exponents is explained as follows

“The local behavior of the dynamics varies among the many directions in state space. Nearby initial conditions may be moving apart along one axis, and moving together along another. For a given point, we imagine a sphere of initial conditions of infinitesimal radius evolving into an ellipse as the flow  $f$  is applied. The natural logarithm of the average growth rate of the longest orthogonal axis of the ellipse was defined to be the first

Lyapunov exponent.

A positive Lyapunov exponent signifies growth along that direction, and therefore exponential divergence of nearby trajectories. The existence of a local expanding direction along an orbit is the hallmark of a chaotic orbit.”

A chaotic attractor can be dissipative (volume-decreasing), locally unstable (orbits do not settle down to stationary, periodic, or quasiperiodic motion) and stable at large scale (i.e. they get trapped in a strange attractor) [7].

## 2.3 Examples of continuous systems that displays chaos

A classic three-dimensional system which display stable fixed points and chaotic behavior for different values of a parameter is the Lorenz model given below. Lorenz was modeling atmospheric convection.

$$\begin{aligned}\dot{x} &= \sigma(y - x) \\ \dot{y} &= x(r - z) - y \\ \dot{z} &= xy - \beta z.\end{aligned}$$

Here  $x$  is proportional to convective intensity,  $y$  to the temperature difference between descending and ascending currents, and  $z$  to the difference in vertical temperature profile from linearity. The parameter  $\sigma$  is the Prandtl number,  $r$  is a ratio of Rayleigh numbers and  $\beta$  is a geometric factor.

For  $\sigma = 10, \beta = 8/3$ , Lorenz found that the system behaved chaotically for  $r \geq 24.74$ . The chaotic attractor is shown in Fig 2.3.1.

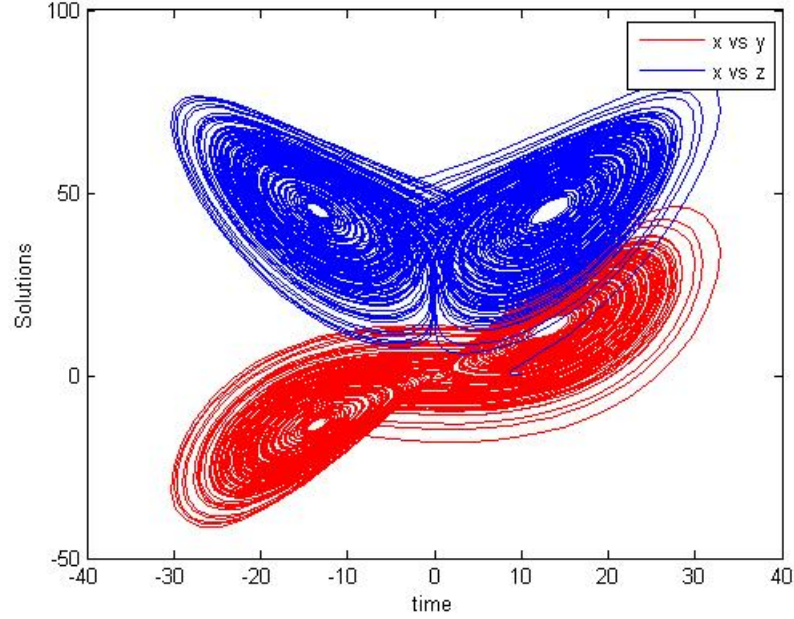


Figure 2.3.1: Lorenz attractor. Red plot is  $x$  vs  $y$ . Blue is  $x$  vs  $z$ .

Figure 2.3.1 depicts the orbit of a single set of initial conditions. This is a numerically observed attractor since the choice of any initial condition in a neighborhood of the chosen set results in a similar figure [7]. This behavior has also been called the *butterfly effect* after the theory that a butterfly flapping its wings can cause significant changes in the weather because of the slight changes it makes in the atmosphere [59].

Another popular system which exhibits a chaotic attractor is by O. Rössler given below.

$$\begin{aligned}\dot{x} &= -y - z \\ \dot{y} &= x + ay \\ \dot{z} &= b + (x - c)z.\end{aligned}$$

This system has only one non-linear term,  $xz$ , as compared to the Lorenz system but is harder to analyze [7].

For the choice of parameters  $a = 0.1, b = 0.1, c = 14$  [7], there is a chaotic attractor shown in Fig. 2.3.2.

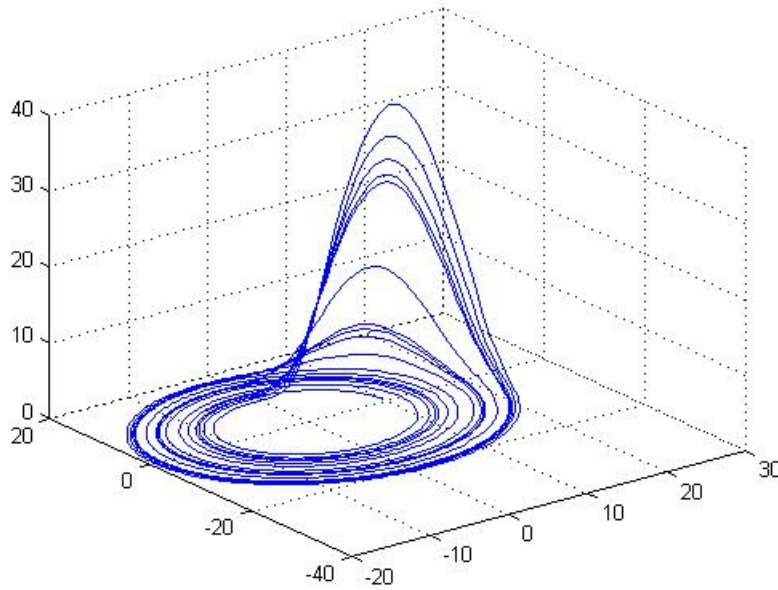


Figure 2.3.2: Rössler attractor

The figures were generated in MATLAB using *ode45*.



Another article which observed chaos for certain parameters in the biological system is by Kot, Sayler and Schulz [60]. They explored a double-monod system with a prey (protozoan) and a predator (bacteria) when the nutrient is being forced into the system out of phase with internal substrate. The system is a non-autonomous continuous dynamical system with ordinary differential equations. The equations used to model that system are as follows [60]:

$$\begin{aligned}\frac{dS}{dt} &= D \left[ S_i \left( 1 + \epsilon \sin \left( \frac{2\pi}{T} t \right) \right) - S \right] - \frac{\mu_1}{Y_1} \frac{SH}{K_1 + S} \\ \frac{dH}{dt} &= \mu_1 \frac{SH}{K_1 + S} - DH - \frac{\mu_2}{Y_2} \frac{HP}{K_2 + H} \\ \frac{dP}{dt} &= \mu_2 \frac{HP}{K_2 + H} - DP\end{aligned}$$

where

1.  $S$  represents the concentration of limiting substrate;
2.  $H$  represent the concentration of the prey;
3.  $P$  represents the predator concentration;
4.  $D$  is the dilution rate;
5.  $\mu_1$  and  $\mu_2$  represent the maximum specific growth rate of the prey and predator respectively;
6.  $Y_1$  is the yield of the prey per unit mass of substrate;
7.  $Y_2$  is the biomass yield of the predator per unit mass of prey.

For ease of calculations, the authors re-scaled the concentrations by the in-flowing substrate concentrations, the prey by its yield constant, predator by both yield constants, i.e.

$$x = \frac{S}{S_i}, y = \frac{H}{Y_1 S_i}, z = \frac{P}{Y_1 Y_2 S_i}, \tau = Dt.$$

The resulting re-scaled equations are as follows:

$$\frac{dx}{d\tau} = 1 + \epsilon \sin(\omega\tau) - x - \frac{Axy}{a+x} \quad (2.1)$$

$$\frac{dy}{d\tau} = \frac{Axy}{a+x} - y - \frac{Byz}{b+y} \quad (2.2)$$

$$\frac{dz}{d\tau} = \frac{Byz}{b+y} - z \quad (2.3)$$

where  $\omega = \frac{2\pi}{DT}$ .

The parameter values are in Table. 2.3.1.

$D = 0.1, S_i = 115$

	$Y_i$	$\mu_i \text{ h}^{-1}$	$K_i \text{ mg/l}$
Prey	0.4	0.5	8
Predator	0.6	0.2	9

Table 2.3.1: Values of parameters for microbial model presented in Kot et al. [60].

In the paper, the authors vary the value of  $\omega$  to observe the behavior of the model. This parameter was chosen because it drives the periodic forcing of the in-flowing substrate. For  $\omega = \frac{5\pi}{6}$  and  $\epsilon = 0.6$  they observed a chaotic model whose simulation is given in Fig. 2.3.3 (also seen in [14]).

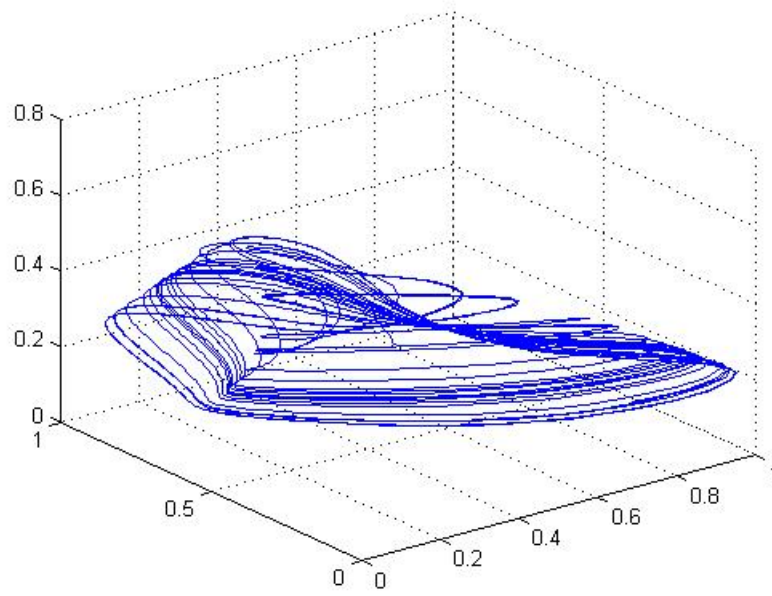


Figure 2.3.3: Manifold plot of the Kot system when  $\omega = \frac{5\pi}{6}$  and  $\epsilon = 0.6$ .

## 2.4 Evaluation of Lyapunov spectrum

As mentioned in Section 2.2, a positive Lyapunov exponent is a measure of a chaotic orbit. The procedure for determining a Lyapunov exponent has been obtained from [6] so the definition from the same article is given below.

Consider a continuous dynamical system in an  $n$ -dimensional phase space. We are observing the long term behavior of an *infinitesimal  $n$ -sphere* of initial conditions. Due to the locally deforming nature of the flow, the sphere eventually becomes a  *$n$ -ellipsoid*. The Lyapunov exponent is calculated for each dimension and it is dependent on the length of the principal axis of the ellipsoid. It is given by

$$\lambda_i = \lim_{t \rightarrow \infty} \frac{1}{t} \log_2 \frac{p_i(t)}{p_i(0)}, \quad (2.4)$$

where  $p_i(t)$  denotes the length of the ellipsoidal principal axis at time  $t$  and  $p_i(0)$  denotes its length at time  $t = 0$ .

The exponents are generally given in decreasing order, i.e.  $\lambda_1 > \lambda_2 > \dots > \lambda_n$  [6].

### 2.4.1 Procedure for calculation of Lyapunov exponents

The meaning of principal axes with initial conditions is required to better understand the definition of Lyapunov exponents provided in [6]. These axes need to evolve with the equations of the system. The issue is we cannot guarantee the condition of small separations for times needed for convergence in a chaotic system. To tackle this issue, the authors use a phase space together with a tangent space approach. A *fiducial trajectory* (center of the sphere) is obtained by the action of the non-linear system on some initial condition. For the definition of trajectories on the points of the sphere, the concept of *linearized system* or *variational equations* is

required.

Consider the Rössler system given below

$$\dot{x} = -y - z$$

$$\dot{y} = x + ay$$

$$\dot{z} = b + (x - c)z.$$

The linearized equations of the above system are constructed using the Jacobian of the right-hand side:

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} & \frac{\partial f_1}{\partial z} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} & \frac{\partial f_2}{\partial z} \\ \frac{\partial f_3}{\partial x} & \frac{\partial f_3}{\partial y} & \frac{\partial f_3}{\partial z} \end{bmatrix}$$

where  $f_i$  is the right-hand side of the  $i^{th}$  differential equation. For a  $n$ -dimensional system we would have an  $n \times n$  matrix.

For the Rössler system the Jacobian is

$$\begin{bmatrix} 0 & -1 & -1 \\ 1 & a & 0 \\ z & 0 & x - c \end{bmatrix}.$$

To set up the variational equations we would need another matrix given by:

$$[\delta] = \begin{bmatrix} \delta_{x1} & \delta_{y1} & \delta_{z1} \\ \delta_{x2} & \delta_{y2} & \delta_{z2} \\ \delta_{x3} & \delta_{y3} & \delta_{z3} \end{bmatrix},$$

where  $\delta_{xi}$  is the component of the  $x$  variation that came from the  $i^{th}$  equation.

The column sums of this matrix are the lengths of the  $x$ ,  $y$ , and  $z$  coordinates of the evolved variation. The rows are the coordinates of the vectors into which the original  $x$ ,  $y$ , and  $z$  components of the variation have evolved.

The linearized equations are:

$$\begin{bmatrix} \dot{\delta}_{x1} & \dot{\delta}_{y1} & \dot{\delta}_{z1} \\ \dot{\delta}_{x2} & \dot{\delta}_{y2} & \dot{\delta}_{z2} \\ \dot{\delta}_{x3} & \dot{\delta}_{y3} & \dot{\delta}_{z3} \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial x} & \frac{\partial f_1}{\partial y} & \frac{\partial f_1}{\partial z} \\ \frac{\partial f_2}{\partial x} & \frac{\partial f_2}{\partial y} & \frac{\partial f_2}{\partial z} \\ \frac{\partial f_3}{\partial x} & \frac{\partial f_3}{\partial y} & \frac{\partial f_3}{\partial z} \end{bmatrix} \begin{bmatrix} \delta_{x1} & \delta_{y1} & \delta_{z1} \\ \delta_{x2} & \delta_{y2} & \delta_{z2} \\ \delta_{x3} & \delta_{y3} & \delta_{z3} \end{bmatrix}.$$

For the Rössler system, it would be:

$$\begin{bmatrix} \dot{\delta}_{x1} & \dot{\delta}_{y1} & \dot{\delta}_{z1} \\ \dot{\delta}_{x2} & \dot{\delta}_{y2} & \dot{\delta}_{z2} \\ \dot{\delta}_{x3} & \dot{\delta}_{y3} & \dot{\delta}_{z3} \end{bmatrix} = \begin{bmatrix} 0 & -1 & -1 \\ 1 & a & 0 \\ z & 0 & x - c \end{bmatrix} \begin{bmatrix} \delta_{x1} & \delta_{y1} & \delta_{z1} \\ \delta_{x2} & \delta_{y2} & \delta_{z2} \\ \delta_{x3} & \delta_{y3} & \delta_{z3} \end{bmatrix}.$$

So now in addition to the original system of  $n$  non-linear equations we will have  $n^2$  additional linearized equations. The system now becomes of length  $n + n^2 = n(n + 1)$ .

Now to obtain the trajectories of points on the surface of the sphere, we consider the action of the linearized system on points very close to the fiducial trajectory. In fact, the principal axes are defined by the evolution via the linearized equations of an initially orthonormal vector frame anchored to the fiducial trajectory [6]. To implement the procedure we solve the new system of  $n(n + 1)$  differential equations with an ode solver such as Runge-Kutta 45 for some initial condition and a time range  $[tstart, tstart + ts]$  where  $tstart$  denotes the initial time and  $ts$  denotes the time step

[6].

Now each vector diverges in magnitude. In a chaotic system, each vector tends to fall along the local direction of most rapid growth. In addition, the finite precision arithmetic of computing the collapse towards a common direction causes the tangent space orientation of all axis vectors to become indistinguishable. To overcome this, repeated Gram-Schmidt reorthonormalization (GSR) procedure is used on the vector frame.

Let the linearized equations act on the initial frame of orthonormal vectors to give a set of vectors  $\{v_1, v_2, \dots, v_n\}$ . In other words, after we solve the system of  $n(n+1)$  equations, consider the components corresponding to the variational equations. Then GSR provides the following orthonormal set  $\{v'_1, v'_2, \dots, v'_n\}$ :

$$\begin{aligned} v'_1 &= \frac{v_1}{\|v_1\|}, \\ v'_2 &= \frac{v_2 - \langle v_2, v'_1 \rangle v'_1}{\|v_2 - \langle v_2, v'_1 \rangle v'_1\|} \\ &\vdots \\ v'_n &= \frac{v_n - \langle v_n, v'_{n-1} \rangle v'_{n-1} - \dots - \langle v_n, v'_1 \rangle v'_1}{\|v_n - \langle v_n, v'_{n-1} \rangle v'_{n-1} - \dots - \langle v_n, v'_1 \rangle v'_1\|} \end{aligned}$$

where  $\langle \cdot \rangle$  denotes the Euclidean inner-product. The orthonormal set thus obtained now serves as the new initial conditions for our linearized system. We then solve the system again, now with these new initial conditions and a new time-range  $[tstart, tstart + ts]$  where  $tstart$  has now been changed to  $tstart + ts$  and  $ts$  denotes the time step. This procedure is repeated  $n$  times.

It is seen that GSR never affects the direction of the first vector in a system, so this vector tends to seek out the most rapidly growing direction in the tangent space [6]. The length of vector  $v_1$  is proportional to  $2^{\lambda_1 t}$  so in this way we can obtain the first Lyapunov exponent  $\lambda_1$ . According to the construction of  $v'_2$ , we are changing the direction of  $v_2$ . So it is not free to chase after the most rapidly growing direction nor the second most. Also note that the vectors  $v'_1$  and  $v'_2$  span the same subspace as  $v_1$  and  $v_2$ . The area defined by the vectors  $v_1$  and  $v_2$  is proportional to  $2^{(\lambda_1+\lambda_2)t}$ . As  $v'_1$  and  $v'_2$  are orthogonal, we may determine  $\lambda_2$  directly from the mean rate of growth of the projection of vector  $v'_2$  on vector  $v'_2$  [6].

Extending this line of thought to  $n$ -dimensions, we see that the subspace spanned by the  $n$  vectors is not affected by the GSR process. The long-term evolution of the  $n$ -volume defined by these vectors is proportional to  $2^{\sum_{i=1}^n \lambda_i t}$ . Projection of the evolved vectors onto the new orthonormal frame correctly updates the rates of growth of each of the principal axes in turn, providing estimates of the Lyapunov exponents.

The MATLAB code corresponding to the FORTRAN code given in [6] is provided in Appendix A.

The next chapter gives examples of biologically relevant systems which will be used in the rest of the thesis.



## Chapter 3

# Examples of biologically relevant systems

In this chapter a brief overview of the different types of systems used throughout this thesis is provided. The systems are the Lotka-Volterra model, ratio-dependent models, predator-prey models that have the Leslie-Gower type functional response and Crowley-Martin type functional response.

### 3.1 Lotka-Volterra systems

The Lotka-Volterra system was initially a pair of equations symbolizing one prey-one predator dynamics. It was developed independently by Alfred Lotka and Vito Volterra in the 1920's. The system has been generalized to  $n$  species systems. A general Lotka-Volterra system is given by:

$$\dot{x}_i = x_i \left( r_i + \sum_{j=1}^n a_{ij} x_j \right) \quad i = 1, 2, \dots, n \quad (3.1)$$

where  $r_i, a_{ij} \in \mathbb{R}$ . These equations are a biologically relevant model for  $n$  interacting species.  $x_i(t)$  denotes the density of species  $i$  at time  $t$ ,  $r_i$  is its intrinsic growth rate and  $a_{ij}$  measures the action of species  $j$  upon the growth rate of species  $i$  (in particular  $a_{ii}$  represents the intra-specific interaction) [39]. The matrix  $A = [a_{ij}]$  is called the **interaction matrix**.

### 3.1.1 Two-dimensional Lotka-Volterra systems

The standard two-dimensional Lotka-Volterra systems considered here are

$$\begin{aligned}\dot{x}_1 &= x_1 (r_1 + a_{11}x_1 + a_{12}x_2) \\ \dot{x}_2 &= x_2 (r_2 + a_{21}x_1 + a_{22}x_2)\end{aligned}$$

The rest points/equilibrium points of this system are obtained by solving:

$$\begin{aligned}x_1 (r_1 + a_{11}x_1 + a_{12}x_2) &= 0 \\ x_2 (r_2 + a_{21}x_1 + a_{22}x_2) &= 0\end{aligned}$$

An *interior rest point* is a rest point  $(x_1, x_2)$  in which  $x_1$  and  $x_2 > 0$ .

Now we classify the systems according to the signs of  $r_i, a_{ij}$  where  $i, j = 1, 2$ .

**Case I**  $a_{11}, a_{22} < 0$  and  $r_1, r_2 > 0$ .

Based on the signs of the coefficients  $a_{ij}$  the systems are classified as below:

1. **Mutualistic system** As defined in [9], in this system the two species benefit

from the presence of each other. Thus  $a_{12}$  and  $a_{21} \geq 0$ . The rest points of this particular system either lie on the coordinate axes or there exists an interior rest point. When there is an interior rest point, all the orbits converge to it and also the determinant  $a_{11}a_{22} - a_{12}a_{21} > 0$ . Otherwise, if the rest points are on the coordinate axes, the orbits diverge to infinity.

2. **Competitive system** As the name suggests, this system consists of competition between different species (i.e. *interspecific competition*) or within one species itself (i.e. *intraspecific competition*). Here  $a_{12}$  and  $a_{21} \leq 0$ . As before, we get either an interior rest point or ones on the coordinate axes. When there is an interior rest point, say  $F$ , two cases arise.

- (a) The rest point  $F$  is a sink which can be shown by the negative eigenvalues of the Jacobian at  $F$ . This is the case of *stable coexistence* [35].
- (b) The rest point  $F$  is a saddle, that is, the Jacobian at that point has a positive and negative eigenvalue. In this case, the orbits converge to either of the rest points on the coordinate axes excluding the origin. This means that depending on the initial condition, one or the other species gets eliminated. This is known as *bistable case* [35].

**Case II:**  $r_1 > 0, r_2 < 0, a_{11} < 0, a_{22} < 0, a_{12} < 0, a_{21} > 0$ .

If there exists an interior rest point, the orbits will converge to it. If no such point exists, the orbits will converge to the biologically relevant rest point (i.e. a rest point where all the coordinates are non-negative) on the coordinate axis  $(-\frac{r_1}{a_{11}}, 0)$  (Recall

$r_1 > 0, a_{11} < 0$ )(by pages 17-20 of [35]).

### 3.1.2 Three-dimensional Lotka-Volterra systems and Heteroclinic cycles

#### 3.1.2.1 Definitions

Let us recall the definitions of  $\omega$ —limit set and  $\alpha$ — limit set from Section 2.2.

- **$\omega$ —limit:** Let  $\dot{x} = f(x)$  be an autonomous ODE where  $x \in \mathbb{R}^n$  and let  $x(t)$  be a solution defined for all  $t \geq 0$  with initial condition  $x(0) = \mathbf{x}$ . The  $\omega$ —limit of  $\mathbf{x}$  is the set of all accumulation points of  $x(t)$ , for  $t \rightarrow +\infty$ :

$$\omega(\mathbf{x}) = \{y \in \mathbb{R}^n : x(t_k) \rightarrow y \text{ for some sequence } t_k \rightarrow +\infty\}$$

- **$\alpha$ — limit:** The definition is similar as above except  $t_k \rightarrow -\infty$  [35].

#### 3.1.2.2 Heteroclinic cycles

When three or more species compete, a very interesting phenomenon may occur. The species take each other's place as the dominant one in a cyclic fashion. The observer may think one species will be the unique survivor and the others are fated to extinction, until suddenly, a revolution occurs. This kind of behavior is due to the presence of a **heteroclinic cycle**. The heteroclinic cycles are cyclic arrangements of saddle rest points and orbits having one saddle point as  $\alpha$ —limit and the next one as  $\omega$ —limit [35]. This means that the orbit will be backward asymptotic to one saddle point and forward asymptotic to the other saddle point.

An example using a Lotka-Volterra type system is shown below[35]:

$$\begin{aligned} \dot{x}_1 &= x_1 (1 - x_1 - 2x_2 - 0.5x_3) \\ \dot{x}_2 &= x_2 (1 - 0.5x_1 - x_2 - 2x_3) \\ \dot{x}_3 &= x_3 (1 - 2x_1 - 0.5x_2 - x_3) \end{aligned} \tag{3.2}$$

The authors chose such a model for the cyclic interaction between the species: if they replace 1 by 2, 2 by 3 and 3 by 1, the equations remain unchanged. When the solution for the system with initial condition  $(0.5, 1, 1.5)$  was plotted, Fig. 3.1.1 was observed.

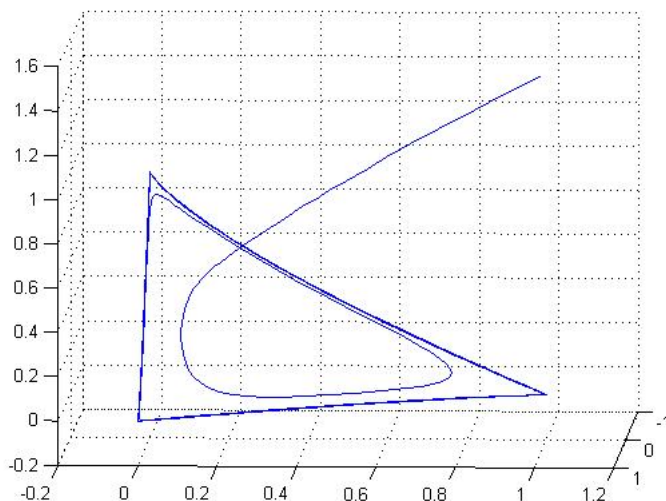


Figure 3.1.1: Heteroclinic cycle.

The heteroclinic cycle is the set consisting of the three saddles  $e_1, e_2, e_3$  (the standard unit vectors) and the three connecting orbits  $o_1, o_2, o_3$ . The state remains for a long time close to the rest point  $e_1$ , travels along  $o_2$  to the vicinity of the rest point  $e_2$ , lingers, then jumps over to  $e_3$  and so on, in cyclic fits and starts [35].

Let us consider some notations [35] concerning heteroclinic cycles occurring in the three-dimensional Lotka-Volterra system:

$$\dot{x}_i = x_i \left( r_i + \sum_{j=1}^3 a_{ij} x_j \right) \quad i = 1, 2, 3. \quad (3.3)$$

The one-species rest points  $\mathbf{F}_i = \left( 0, 0, \dots, \frac{r_i}{-a_{ii}}, \dots, 0 \right)$  are biologically relevant only if  $r_i > 0$  and  $a_{ii} < 0$ . Also they are saddles, since the Jacobian at  $F_i$  will have the  $i^{th}$  entry as  $\frac{a_{ii} r_i}{-a_{ii}} < 0$  and the rest of the diagonal entries as positive. So we can rewrite the equation in the form

$$\dot{x}_i = r_i x_i \left( 1 - \sum_{j=1}^3 c_{ij} x_j \right) \quad i = 1, 2, 3. \quad (3.4)$$

Let

$$\alpha_i = \frac{c_{i-1,i}}{c_{ii}} \quad \beta_i = \frac{c_{i+1,i}}{c_{ii}} \quad (3.5)$$

where the indices are calculated modulo 3. If there exists a heteroclinic cycle, then

$$\alpha_i > 1 > \beta_i.$$

Here  $\beta_i$  may be negative.

## 3.2 Kolmogorov theorem

The Kolmogorov theorem [40, 56], is a very useful tool in determining system parameters in ecological systems. It assures the existence of either a stable equilibrium point or a stable limit cycle in 2D systems provided certain conditions are satisfied. Consider the following prey-predator model described by the system of equations [33]

$$\begin{aligned}\frac{dH}{dt} &= HF(H, P) \\ \frac{dP}{dt} &= PG(H, P)\end{aligned}\tag{3.6}$$

where  $H$  is the prey population at any instant of time and  $P$  is the predator population at the same instant of time.  $F$  and  $G$  are continuous functions of  $H$  and  $P$  with continuous first partial derivatives in the domain  $H \geq 0, P \geq 0$ .

**Theorem 3.2.1. *Kolmogorov Theorem:*** *The 2D system (3.6) possesses a stable equilibrium point or a stable limit cycle if the following five conditions and four requirements are satisfied.*

*Conditions*

$$\begin{aligned}1. \frac{\partial F}{\partial P} < 0 \quad 2. H \left( \frac{\partial F}{\partial H} \right) + P \left( \frac{\partial F}{\partial P} \right) < 0 \quad 3. \frac{\partial G}{\partial P} < 0 \\ 4. H \left( \frac{\partial G}{\partial H} \right) + P \left( \frac{\partial G}{\partial P} \right) > 0 \quad 5. F(0, 0) > 0\end{aligned}$$

*Requirements: There exist quantities  $A, B, C$  such that*

$$\begin{aligned}6. F(0, A) = 0, A > 0 \quad 7. F(B, 0) = 0, B > 0 \\ 8. G(C, 0) = 0, C > 0 \quad 9. B > C\end{aligned}$$

The author R.M. May [56, 33] gives a biological interpretation of the conditions and requirements as follows.

1. The per capita rate of change of the prey density is a decreasing function of the number of predators.
2. The rate of change of prey density is a decreasing function of both densities.
3. The per capita rate of change of the predator density is a decreasing function of the number of predators.
4. The rate of change of predator density is an increasing function of both densities.
5. When both the population densities are low, the prey has a positive rate of increase.
6. There is a predator population density sufficiently large to stop further prey growth, even when the prey is scarce.
7. There is a bound  $B$  on prey growth even when predators are not present.
8. A critical prey size  $C$  is required that stops further increase in predators, even if they are rare.
9. The minimum prey level that will allow an extremely sparse predator population to grow must be a level at which the prey can also grow, i.e. unless  $B > C$ , the system will collapse.

May [56] also suggested the constraints can be relaxed to equality in certain cases.



The authors Upadhyay et al. in [34, 67] stated a conjecture which uses Kolmogorov 2D subsystems (2D subsystems that satisfy the Kolmogorov theorem) to determine parameters for a 3D system. The conjecture is

*Two coupled Kolmogorov-systems in the oscillatory mode would yield either cyclic (stable limit cycles and quasi-periodicity) or chaotic solutions depending on the strength of coupling between the two.*

They divided their original 3D food chain model which consisted of a prey, intermediate predator (predator 1) and a specialist predator (predator 2) into two subsystems: one consisted of the prey and predator 1 and the other of predators 1 and 2. In the second subsystem predator 1 acts a prey for predator 2. The authors called this method the *Pseudo-Prey method*. The diagram depicting the relationship from [67] is Fig. 3.2.1. This shows an interesting way to choose parameters of a 3D system which can be divided into two subsystems so as to obtain chaos.

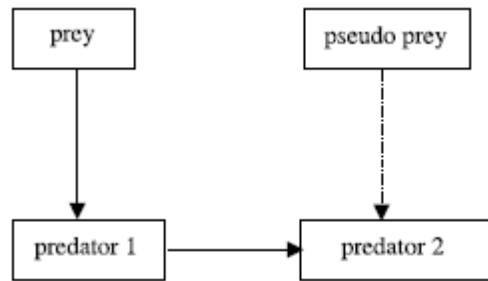


Figure 3.2.1: Relationship between the food chain species and pseudoprey [67].

### 3.3 Ratio-dependent systems using Michaelis-Menten-Holling type interaction

A major concept in predator-prey models is the predator functional response [2]. Different papers [46, 16, 17] argued that, because predators can only handle a finite number of prey in one unit of time, the prey death rate should be a nonlinear function of prey density

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

where  $N, P$  are the biomass densities of the prey and predator respectively,  $a$  is the prey's per-capita rate of change in absence of predation,  $K$  is the carrying capacity and  $b(N)$  is the functional response of the predator to prey density.

Holling carried out some behavioral experiments, in which predators (sometimes blind-folded students) searched for different densities of prey (sometimes sandpaper disks). Using these experiments, Holling derived his famous “disk” equation which was identical to the well-known Michaelis-Menten equation of enzyme kinetics [45],

$$b(N) = \frac{mN}{w + N},$$

where  $m$  is the maximum predator attack rate and  $w$  is the prey density where the attack rate is half-saturated. The **Michaelis-Menten-Holling** equation can be extended to account for general predators that switch from one prey species to another.

Another popular example of the Michaelis-Menten kinetics are found in chemostat models [20]. A chemostat is a device for harvesting bacteria. Nutrients are replenished

as they are being consumed to maintain a required level of bacteria concentration. A two-dimensional model of one species of bacteria and the nutrient is given below:

$$\begin{aligned}\frac{dN}{dt} &= \left( \frac{K_{max}C}{K_n + C} \right) N - \frac{FN}{V} \\ \frac{dC}{dt} &= -\alpha \left( \frac{K_{max}C}{K_n + C} \right) N - \frac{FC}{V} + \frac{FC_0}{V}.\end{aligned}$$

$N$  denotes the bacterial population density,  $C$  the nutrient concentration in the growth chamber,  $C_0$  the nutrient concentration in the reservoir,  $Y$  the yield constant,  $V$  the volume of the growth chamber and  $F$  the intake/output flow rate. The rate of growth of the bacteria increases with nutrient availability only up to some limiting value.

The mechanism that incorporates this effect is Michaelis-Menten kinetics which is shown by the term

$$K(C) = \frac{K_{max}C}{K_n + C}, \quad (3.7)$$

where  $K_{max}$  denotes the upper bound for  $K(C)$  and for  $C = K_n$ ,  $K(C) = \frac{1}{2}K_{max}$ .

The figure depicting Michaelis-Menten kinetics [20] is Fig. 3.3.1.

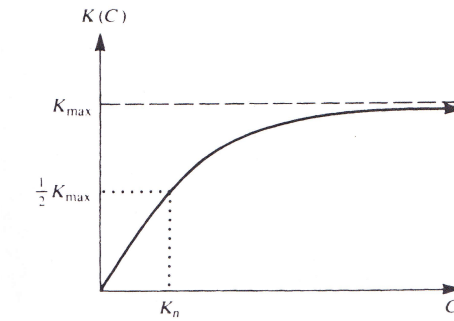


Figure 3.3.1: Michaelis-Menten kinetics [20].

### 3.4 Predator-prey models with Leslie-Gower functional response

The Leslie-Gower two dimensional model [52, 33] leads to asymptotic solutions tending to a stable equilibrium, which is independent of the initial conditions and depends on intrinsic factors governing the biology of the system. The equations of the Leslie-Gower model are

$$\begin{aligned}\frac{dP}{dt} &= (a_1 - c_1 Z)P \\ \frac{dZ}{dt} &= \left( a_2 - c_2 \left( \frac{Z}{P} \right) \right) Z\end{aligned}$$

where  $P$  and  $Z$  denote the density of the prey and predator population respectively at time  $t$ . The parameters are all positive and are given by:

$a_1$  : intrinsic growth rate of prey;

$c_1$  : effect of the density of the predator population on the population growth of the prey;

$a_2$  : intrinsic growth rate of the predator;

$c_2$  : number of prey necessary to support each individual predator.

The factor  $-c_2 \left( \frac{Z}{P} \right)$  indicates the growth rate of the predator is limited. In this model, the following assumptions are inherent:

1. The rate of increase of the predator population has an upper limit.
2. Intraspecific competition has negligible effect on prey's population growth.

As mentioned before, the model depends only on the intrinsic attributes of the interacting system, that is, the parameters  $a_1, c_1$ , and so on.

### 3.5 Predator-prey models with the Crowley-Martin functional response

The Crowley-Martin type of functional response [15] is a predator-dependent functional response, i.e. the response is a function of both prey and predator abundance because of predator interference. The response was observed in a laboratory study of a species of dragonfly. The authors modeled the predation rate per predator (prey per predator per time)  $F$  as proportional to the prey density (per area)  $H$ . The predators are present at density  $P$  per area. Let  $P_1$  be the density of one less than the total number of predators. Interference between predators is assumed and therefore each predator experiences a density  $P_1$  of other predators due to interference.

The authors consider two possibilities:

- Possibility 1: that feeding and interference simply compete with each other to distract the predator's attention. In this case the predation rate  $F$  is given by

$$F = \frac{aH}{(1 + abH + cP_1)}.$$

This is called the *distraction model*.

- Possibility 2: that interference takes precedence over feeding. Using that possibility, the predation rate  $F$  is given by

$$F = \frac{aH}{(1 + abH)(1 + cP_1)}.$$

This is called the *pre-emption model*.

In both cases,  $a$  is the attack coefficient,  $b$  is the time spent by the predator to process the prey and  $c$  is the interference coefficient.

For the distraction model, predation rates are most sensitive to predator density at intermediate prey densities; at high prey densities, increasing predator density has little inhibitory effect on predation rates. In the pre-emption model, predation rates are most sensitive to predator density at high prey densities. Therefore the effects of predator interference on feeding rate remain important all the time whether an individual predator is processing or searching for a prey. The authors provide a graphical comparison of the two models [15] which is shown in Fig. 3.5.1

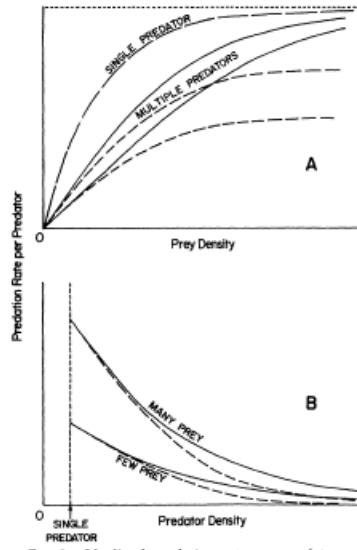


Figure 3.5.1: The distraction and pre-emption model (dashed lines)[15].

These are only a few types of biologically relevant models. Some other examples involve the Holling types [29], Holling-Tanner ratio-dependent type [64], Beddington-DeAngelis type [11, 24], Ivlev type [32], Rosenzweig-MacArthur model [53].

As mentioned in the introduction, we wish to use permanence/persistence to measure the thriving/survival of the species. The following chapter defines these concepts and provides methods to prove the existence of permanence/persistence in dynamical systems.

# Chapter 4

## Permanence of dynamical systems

The most frequently used modeling framework in mathematical biology is the autonomous ordinary differential equations of the form:

$$\dot{x}_i = x_i f_i(x). \tag{4.1}$$

Extinction or survival of the species are important points to consider for any ecological system. Stability notions have been introduced and studied in different manners: “cooperativity” by Schuster et al. [43], “permanent coexistence” by Hutson and Vickers [69], “permanence and viability” by Aubin and Sigmund [5].

Certain terms which will be referred to are defined below:

- A set is **invariant** for (4.1) if a solution with initial values in that set remains in the set for all time [31]. To be biologically relevant, (4.1) is only considered in the positive cone  $\mathbb{R}_+^n$ . A point to note is this set, its interior ( $\text{int}\mathbb{R}_+^n$ ) and its boundary ( $\partial\mathbb{R}_+^n$ ) are all invariant. Clearly points in  $\partial\mathbb{R}_+^n$  denote situations where at least one species is absent.



- To recall, a **fixed point/rest point/equilibrium point** is a point where the right-hand side of (4.1) is zero for each  $i$ .
- An **interior rest point** is a rest point in  $\text{int } \mathbb{R}_+^n$ .

## 4.1 Background information

In the paper ‘Permanence and dynamics of biological systems’ [31], the authors Hutson and Schmitt provide a historical background into the development of permanence. Stability notions in biology is a subject of considerable interest. The mathematical treatments of such notions which developed into a clear pattern is described.

For the system (4.1) it was required that there should be a unique interior rest point and it should be **globally asymptotically stable** (for initial values in  $\text{int } \mathbb{R}_+^n$ ), i.e. all perturbations would eventually be compensated for, and the system would return to the rest point. Volterra invented a rather clever Lyapunov function which proved the global asymptotic stability of the interior rest point. Unfortunately, the function worked for Lotka-Volterra equations of two species but it wasn’t adequate for dimension  $\geq 3$ .

Another criterion along the same lines is that of local asymptotic stability where it is only required that all orbits with initial values sufficiently close to the rest point should return to it. This property was shown using eigenvalues of the Jacobian of the right hand side of (4.1). If the eigenvalues had negative real parts, the rest point was locally stable. The drawback of this property is that ‘sufficiently close’ is not specific enough. Another question arose: why should there only be one interior rest point?

Also, why should the system even go to rest? There are examples (e.g. the lynx-hare cycle [56]) in which communities that oscillate violently could also survive perfectly well.

By the sixties, there were some doubts among biologists that either local or global asymptotic stability was not enough. Papers by R.C. Lewontin [55] and J. Maynard Smith [36] give an intuitive approach to **dynamic boundedness** and **permanence** which are predecessors of the formal concept of **permanence**. But there were no mathematical ideas that seemed helpful in treating these concepts. To meet these requirements, the idea of **weak persistence**, that is

$$\limsup_{t \rightarrow \infty} x_i(t) > 0 \quad \forall i \quad (4.2)$$

was introduced in [26]. A disadvantage of this concept is that orbits of a weakly persistent system may approach  $\partial\mathbb{R}_+^n$ .

The stronger condition of **permanence** that avoids this difficulty was introduced in [43] and is based on  $\partial\mathbb{R}_+^n$  being repelling. The system (4.1) is said to be permanent if there are numbers  $m, M$  with  $0 < m \leq M < \infty$  such that given any  $x = x(0) \in \text{int}\mathbb{R}_+^n$  there is a  $t_u$  such that

$$m \leq x_i(t) \leq M(t > t_u, i = 1, \dots, n). \quad (4.3)$$

Some obvious advantages of this definition are noted. First, it is global, the quantities  $m, M$  being independent of the initial values. Secondly, no solution can approach the boundary. Thirdly, only the behavior near  $\partial\mathbb{R}_+^n$  is relevant. Lastly, any asymptotic behavior consistent with (4.1) is allowed; even chaotic behavior. One clear disadvan-

tage is the definition does not say how large  $m$  need be.

A second approach to permanence can be traced to a paper by Freedman and Waltman [27] in 1984 where it is observed that a careful analysis of the flow in the boundary led to convenient conditions for **strong persistence** (similar to weak persistence except it is  $\liminf$ ).

Another approach to permanence is present in [5] where the authors talk about two concepts in non-equilibrium theory namely *permanence* and *viability*. They define system to be permanent if the boundary (including infinity) is an unreachable repellor, or equivalently if there exists a compact subset in the interior of the state space where all orbits starting from the interior eventually end up. They are mostly concerned with ecological equations of the type

$$\dot{x}_i = x_i f_i(x) \tag{4.4}$$

on  $\mathbb{R}_+^n$  or replicator equations

$$\dot{x}_i = x_i(f_i(x) - \sum x_i f_i) \tag{4.5}$$

which have been widely investigated in population genetics, population ecology, the theory of prebiotic evolution of self-replicating polymers and socio-biological studies of evolution.

They go on to state a sufficient condition for permanence with the help of an ‘average Lyapunov function’  $P$ . The function  $P$  is defined on the state space, vanishing on the boundary and strictly positive in the interior, such that  $\dot{P} = P\psi$  where  $\psi$  is a

continuous function with the property that for some  $T > 0$

$$\frac{1}{T} \int_0^T \psi(x(t)) dt > 0 \quad \forall x \text{ on the boundary .}$$

Permanence can also be usefully applied to systems of difference equations, differential equations with delays, functional differential equations.

They [5] then introduce the concept of *viability* for equations of the form

$$\dot{x} = f(x, u) \tag{4.6}$$

where  $u$  is a control depending on the state  $x$ , i.e.  $u \in F(x)$ . An additional constraint on the system is that it remains in a certain *viability domain*  $K$  which is assumed to be closed in  $\mathbb{R}^n$ . A trajectory solving (4.6) is viable if

$$x(t) \in K \quad \text{for all } t. \tag{4.7}$$

The restrictions at the boundary of  $K$  were described using the contingent cone to  $K$  at  $x$  defined by

$$T_k(x) = \left\{ v \in \mathbb{R}^n : \liminf_{h \rightarrow 0^+} \frac{d_k(x + hv)}{h} = 0 \right\}$$

where  $d_k(x + hv)$  is the distance from  $x + hv$  to  $K$ . They then introduce the feedback regulation map  $R$  defined by

$$R(x) = \{u \in F(x) | f(x, u) \in T_k(x)\} . \tag{4.8}$$

They observed that any viable trajectory of the controlled system is a solution to the ‘feedback’ differential inclusion (the function  $f$  is a set rather than a single point)

$$\dot{x} = f(x, u) \quad \text{with } u \in R(x). \quad (4.9)$$

A necessary and sufficient condition is also provided for viability. Interpretations of equation (4.6) and viable trajectories in biological evolution and economics is also discussed.

In the paper [39], the author analyzes ecological systems of the Lotka-Volterra type with one prey and several predators. The general form of the system considered by her is as follows:

$$\dot{x}_i = x_i \left( r_i - \sum_{j=1}^n a_{ij} x_j \right) \quad i = 1, 2, \dots, n \quad (4.10)$$

where  $x_i(t)$  denotes the density of species  $i$  at time  $t$ ,  $r_i$  its intrinsic growth rate and  $a_{ij}$  measures the action of species  $j$  upon the growth rate of species  $i$  (in particular  $a_{ii}$  represents the crowding effect within one species) [39]. One of main results of this paper is the following

**Theorem 4.1.1.** *Whenever system (4.10) is permanent or robustly weakly persistent the following three properties are valid:*

- i There exists an interior equilibrium.*
- ii The determinant of the interaction matrix  $A$  of the whole system is positive.*

*iii The determinant of the interaction matrix of any  $n - 1$  species subsystem is positive whenever the corresponding  $n - 1$  species fixed point exists.*

The system (4.10) is *robustly weakly persistent* if it remains weakly persistent under small perturbations of the parameters  $a_{ij}$ .

The author goes on to prove necessary and sufficient conditions for the permanence (or weak persistence) of three-species and four-species multiple predator models. The conditions are combinations of the ones listed above in Theorem 4.1.1.

The author also derived conditions for permanence in higher dimensional prey-predator systems linked by interspecific competition of prey in [38].

A paper which dealt with a non-traditional prey dependent model is ‘Persistence and Extinction of One-Prey and Two-Predators System’ by Dubey and Upadhyay [54]. They proposed and analyzed a mathematical model of one prey-two predators system in which the predator interference is based on the ratio-dependent theory. The two predators are in a state of competition for the single prey. Criteria for local stability, instability and global stability of the non-negative equilibria are also obtained. The paper then goes to obtain sufficient conditions for the permanent co-existence of the species.

Permanence of a local dynamical system in a topographical setting has also been addressed by the authors Fonda and Giodani [22]. They provide a necessary and sufficient condition for permanence. An illustrative application to a two-dimensional Lotka-Volterra model has also been provided.

Even permanence of non-autonomous two-dimensional predator-prey models were studied in [49]. These models were based on modified Leslie-Gower and Holling-Type II schemes and also incorporated a time-delay factor. Using Lyapunov functionals, sufficient conditions for the global stability of the solutions were also established.

Another paper that deals with non-autonomous systems is by Nie et al. [51]. They consider a multi-species Lotka-Volterra type competitive system with delays and feedback controls. They use the following condition to prove permanence:

$$m \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq M \quad (i = 1 \dots n)$$

for any positive solution  $(x_1(t), x_2(t), \dots, x_n(t), u_1(t), u_2(t), \dots, u_n(t))$ . Here  $u_i(t)$  are control variables. This is established in integral form and is independent of feedback controls.

In the paper ‘Dynamics of a non-autonomous ratio-dependent predator-prey system’ [73], the authors investigate a non-autonomous ratio-dependent predator-prey system. They use the same condition for permanence as in [51]. Their proof involves obtaining bounds on the derivatives of the solutions. Conditions for existence, uniqueness and stability of a positive periodic solution and a positive almost-periodic solution are obtained for the periodic and almost-periodic cases respectively.

The authors of [32] investigate a predator-prey system with a special type of functional response, namely the Ivlev-type. The Ivlev-type response which is both mono-

tonically increasing and uniformly bounded is given by

$$p(x) = h(1 - \exp(-cx)) \text{ where } c, h > 0$$

where  $p(x)$  is the predation rate,  $h$  the maximum rate of predation and  $c$  is a constant representing the decrease in motivation to hunt.

Impulsive control strategies containing a biological control (periodic impulsive immigration of the predator) and a chemical control (periodic pesticide spraying) have also been applied to the model. They derive conditions for permanence using the result

$$m \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq M \quad (i = 1 \dots n)$$

and by using the comparison results of impulsive differential inequalities. In addition to this, they also add a forcing term to the prey population's intrinsic growth rate and then find the conditions for the stability and for the permanence of the system.

The papers [63, 71] deal with permanence of Kolmogorov type (Section 3.2) non-autonomous systems. The authors of [71] deal with a system of partial differential equations. They are concerned with obtaining a condition of permanence for two-species Kolmogorov periodic predator-prey models with diffusion. They apply the average Lyapunov function method.

In [63], the authors also use the method of Lyapunov-like functions. They deal with the  $n$ -species Lotka-Volterra type systems with distributed delays (i.e. non-autonomous Lotka-Volterra system). They construct  $n$  Lyapunov-like functions which are regarded as boundary functions of some compact region inside the positive cone in  $\mathbb{R}^n$ .



Most of the papers reviewed dealt with continuous systems. The authors of [70] investigate the long term survival of species in models governed by Lotka-Volterra difference equations which are discrete dynamical systems. The criterion used is the definition of permanence, that is a system is permanent when the populations with all positive initial values must eventually all become greater than some fixed positive number. They derive applicable criteria for permanence in a wide range of cases.

The authors of [41] study Lotka-Volterra systems with  $N$  species and  $n$  resources with  $n < N$ . With a change of variables, they reduce the initial system to a system of  $n$  differential equations. They show the existence of chaotic behavior for such systems. They show this by taking a finite family of hyperbolic dynamics and generate a sufficiently large Lotka-Volterra model with an appropriate choice of parameters. The paper then goes to investigate the plankton paradox problem: how many species can share a bounded number of resources? To show this, they describe the construction of strongly persistent Lotka-Volterra systems, which have chaotic behavior. This indicates that the concepts of chaos and permanence are not mutually exclusive.

Some other papers which provide conditions for permanence/persistence and also observe chaos in the numerical simulations are [10, 67, 68] to name a few. Each of the papers investigates the two phenomena separately and does not mention a link between them.

The next section provides some methods to prove permanence in different systems.

## 4.2 Methods to prove permanence

From [35], a dynamical system is said to be permanent if there exists a  $\delta > 0$  such that  $x_i(0) > 0$  for  $i = 1 \dots n$  implies

$$\liminf_{t \rightarrow +\infty} x_i(t) > \delta$$

for  $i = 1 \dots n$ .

Here  $\delta$  does not depend on the initial values  $x_i(0)$ .

This section gives a summary of some methods to prove permanence since using the general definition of permanence is hard. One subsection deals with permanence in Lotka-Volterra systems. The next subsection deals with permanence in biologically relevant systems using boundary rest points and the last shows how to prove permanence using a type of an average Lyapunov function.

### 4.2.1 Necessary and sufficient conditions for permanence of Lotka-Volterra systems

This subsection gives a necessary and sufficient condition for permanence of Lotka-Volterra system. An example of how to use the theorem is provided. Additionally, the condition is also used to show how chaos could be related to permanence.

In pages 206-207 of [35] the necessary and sufficient conditions for permanence of a Lotka-Volterra system  $\dot{x} = x(r + Ax)$ , where  $x \in \mathbb{R}^n$ ,  $r$  is the vector growth (or death) rates and  $A$  is the interaction matrix, are specified as follows.

1. There exists an interior rest point  $\hat{x} = (\hat{x}_1, \hat{x}_2, \hat{x}_3)$  (i.e.  $\hat{x}_1 > 0, \hat{x}_2 > 0, \hat{x}_3 > 0$ )
2.  $\det(-A) > 0$
3. The two species subsystems are uniformly bounded and not bistable.

For example, if the two-species subsystem (say  $x_3 = 0$ ) is mutualistic and the determinant  $a_{11}a_{22} - a_{12}a_{21} > 0$ , it was seen in Section 3.1.1 that the interior rest point is stable.

Or if the system is competitive, it has a stable interior rest point or only one stable rest point at the boundary.

Another point to note, this condition excludes the cases when the interior rest point is a saddle (when the subsystem has **two** boundary rest points) or the degenerate cases of a line of rest points or that the isoclines intersect on an unstable rest point on a coordinate axis [35].

4. If the system admits a heteroclinic cycle, then the following equation holds:

$$\prod_{i=1}^3 (\alpha_i - 1) < \prod_{i=1}^3 (1 - \beta_i) \quad (4.11)$$

where  $\alpha_i, \beta_i$  are as defined in Section 3.1.2.2.

If the system satisfies all 4 conditions, then it is **robustly permanent**. If it satisfies just the first three, then it is permanent. An example of a permanent and chaotic Lotka-Volterra system is shown in Section 4.2.1.1.

#### 4.2.1.1 Example of a permanent and chaotic Lotka-Volterra system

Let us consider an example of a Lotka-Volterra system [35] that is both permanent and chaotic [23].

The three-dimensional Lotka-Volterra system under consideration is as follows:

$$\dot{x}_i = x_i \left( r_i + \sum_{j=1}^3 a_{ij} x_j \right) \quad i = 1, 2, 3 \quad (4.12)$$

with

$$r_1 = 1, \quad r_2 = 1, \quad r_3 = -1 \quad \text{and} \\ A = \begin{bmatrix} -1 & -1 & -10 \\ -1.5 & -1 & -1 \\ 5 & 0.5 & -0.01 \end{bmatrix}.$$

The expanded version of the Lotka-Volterra equations is

$$\begin{aligned} \dot{x}_1 &= x_1 (1 - x_1 - x_2 - 10x_3) \\ \dot{x}_2 &= x_2 (1 - 1.5x_1 - x_2 - x_3) \\ \dot{x}_3 &= x_3 (-1 + 5x_1 + 0.5x_2 - 0.01x_3). \end{aligned} \quad (4.13)$$

#### 4.2.1.2 Permanence criterion for the system

**Lemma 4.2.1.** *The system (4.13) is permanent.*

*Proof.* Let us consider each of the conditions for permanence for the system (4.13).

1. There exists an interior rest point

(.1184366364, .8157652323, 0.6579813133e - 2) given by solving the following system:

$$\begin{aligned}
1 - x_1 - x_2 - 10x_3 &= 0 \\
1 - 1.5x_1 - x_2 - x_3 &= 0 \\
1 + 5x_1 + 0.5x_2 - 0.01x_3 &= 0
\end{aligned} \tag{4.14}$$

2.  $\det(-A) = 37.995 > 0$

3. Next we consider each two-species subsystem which are uniformly bounded:

Case 1:  $x_3 = 0$ . The subsystem is as follows:

$$\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - x_2) \\
\dot{x}_2 &= x_2(1 - 1.5x_1 - x_2)
\end{aligned}$$

So this system is competitive and it has only one stable rest point  $(x_1 = 1, x_2 = 0)$  at the boundary and thus it is not bistable.

Case 2:  $x_2 = 0$ . The subsystem is as follows:

$$\begin{aligned}
\dot{x}_1 &= x_1(1 - x_1 - 10x_3) \\
\dot{x}_3 &= x_3(-1 + 5x_1 - 0.01x_3)
\end{aligned}$$

This subsystem is neither mutualistic or competitive. It has an interior rest point namely  $x_1 = 0.2001599680$ ,  $x_3 = 0.07998400320$ . This rest point is stable as the Jacobian at this point has eigenvalues with negative real parts

and as in Section 3.1.1. So this subsystem is also not bistable.

Case 3:  $x_1 = 0$ . The subsystem is as follows:

$$\begin{aligned}\dot{x}_2 &= x_2(1 - x_2 - x_3) \\ \dot{x}_3 &= x_3(-1 + 0.5x_2 - 0.01x_3)\end{aligned}$$

This subsystem is neither mutualistic or competitive. It does not have an interior rest point. As seen in Section 3.1.1, the orbits all converge to the rest point on the coordinate axes, namely  $(x_2 = 1, x_3 = 0)$ . So again the system is not bistable.

4. A heteroclinic cycle exists if there are 3 one species rest points, namely  $F_1, F_2, F_3$  (from Section 3.1.2.2). The one species rest points  $F_i$  exist if  $r_i > 0$  and  $a_{ii} < 0$  for  $i = 1, 2, 3$ . In our example,

$$\begin{aligned}r_1 &= 1 > 0 \text{ and } a_{11} = -1 < 0 \\ r_2 &= 1 > 0 \text{ and } a_{22} = -1 < 0 \\ r_3 &= -1 < 0 \text{ and } a_{33} = -0.01 < 0.\end{aligned}$$

So we can see that  $F_3$  does not exist and hence a heteroclinic cycle does not exist.

Thus our system is permanent. □

#### 4.2.1.3 Stability analysis

Table 4.2.1 provides the stability analysis for the Lotka-Volterra system (4.13). The Lyapunov spectrum has been calculated only for points with negative divergence. The negative divergence indicates the solutions are bounded.

Rest point $((x_1, x_2, x_3))$	Eigenvalues	Stability	Maximum Lyapunov exponent	Divergence
$(0, 0, 0)$	1 1 -1	Unstable	N/A	positive
$(0, 1, 0)$	-1 0 -0.5	Unstable	0.0009	negative
$(1, 0, 0)$	-1 -0.5 4	Unstable	N/A	positive
$(.2001599680, 0., 0.079984)$	$-.100479904032000 + 0.889125222282289I$ $-.100479904032000 - 0.889125222282289I$ $0.619776044800000$	Unstable	N/A	positive
$(.1184366364, .8157652323, 0.6579813133e - 2)$	$-.966926554652232$ $0.163294437447653e - 1 + 0.157205778092898I$ $0.163294437447653e - 1 - 0.157205778092898I$	Unstable	0.0241	negative

Table 4.2.1: Maximum Lyapunov Exponent for rest points of (4.13).

As is seen in Table 4.2.1, chaos is observed for the interior rest point  $(.1184366364, .8157652323, 0.6579813133e - 2)$ .

The chaotic manifold is shown in Fig. 4.2.1

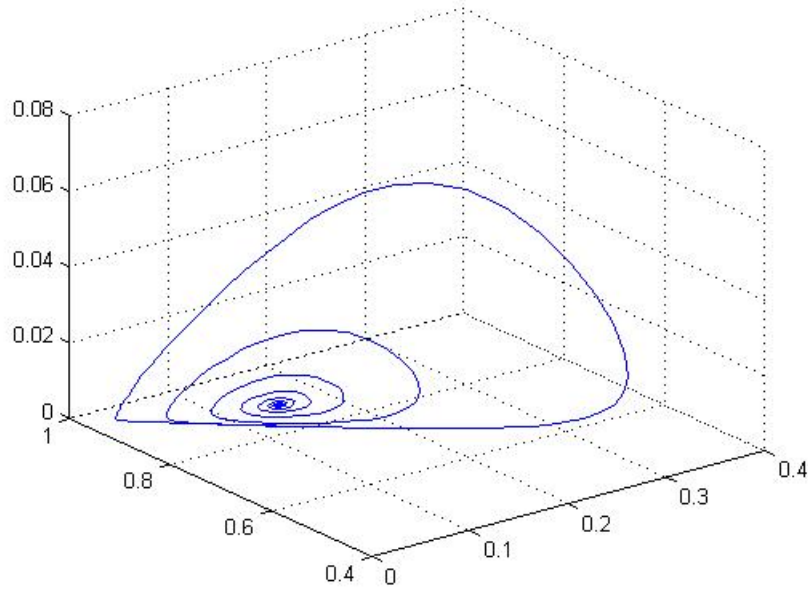


Figure 4.2.1: Lotka-Volterra attractor for system (4.13).



#### 4.2.1.4 Does chaos imply permanence in three-dimensional Lotka-Volterra systems?

We wish to use the necessary and sufficient conditions for permanence specified in Section 4.2.1 to find a connection between chaos and permanence of some Lotka-Volterra systems.

Consider the following general three-dimensional two prey, one predator Lotka-Volterra system with  $a_{ii} < 0$  for  $i = 1, 2, 3$ :

$$\begin{aligned} \dot{x}_1 &= x_1 (1 + a_{11}x_1 + a_{12}x_2 + a_{13}x_3) \\ \dot{x}_2 &= x_2 (1 + a_{21}x_1 + a_{22}x_2 + a_{23}x_3) \\ \dot{x}_3 &= x_3 (-1 + a_{31}x_1 + a_{32}x_2 + a_{33}x_3) \end{aligned} \tag{4.15}$$

where  $r = \begin{bmatrix} 1 \\ 1 \\ -1 \end{bmatrix}$  and  $A = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$

The interior rest point is obtained by solving

$$-r = Ax \tag{4.16}$$

Recall the necessary and sufficient conditions for permanence

1. There exists an interior rest point  $\hat{x} = (\hat{x}_1, \hat{x}_2, \hat{x}_3)$  (i.e.  $\hat{x}_1 > 0, \hat{x}_2 > 0, \hat{x}_3 > 0$ )
2.  $\det(-A) > 0$
3. The two species subsystems are uniformly bounded and not bistable.

4. If the system admits a heteroclinic cycle, then the following equation holds:

$$\prod_{i=1}^3 (\alpha_i - 1) < \prod_{i=1}^3 (1 - \beta_i) \quad (4.17)$$

where  $\alpha_i, \beta_i$  are as defined in Section 3.1.2.2.

In our case, since  $r_3 < 0$  and  $a_{33} < 0$ , therefore  $F_3$  does not exist and hence a heteroclinic cycle does not exist.

**Theorem 4.2.2.** *Assume there exists a chaotic orbit near the interior rest point which implies the interior rest point is unstable and the orbit is bounded and aperiodic. Then the system (4.15) is permanent when  $b = x_1x_2M_{33} + x_2x_3M_{11} + x_1x_3M_{22} < 0$ , where  $M_{ii}$  is the minor of the Jacobian  $D$  at the unique rest point  $\bar{x}$ . Also assuming the eigenvalues of  $D$  are real.*

*Proof.*  $D$  denotes the Jacobian of (4.15) at the unique interior rest point  $\bar{x}$ . We have the following results:

- From linear algebra, the determinant of a matrix is the product of the eigenvalues and the trace is the sum of the eigenvalues.
- Descartes' Rule of sign states that if the terms of a single-variable polynomial with real coefficients are ordered by descending variable exponent, then the number of positive roots of the polynomial is equal to the number of sign differences between consecutive nonzero coefficients.
- An orbit is bounded if the divergence at the initial condition is negative, i.e. the trace of the Jacobian at the initial condition is negative.

- We have a relationship between the Jacobian  $D$  and the matrix  $A$ :

$$D = [d_{ij}] = [\bar{x}_i a_{ij}] \implies \det(D) = \bar{x}_1 \bar{x}_2 \bar{x}_3 \det(A) \quad (4.18)$$

From (4.18), we have that  $\det(D)$  and  $\det(A)$  have the same sign.

- Also since the interior rest point is unique,  $A$  is non-singular, i.e.,  $\det(A) \neq 0 \implies \det(D) \neq 0$ . This implies that the eigenvalues of  $D$  are non-zero.

### Sign analysis

Since the rest point is unstable, at least one eigenvalue of the Jacobian  $D$  has a positive real part. The possible sign combinations of the real eigenvalues are as follows:

Case 1 + + +

Case 2 + + -

Case 3 + - -

Case 1 cannot occur as the orbit is bounded, therefore the trace is negative and at least one eigenvalue is negative.

We are hoping that a chaotic orbit near the rest point can replace one or more conditions for permanence of Lotka-Volterra systems. Considering the condition  $\det(-A) > 0 \implies \det(A) < 0$  and  $\therefore \det(D) < 0$ , we can exclude Case 3 as well.

Consider the Case 2 + + - of the real eigenvalues. The characteristic equation of  $D$  is

$$x^3 - \text{trace}(D)x^2 + bx - \det(D) = 0 \quad (4.19)$$

where  $b = x_1x_2M_{33} + x_2x_3M_{11} + x_1x_3M_{22}$ ,  $\text{trace}(D) < 0$ ,  $\det(D) < 0$ . Since we have two positive eigenvalues, for two sign changes in the coefficients of the equation, we should have  $b < 0$  by Descartes' Rule of sign.

Consider the two species subsystems:

Case:  $x_3 = 0$     1. Stable interior rest point which implies  $M_{33} > 0$ ,  $a_{12} > a_{22}$  and  $a_{21} > a_{11}$   
or

2. Only one stable rest point at the boundary  $a_{11} > a_{21}$  or  $a_{12} > 0$ .

Case:  $x_2 = 0$     1. Stable interior rest point which implies  $M_{22} > 0$ ,  $-a_{13} > a_{33}$   
and  $a_{31} + a_{11} > 0$

2. Only one stable rest point at the boundary  $-a_{11} > a_{31}$ .

Case:  $x_1 = 0$     1. Stable interior rest point which implies  $M_{11} > 0$ ,  $-a_{33} - a_{23} > 0$   
and  $a_{32} + a_{22} > 0$

2. Only one stable rest point at the boundary  $-a_{22} > a_{32}$ .

Combinations of the above cases could give us  $b < 0$  thus leading to two positive eigenvalues. This then leads to  $\det(D) < 0$  which leads to our second condition for permanence by the relation (4.18). The previous analysis implies that chaos does in fact give rise to permanence under certain parameter values.  $\square$

This analysis unfortunately only uses the unstable nature of the interior rest point which can happen even in non-chaotic cases. Also this is specific to the three-dimensional two prey, one predator Lotka-Volterra system with  $a_{ii} < 0$  for  $i = 1, 2, 3$ .

### 4.2.2 Condition for permanence using boundary rest points

As mentioned before, the general definition of permanence is hard to apply. The following definitions will be needed for Theorem 4.2.3 to prove permanence of systems using boundary rest points (i.e., boundary rest points are rest points with at least one coordinate is zero).

- A rest point  $\bar{x}$  of (4.1) is **saturated** if  $f_i(\bar{x}) \leq 0$  for all  $i$  (the equality sign must hold whenever  $\bar{x}_i > 0$ ). A rest point in the interior is trivially saturated. The quantities  $f_i(\bar{x})$  are the eigenvalues of the Jacobian of (4.1) at  $\bar{x}$  whose eigenvectors are transversal to the boundary face of  $\bar{x}$ . Thus they are called **transversal eigenvalues**.
- A **degenerate saturated rest point** is one which has a zero transversal eigenvalue.
- A **regular rest point** is one which has non-zero eigenvalues.
- If  $\bar{x}$  is a regular rest point of (4.1), then the **index**  $\mathbf{i}(\bar{x})$  is the sign of the Jacobian  $D_{\bar{x}}f$ . Hence

$$\mathbf{i}(\bar{x}) = (-1)^k$$

where  $k$  is the number of real negative eigenvalues of the Jacobian. For  $n = 2$ , for example, the index of a center, a sink or a source is  $+1$ , while that of a saddle is  $-1$  [35].

**Theorem 4.2.3.** *If the system  $\dot{x}_i = x_i f_i(x_1, x_2, \dots, x_n)$   $i = 1, 2, \dots, n$ , does not have regular saturated boundary rest points, it is permanent [28].*

*Proof.* Proof can be found in the paper [28]. □

#### 4.2.2.1 Permanence of Lotka-Volterra system (4.13) using boundary rest points

Let us also consider the nature of the rest points of the Lotka-Volterra system in Section 4.2.1.1 given by

$$\begin{aligned} \dot{x}_1 &= x_1 (1 - x_1 - x_2 - 10x_3) \\ \dot{x}_2 &= x_2 (1 - 1.5x_1 - x_2 - x_3) \\ \dot{x}_3 &= x_3 (-1 + 5x_1 + 0.5x_2 - 0.01x_3) \end{aligned} \tag{4.20}$$

at the boundary:

Rest point	Value of $f_i$
$(0, 0, 0)$	$f_1(0, 0, 0) = 1 > 0$ $f_2(0, 0, 0) = 1 > 0$ $f_3(0, 0, 0) = -1 < 0$
$(1, 0, 0)$	$f_2(1, 0, 0) = -0.5 < 0$ $f_3(1, 0, 0) = 4 > 0$
$(0, 1, 0)$	$f_1(0, 1, 0) = 0$ $f_3(0, 1, 0) = -0.5 < 0$
$(0.2001599680, 0, 0.07998400320)$	$f_2(0.2, 0, 0.08) = 0.62 > 0$

Table 4.2.2: Check of permanence of Lotka-Volterra system (4.13) using boundary rest points.

The rest point  $(0, 1, 0)$  is a degenerate saturated rest point (i.e. one transversal eigenvalue is 0) which is allowed for permanence. We have also seen it is chaotic in Section 4.2.1.1.

### 4.2.3 Condition for permanence using average

#### Lyapunov functions

From [35] we have an additional method to prove permanence:

**Theorem 4.2.4.** *Let us consider a dynamical system on  $S_n$  leaving the boundary invariant. Let  $\sigma : S_n \rightarrow \mathbb{R}$  be a differentiable function vanishing on the boundary of  $S_n$  ( $bdS_n$ ) and strictly positive in the interior of  $S_n$  ( $intS_n$ ). If there exists a continuous function  $\psi$  on  $S_n$  such that the following two conditions hold*

$$\text{for } x \in intS_n, \quad \frac{\dot{\sigma}(x)}{\sigma(x)} = \psi(x) \quad (4.21)$$

$$\text{for } x \in bdS_n, \quad \int_0^T \psi(x(t))dt > 0 \text{ for some } T > 0, \quad (4.22)$$

*then the dynamical system is permanent.*

The proof of the theorem is given in pages 147-148 of [35]. Here the function  $\sigma(X)$  is said to be an *average Lyapunov function* since its time average acts like a Lyapunov function.

#### 4.2.3.1 Example of a permanent and chaotic food-chain model with Crowley-Martin type functional response

In [68], a three-species food-chain model, consisting of a hybrid type of prey-dependent and predator-dependent functional responses is investigated for persistence and chaos. We shall also derive conditions for permanence using the theorem in Section 4.2.3 for the parameter values given in [68] that give chaos.



The model simulates a tritrophic level food chain (a food chain with three levels: a prey, an intermediate predator and the top predator) and is given below

$$\begin{aligned}\dot{X} &= a_1X(1 - \frac{X}{K} - \frac{wXY}{X+D}) \\ \dot{Y} &= -a_2Y + \frac{w_1XY}{X+D_1} - \frac{w_2YZ}{1+dY+bZ+bdYZ} \\ \dot{Z} &= -cZ + \frac{w_3YZ}{1+dY+bZ+bdYZ}\end{aligned}$$

Here  $X(T)$  denotes the population density of the prey,  $Y(T)$  denotes the population density of the intermediate predator and  $Z(T)$  denotes the population density of the top predator. The intermediate predator  $Y$  feeds on the prey  $X$  according to the Holling type-II (or Michaelis-Menten- Holling, Section 3.3) functional response and the top predator  $Z$  preys upon  $Y$  according to the Crowley-Martin type functional response (Section 3.5).

The parameters are defined as follows:

- $a_1$ : intrinsic growth rate of the prey;
- $K$ : carrying capacity of the prey in absence of predation;
- $w, w_1$ : maximum value which per capita reduction rate of  $X$  can attain;
- $D, D_1$ : measure the extent to which the environment can provide protection to prey  $X$  and  $Y$  respectively;
- $w_2, w_3, b, d$ : saturating Crowley-Martin type functional response parameters in which  $b$  measures the interference among the predators;
- $a_2, c$ : death rates of predators  $Y$  and  $Z$  respectively.

The authors reduced the number of parameters by non-dimensionalizing the model by using the following conversions:

$$t = a_1 T, x = \frac{X}{K}, y = \frac{wY}{a_1 K}, z = \frac{w w_2 Z}{a_1^2 d K}, w_4 = \frac{D}{K}, w_5 = \frac{a_2}{a_1}, w_6 = \frac{w_1}{a_1}$$

$$w_7 = \frac{D_1}{K}, w_8 = \frac{a_1 b}{w_2}, w_9 = \frac{a_1^2 b d K}{w w_2}, w_{10} = \frac{w}{a_1 d K}, w_{11} = \frac{c}{a_1}, w_{12} = \frac{w_3}{a_1 d}.$$

The dimensionless equations are:

$$\begin{aligned}\dot{x} &= x \left[ (1-x) - \frac{y}{x+w_4} \right] \\ \dot{y} &= y \left[ -w_5 + \frac{w_6 x}{x+w_7} - \frac{z}{y+(w_8+w_9 y)z+w_{10}} \right] \\ \dot{z} &= z \left[ -w_{11} + \frac{w_{12} y}{y+(w_8+w_9 y)z+w_{10}} \right]\end{aligned}$$

The paper goes on to provide conditions for boundedness of the system and existence of the rest points both boundary and interior. The boundary rest points are given by

$$E_0 = (0, 0, 0), E_1 = (1, 0, 0) \text{ and } E_2 = (\tilde{x} = \frac{w_5 w_7}{w_6 - w_5}, \tilde{y} = (1 - \tilde{x})(\tilde{x} + w_4), 0).$$

$E_0, E_1$  always exist and  $E_2$  exists if

$$0 < \frac{w_5 w_7}{w_6 - w_5} < 1 \tag{4.23}$$

The parameter values given in [68] are as follows:

$$w_4 = 0.25, w_6 = 0.8, w_7 = 0.25, w_8 = 0.01, w_9 = 0.1, w_{10} = 0.28, w_{12} = 0.25.$$

The system is given by

$$\begin{aligned}\dot{x} &= x \left[ (1-x) - \frac{y}{x+0.25} \right] \\ \dot{y} &= y \left[ -w_5 + \frac{0.8x}{x+0.25} - \frac{z}{y+(0.01+0.1y)z+0.28} \right] \\ \dot{z} &= z \left[ -w_{11} + \frac{0.25y}{y+(0.01+0.1y)z+0.28} \right].\end{aligned}\tag{4.24}$$

The authors choose to vary the death rates of the predators, namely  $w_5, w_{11}$  to check for chaos. The conditions for permanence will be in terms of the very same parameters.

**Theorem 4.2.5.** *Assuming the rest points  $E_0, E_1, E_2$  exist and using Theorem 4.2.4 (Section 4.2.3), we need*

$$-w_{11} + \frac{0.25\tilde{y}}{\tilde{y}+0.28} > 0$$

*for the system (4.24) to be permanent.*

*Proof.* Let the Lyapunov function be

$$\sigma(X) = x^{p_1} y^{p_2} z^{p_3}$$

where  $p_1, p_2, p_3 > 0$  and are constants. Clearly  $\sigma(X)$  is a non-negative  $C^1$  function defined in  $\mathbb{R}_+^3$ .

Consider

$$\begin{aligned}
\psi(X) &= \frac{\dot{\sigma}(X)}{\sigma(X)} \\
&= p_1 \frac{\dot{x}}{x} + p_2 \frac{\dot{y}}{y} + p_3 \frac{\dot{z}}{z} \\
&= p_1 \left( (1-x) - \frac{y}{x+0.25} \right) \\
&\quad + p_2 \left( -w_5 + \frac{0.8x}{x+0.25} - \frac{z}{y+(0.01+0.1y)z+0.28} \right) \\
&\quad + p_3 \left( -w_{11} + \frac{0.25y}{y+(0.01+0.1y)z+0.28} \right)
\end{aligned}$$

The condition for the existence of  $E_2$  is given by 4.23 and there are no periodic orbits in the boundary.

To obtain permanence, we need to show  $\psi(X) > 0 \forall$  equilibria  $X \in \text{bd}\mathbb{R}_+^3$ , i.e. the following conditions have to be satisfied:

$$\psi(E_0) = p_1 - p_2 w_5 - p_3 w_{11} > 0 \quad (4.25a)$$

$$\psi(E_1) = p_2 \left( -w_5 + \frac{0.8}{1.25} \right) - p_3 w_1 > 0 \quad (4.25b)$$

$$\psi(E_2) = p_3 \left( -w_{11} + \frac{0.25\tilde{y}}{\tilde{y}+0.28} \right) > 0 \quad (4.25c)$$

We note that by increasing  $p$  to a sufficiently large value,  $\psi(E_0)$  can be made positive.

From (4.23), and by making  $p_2$  sufficiently large,  $\psi(E_1) > 0$ .

From (4.25c):

$$-w_{11} + \frac{0.25\tilde{y}}{\tilde{y}+0.28} > 0 \quad (4.26)$$

and if (4.26) is satisfied,  $\psi(E_2) > 0$  and thus, we obtain permanence.  $\square$

So to obtain permanence using an average Lyapunov function, we need conditions (4.23) and (4.26).

#### 4.2.3.2 Parameters for which chaos is obtained

In [68], chaos was obtained for  $w_5 = 0.25$  and  $w_{11} = 0.01, 0.035$ .

When  $w_5 = 0.25$ , Condition (4.23), namely  $0 < \frac{w_5 w_7}{w_6 - w_5} < 1$ , is satisfied with  $E_2 = (\tilde{x}, \tilde{y}, 0) = (0.1136, 0.3222, 0)$ .

Condition (4.26) (i.e.  $-w_{11} + \frac{0.25\tilde{y}}{\tilde{y} + 0.28} > 0$ ) from the proof becomes  $w_{11} < 0.1407$  which is satisfied by both given values of  $w_{11}$ . So the system is both chaotic and permanent.

They also obtained chaos for  $w_5 = 0.375$  and  $w_{11} = 0.03$ .

When  $w_5 = 0.375$ , Condition (4.23) is satisfied with  $E_2 = (0.2206, 0.3668, 0)$  and

Condition (4.26) becomes  $w_{11} < 0.1118$  which is again satisfied by the given value of  $w_{11}$ . So the system is both chaotic and permanent.

The chaotic manifold when  $w_5 = 0.25$  and  $w_{11} = 0.01$  is recreated in Fig. 4.2.2.

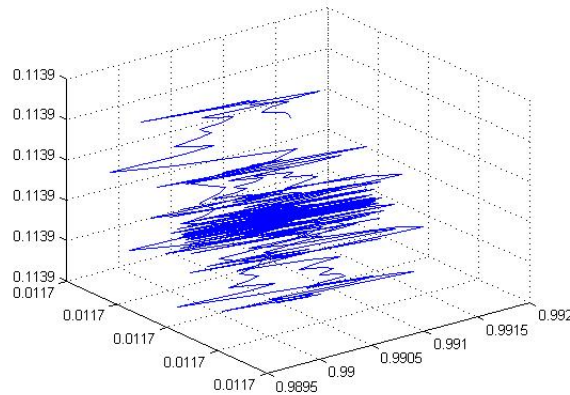


Figure 4.2.2: Chaotic attractor when  $w_5 = 0.25$  and  $w_{11} = 0.01$ .

## 4.3 Chaos implies persistence in three-dimensional systems

As mentioned before, both chaos and persistence have been studied separately for the same model ([10, 67, 68]). Previously, a connection between these two concepts had not been established. We establish a link between chaos and persistence in three-dimensional systems using the Poincaré–Bendixson Theorem.

**Theorem 4.3.1.** *Assuming there are no crisis manifolds, three dimensional biologically relevant systems  $\dot{x} = xf(x)$  where  $x \in \mathbb{R}^3$  which exhibit chaotic behavior (i.e. they have a positive Lyapunov exponent) are also persistent (i.e.  $\limsup_{t \rightarrow +\infty} x_i(t) > 0$  for  $i = 1, 2, 3$ ).*

*Proof.* If the trajectory of a chaotic orbit touches the boundary of  $\mathbb{R}^3$  (i.e., one of the species becomes extinct), the system would become two-dimensional. By the Poincaré–Bendixson Theorem, two-dimensional systems cannot exhibit chaos. So the orbit couldn't revert to its chaotic state. Thus the system is persistent.  $\square$

We will further investigate how chaotic orbits present in any continuous system can be used to push the system into permanence. We shall use control theory which is detailed in the chapters that follow.

# Chapter 5

## Control using chaos

As we saw in the Section 4.3, chaos does imply persistence in three-dimensional systems. However, it is hard to prove this result analytically for higher dimensional systems. In this chapter, we consider systems which are chaotic and non-permanent. To show how chaos can be beneficial to the system, i.e. how it can be used to obtain permanence, we employ control theory on the chaotic orbits to push the system into permanence.

Using controls on the chaotic nature of the system, we obtain a desired state without changing the system completely. The first section gives a brief description of different control methods which use chaos to control the system. The next section gives a summary of the linear quadratic regulator (LQR) method [57]. The last section describes the control algorithm from [66] which will be used in the next chapter to push the system from non-permanence to permanence.

## 5.1 Background information

This section provides a short review of some methods for using chaos for control.

Among the first proponents of using a chaotic attractor to control a system were E. Ott, C. Grebogi and J. A. Yorke in [25]. They observed that a chaotic attractor has typically embedded within it an infinite number of unstable periodic orbits. They wished to use these existing unstable orbits. Their approach was to first determine some of the unstable low-period periodic orbits that are embedded in the chaotic attractor. They then chose one which yields improved system performance. They then tailored their small time-dependent parameter perturbations so as to stabilize the existing orbit.

They note that if the attractor is not chaotic but periodic, then small parameter perturbations can only change the orbit slightly. This makes it hard to improve the system without making large alterations to the existing system.

They then go on to describe the popular method which is now described as the **OGY** method with a numerical example. The method utilizes delay coordinate embedding, and so is applicable to experimental situations in which *a priori* analytical knowledge of the system dynamics is not available.

In the ecological context, the method is applicable in the control of pests, insects and other natural populations, offering a fast converging solution [61]. A simple numerical example was also explored to support this claim.



Two other popular control methods using chaos were suggested by K.Pyragas in [42]. Both methods (known as **Pyragas methods**) were control in the form of feedback. They were based on the construction of a special form of a time-continuous perturbation, which does not change the form of the desired unstable periodic orbit, but under certain conditions can stabilize it. The first method used a combined feedback with a periodic external force of a special form. The second method did not require any external force, but it was based on a self-controlling delayed feedback. Both the methods are applicable to experimental situations. In particular, the second method does not require any computer analysis of the system and can be thus more convenient in an experimental setting. The methods were applied to the Lorenz and Rössler systems.

Both the Pyragas and OGY methods are part of a general class of methods called **closed loop** or **feedback** methods which can be applied based on knowledge of the system obtained through solely observing the behavior of the system as a whole over a suitable period of time.

The paper [50] provided a method that converted a chaotic attractor to a desired attracting time periodic motion by controlling temporal perturbations through an accessible system parameter. The time periodic motion is obtained by stabilizing one of the infinite number of unstable periodic orbits embedded in the chaotic attractor. They applied the method to two discrete systems, namely the Hénon map and to a periodically forced mechanical system (a four-dimensional map). This method is applicable to continuous systems as well by considering the discrete time system obtained from the induced dynamics on a Poincaré section.

The paper did not discuss the effect of noise. Also the paper has only considered

a case where there is only a single control parameter available for adjustment. An advantage of the method is that it can be applied even without full knowledge of the system dynamics. It only requires the location of the desired periodic orbit, the linearized dynamics about the periodic orbit, and the dependence of the location of the periodic orbit on small variation of the control parameter.

The author of [19] states that there is an evolutionary advantage of controlling chaos. A chaotic system has many different patterns of motion. Very small changes in the initial conditions can greatly alter the system's trajectory. The author uses the one-dimensional Ricker's difference model to explain how these properties can be exploited to control the chaotic dynamics of a population. In some cases, the population can apply some small perturbations to itself and can drive the density of the population to a stable state.

In [74], the authors present a method to demonstrate that species extinctions due to transient chaos can be effectively prevented by applying small, ecologically feasible perturbations to the populations at appropriate but rare times. Transient chaos occurs when the tip of the chaotic attractor touches the basin boundary (i.e. a *crisis*). The crisis creates 'holes' on the basin boundary from which trajectories can now leak through the holes and enter a region where one species goes extinct. If it is determined that the populations are close to a dangerous region, small but deliberately chosen perturbations to the population can be applied to guarantee that no immediate exit from the hole occurs.

The authors Sprott et al. [37] applied a periodic perturbation to an accessible system parameter of several different chaotic systems of increasing dimension. This kind of control is an example of an open-loop control scheme (i.e. the control is

independent of the system's state). The numerical systems that were examined in [37] were the logistic equation (a one-dimensional quadratic map), the Lorenz equations (a three-dimensional quadratic flow), the Rössler equations (another three-dimensional quadratic flow), a coupled Lorenz cell model (a 96-dimensional polynomial flow), the Yoshida equations, which model magnetic fluctuations in a plasma fusion device (a nine-dimensional polynomial flow), and a neural net model for a fluctuating plasma (a 64-dimensional nonlinear map). In every case, the optimum frequency to obtain control was found to be the frequency of the unstable periodic orbit obtained from the dynamical fluctuations of the system. Also the perturbation amplitude applied was minimum. They also found that a given frequency could stabilize more than one unstable orbit and that the best frequencies to perturb were not always the ones with the most power.

The author of [66] first provides a motivation of why chaotic behavior in nonlinear systems is useful to set up a control design. He mentions that chaotic behavior is useful in moving a system to various points in the state space without changing the system drastically. The reasoning is very similar to the one used by the creators of the OGY method [25]. The paper then gives a chaotic control algorithm where two ingredients are needed: a chaotic attractor and a **controllable target**. If chaos does not exist, it can be created using **open loop control** (where the control function  $U$  is a function of time). A controllable target is any subset of the domain of attraction to an equilibrium point, under a corresponding feedback control law, that has a non-empty intersection with the chaotic attractor [66]. The controllable target should be large enough so that one does not have to wait too long for the system to reach it. The method is as follows [66].

The system is first linearized about the desired fixed point solution. If necessary,

a feedback controller is then designed so that this reference solution has suitable stability properties.

Then, based on this stable linear system, a Lyapunov function is obtained. For this function, a level curve is determined such that, whenever the state of the nonlinear system is within this level curve, the feedback controller will drive the nonlinear system to the desired equilibrium solution.

The **Linear Quadratic Regulator (LQR)** method is used to design the full state variable feedback controller that will assure the asymptotic stability of the origin.

The chaotic control algorithm is then used with three different systems viz the Hénon map, bouncing ball system, two-link pendulum system. The first two are discrete and the third is a four-dimensional continuous system. Further detailed examples on how to control an inverted pendulum and a bouncing ball were provided in [72].

The paper [47] studied the optimal stabilization of the steady state of a Lotka-Volterra model. They did this by introducing control functions to the system. The functions ensuring the required stabilization was obtained as a function of the state variables. Two-dimensional models were presented as examples and numerical simulation was also presented. In addition, they also looked into the optimal control ensuring the synchronization of these models which is not relevant to this thesis.

As a follow-up to [47], the optimal control of the Lorenz system with unknown parameters was studied in [58]. Controls were introduced in each equation. Based on the Lyapunov-Bellman method, an optimal control law was obtained such that the trajectory of the Lorenz system is optimally stabilized to an equilibrium point of the uncontrolled system. Further, another optimal control law is also applied to achieve the state synchronization of two identical Lorenz systems. Numerical results

to demonstrate the effectiveness of the proposed control scheme were also provided.

In [48], an investigation on optimization of the feedback control of chaos is carried out. The main objective is to show that evolutionary algorithms can be used for this optimization. The stochastic optimization algorithm SOMA (self-organizing migrating algorithm) was used in four versions. This algorithm is based on the social behavior of competitive-cooperating individuals. The one-dimensional logistic equation and two-dimensional Henon map were used as examples of deterministic chaotic systems. For each version of the algorithm, simulations were carried out to show and check for robustness of applied method as compared to the OGY method.

The authors of [4] reviewed the problems and methods of control of chaos developed in the nineties. The open-loop control based on periodic system excitation, the method of Poincaré map linearization (OGY method) and the method of time-delayed feedback (Pyragas method) were discussed in detail. They also presented results obtained within the framework of linear, nonlinear and adaptive control as well as discrete systems, neural networks and fuzzy systems.

The next sections give a detailed description of the chaotic control algorithm [66] and how it is used to obtain a desired permanent state for the biologically relevant systems.

## 5.2 Linear Quadratic Regulator (LQR) method

This section provides a brief description of the linear quadratic regulator (LQR) and describes how to design a control based on it. This method is used in the algorithm specified in Section 5.3.

The infinite horizon, linear quadratic regulator (LQR) is given by

$$\begin{aligned}\dot{x} &= Ax + Bu \quad x \in \mathbb{R}^n, u \in \mathbb{R}^n \\ J &= \int_0^\infty (x^t Q x + u^t R u) dt\end{aligned}$$

where  $Q$  and  $R$  are symmetric positive definite matrices to be chosen as part of the control design process. We maximize  $J$  and find that  $u(x)$  is given by

$$u(x) = -Kx, \tag{5.1a}$$

$$K = R^{-1} B^T S, \tag{5.1b}$$

$$SA + A^T S - SBR^{-1} B^T S + Q = 0 \tag{5.1c}$$

The equation (5.1c) is called the *algebraic Riccati equation*.

The simplest choices of  $Q$  and  $R$  are  $I$  and  $\rho I$  respectively where  $\rho$  can be varied to maximize  $J$ .

Also  $K$  can be obtained in MATLAB via the following command:

$$K = lqr(A, B, Q, R).$$

### 5.3 Chaotic control algorithm [66]

The control algorithm specified in [66] and [72] consists of using open loop control (i.e. a control function of time) to generate chaotic motion and then waiting for the system to move into the controllable target. A controllable target is any subset of the domain of attraction to an equilibrium point, under a corresponding feedback control law, that has a non-empty intersection with the chaotic attractor [66]. The

controllable target should be large enough so that one does not have to wait too long for the system to reach it.

Consider the system of non-linear differential equations given by

$$\dot{X} = F[X, U] \quad (5.2)$$

where  $F = [F_1, \dots, F_{N_X}]$  is an  $N_X$  dimensional vector function of the state vector  $X = [X_1, \dots, X_{N_X}]$ , and control vector  $U = [U_1, \dots, U_{N_U}]$ . The control will, in general, be bounded, and it is assumed that at every time  $t$ , the control  $U$  must lie in a subset of the control space  $\mathcal{U}$  defined by the inequalities

$$U_{i_{min}} \leq U_i \leq U_{i_{max}} \quad \text{for } i = 1, \dots, N_U.$$

The control can also be of two kinds

$$U = \begin{cases} U(t) & \text{open loop control} \\ U(X) & \text{closed loop control} \end{cases}$$

Assume that for all  $t$  there exists a control  $\hat{U}(t)$  such that the system (5.2) has a chaotic attractor. Also assume that for a specified constant control,  $\bar{U}$ , there is a corresponding rest point (or fixed point) of interest which is near the chaotic attractor. The rest point  $\bar{X}$  is such that

$$F(\bar{X}, \bar{U}) = 0. \quad (5.3)$$

The method is used to design a full state variable feedback controller, i.e. a closed loop control, such that the rest point will be asymptotically stable.

### 5.3.1 Steps of the algorithm

1. Linearizing  $\dot{X} = F[X, U]$  about the rest point  $\bar{X}$  we get

$$\dot{x} = Ax + Bu \quad (5.4)$$

where

$$x = X - \bar{X}$$

$$u = U - \bar{U}$$

$$A = \left. \frac{\partial F}{\partial X} \right|_{\bar{X}, \bar{U}}$$

$$B = \left. \frac{\partial F}{\partial U} \right|_{\bar{X}, \bar{U}}$$

Now the origin is the rest point for (5.4) at control  $u(t) \equiv 0$ . We are going to get a control such that the origin becomes stable.

2. **LQR method:** Apply the LQR method (Section 5.2) to determine gains  $K$



such that the required closed loop control is

$$u(x) = -Kx \quad (5.5)$$

The gain matrix  $K$  is given by (5.1c) in Section 5.2.

3. **Verification of optimal control:** Under the closed loop control given by (5.5), the linearized system is given by:

$$\dot{x} = \hat{A}x \quad (5.6)$$

where

$$\hat{A} = A - BK$$

A Lyapunov function of the form

$$V(x) = x^t P x \quad (5.7)$$

may now be determined for the linear stable controlled system (5.6) using the continuous Lyapunov equation

$$P\hat{A} + \hat{A}^T P = -\hat{Q}$$

where  $\hat{Q}$  is a positive definite matrix.

For the stable linear system, starting from any point in state space, the solution obtained for  $P$  will result in the property that  $\dot{V} < 0$  for every point of the linear

system (5.6) except at the origin where  $V = 0$ . This will prove that the origin is asymptotically stable for (5.4). This, in turn, implies that for the nonlinear system (5.2), the rest point will be asymptotically stable in some neighborhood containing the rest point.

We shall use this algorithm and the chaotic nature of a model to go from non-permanence to permanence. The algorithm originally was only used to move to a stable fixed rest point. We take it a step further by making sure there is permanence in the system.

## Chapter 6

# Applications of the control algorithm to predator-prey Models

In this chapter, we will investigate three different types of predator-prey models. The models are of Lotka-Volterra type, ratio-dependent and Leslie-Gower type. In each case harvesting of one species is introduced and chaotic behavior is observed for certain parameter values. For the same parameter values, non-permanence of the species is also observed. Using the chaotic control algorithm in Section 5.3, we construct a closed loop control (i.e. a control which is a function of the state of the system) which steers the system towards permanence. The systems were chosen for their different types of functional responses and the harvesting of one species was relatively easy to introduce. The different models show the versatility of the algorithm.

## 6.1 Control through harvesting in a predator-prey model

First we shall apply the control algorithm to a Lotka-Volterra type (Section 3.1) two-prey, one-predator model from [30] where the predator is harvested at a constant rate. Here the harvesting of the predator will act as a control.

The population dynamics model involves three interacting species, namely the prey  $N_1, N_2$  and the predator  $P$ . The harvesting is given by a harvesting function  $H(P)$ . The dynamics is described by Lotka-Volterra type equations given by

$$\begin{aligned}\dot{N}_1 &= N_1(r_1 - a_{11}N_1 - a_{12}N_2 - a_{13}P) \\ \dot{N}_2 &= N_2(r_2 - a_{21}N_1 - a_{22}N_2 - a_{23}P) \\ \dot{P} &= P(-r_3 + a_{31}N_1 + a_{32}N_2) - H(P)\end{aligned}\tag{6.1}$$

We will consider the harvest function  $H(P) = H_p$  where  $H_p$  is a constant and  $0 < H_p < 1$ . This is called constant harvest quota.

The parameters chosen are the same as in [30] and are as follows:

$$r_1 = r_2 = r_3 = a_{11} = a_{12} = a_{22} = a_{23} = 1, a_{21} = 1.5, a_{32} = 0.5, a_{13} = 5, a_{31} = 2.5.$$

Since  $a_{12} < a_{21}$ , the first prey has a competitive advantage, i.e.  $N_1$  is the dominant and  $N_2$  the sub-dominant prey. Consider the two-dimensional subsystem of the preys without predation:

$$\begin{aligned}\dot{N}_1 &= N_1(r_1 - a_{11}N_1 - a_{12}N_2) \\ \dot{N}_2 &= N_2(r_2 - a_{21}N_1 - a_{22}N_2)\end{aligned}$$

The relation

$$a_{11}a_{22} - a_{12}a_{21} < 0$$

implies that the system does not have an interior rest point, i.e. both the species  $N_1, N_2$  do not coexist. This shows the system is unstable without predation. [75]

### 6.1.1 Boundedness of the solutions

Following methods similar to those in [62, 21, 1], we can prove that the solutions of (6.1) are bounded.

**Theorem 6.1.1.** *All the solutions of the system (6.1) which initiate in  $\mathbb{R}_+^3$  are uniformly bounded*

*Proof.* Let  $W = N_1 + N_2 + 2P$ . Then

$$\dot{W} = \dot{N}_1 + \dot{N}_2 + 2\dot{P}$$

Along the solutions of 6.1, we have

$$\begin{aligned} \dot{W} &= N_1(1 - N_1 - N_2 - 5P) \\ &\quad + N_2(1 - 1.5N_1 - N_2 - P) \\ &\quad + 2P(-1 + 2.5N_1 + 0.5N_2) - 2H_p \\ &= N_1(1 - N_1) + N_2(1 - N_2) - 2.5N_1N_2 - 2P - 2H_p \\ &\leq N_1(1 - N_1) + N_2(1 - N_2) - 2P \end{aligned}$$

For each constant  $D > 0$ , the following inequality holds:

$$\dot{W} + DW \leq N_1(1 - N_1 + D) + N_2(1 - N_2 + D) + 2P(D - 1)$$

Now if we take  $D$  such that  $0 < D < 1$  and the maximum value of both the expressions  $N_1(1 - N_1 + D)$ ,  $N_2(1 - N_2 + D)$  w.r.t  $N_1$  and  $N_2$  respectively, is  $\frac{1+D}{2}$  we get,

$$\begin{aligned} \dot{W} + DW &\leq 1 + D = K \\ \implies 0 &\leq W(N_1, N_2, P) \leq \frac{K}{D} + W(N_1(0), N_2(0), P(0))e^{-Dt} \\ \implies 0 < W &\leq \frac{K}{D} \quad \text{as } t \rightarrow \infty \end{aligned}$$

Hence all solutions of (6.1) that initiate in  $\mathbb{R}_+^3$  are confined in the region.  $\square$

### 6.1.2 Chaos control algorithm to the harvesting model

The harvesting model is as follows:

$$\begin{aligned}\dot{N}_1 &= N_1(1 - N_1 - N_2 - 5P) \\ \dot{N}_2 &= N_2(1 - 1.5N_1 - N_2 - P) \\ \dot{P} &= P(-1 + 2.5N_1 + 0.5N_2) - H_p\end{aligned}\tag{6.2}$$

Here we consider the control  $U = H_p$ . The control  $\hat{U}$  for which we get chaos is  $\hat{U} = H_p = 0.02$  (obtained from [30]). The chaos is indicated by a positive Lyapunov exponent 0.0474 at the initial conditions (which is the interior rest point)  $(0, 4899, 0.2040, 0.0612)$ .

We also check to see if the system is non-permanent for these parameter values.

**Check for Permanence.** The system is of the form  $\dot{x}_i = x_i f(x_i)$  where  $x_1 = N_1, x_2 = N_2, x_3 = P$  and

$$\begin{aligned}f_1(N_1, N_2, P) &= 1 - N_1 - N_2 - 5P \\ f_2(N_1, N_2, P) &= 1 - 1.5N_1 - N_2 - P \\ f_3(N_1, N_2, P) &= -1 + 2.5N_1 + 0.5N_2 - \frac{0.02}{P}\end{aligned}$$

Now as mentioned before, the system is permanent if it does not have regular, saturated boundary rest points, i.e for the rest point  $\bar{x}$ ,  $f_i(\bar{x}) > 0$  for some  $i$  when  $\bar{x}_i = 0$ .

For this particular system, consider the biologically valid rest points  $\bar{x} = (\bar{N}_1, \bar{N}_2, \bar{P})$  and the values of  $f_i(\bar{x}) > 0$  for some  $i$  when  $\bar{x}_i = 0$ . So we can see from Table 6.1.1, the

Rest point	Value of $f_i$
$A = (0.4763932022, 0, 0.1047213596)$	$f_2(A) = 0.18 > 0$
$B = (.9236067978, 0, 0.1527864045e - 1)$	$f_2(B) = -0.4013 < 0$

Table 6.1.1: Check of permanence of (6.2) using boundary rest points.

system does indeed have a saturated rest point, namely  $B = (.9236067978, 0, 0.1527864045e - 1)$ , so it is not permanent.

The chaotic manifold can be seen in Fig. 6.1.1.

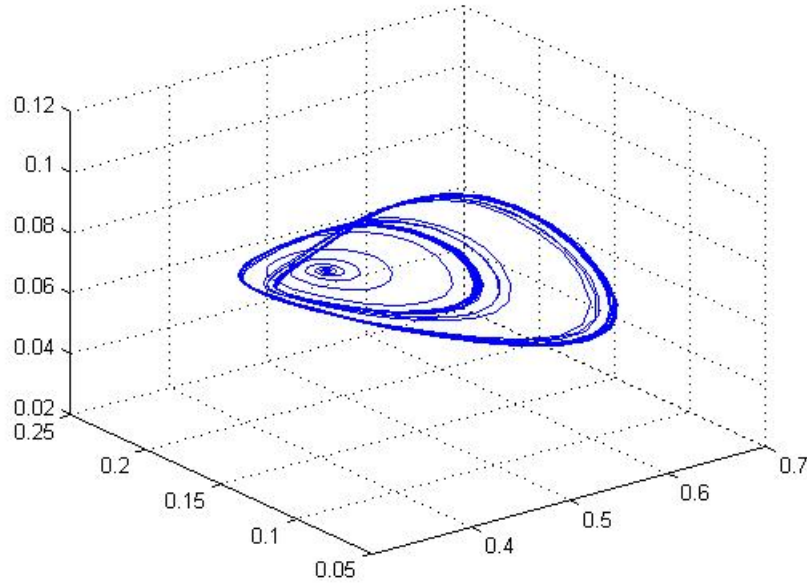


Figure 6.1.1: Chaotic manifold when  $h = 0.02$ .



### 6.1.3 Application of the algorithm specified in Section 5.3

Our desired state is permanence. The specific control we wish to obtain is  $\bar{U} = H_p = 0.035$  and the interior rest point to the system

$$\begin{aligned}\dot{N}_1 &= N_1(1 - N_1 - N_2 - 5P) \\ \dot{N}_2 &= N_2(1 - 1.5N_1 - N_2 - P) \\ \dot{P} &= P(-1 + 2.5N_1 + 0.5N_2) - 0.035\end{aligned}$$

is  $\bar{X} = (N_1 = 0.5816, N_2 = 0.0549, P = 0.0727)$ . The system is found to be permanent by checking the boundary rest points using the MATLAB code given in Appendix B. In the code, the boundary rest points were obtained and were checked to see if they were regular saturated rest points. If the rest points were not saturated, the system was permanent (Section 4.2.2).

So  $\bar{X} = (0.5816, 0.0549, 0.0727)$  and  $\bar{U} = (0.035)$ .

For the linearization step 1 we get the matrices A and B as follows:

$$A = \frac{\partial F}{\partial X} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} -0.5816 & -0.5816 & -2.9080 \\ -0.0824 & -0.0549 & -0.0549 \\ 0.1817 & 0.0363 & 0.4814 \end{bmatrix}$$

$$B = \frac{\partial F}{\partial U} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} 0 \\ 0 \\ -1 \end{bmatrix}$$

We choose the matrices  $Q = I_3$  and  $R=[1]$  which are positive definite.

Applying the *lqr* routine of MATLAB, the gains matrix  $K$  is obtained as

$$K = \begin{bmatrix} 0.2761 & -0.2112 & -2.1591 \end{bmatrix}.$$

So our feedback control given by (5.5) is

$$\begin{aligned} u(x) &= -Kx \\ &= -0.2761N_1 - 0.2112N_2 - 2.1591P. \end{aligned}$$

To confirm the origin is asymptotically stable, the Lyapunov function has also been calculated.

From step 3 of the algorithm, we have

$$\begin{aligned} \hat{A} &= A - BK \\ &= \begin{bmatrix} -0.5816 & -0.5816 & -2.9080 \\ -0.0824 & -0.0549 & -0.0549 \\ 0.4579 & -0.1749 & -1.6777 \end{bmatrix}. \end{aligned}$$

We choose  $\hat{Q} = Q = I_3$  and we obtain  $P$  using the *lyap* function in MATLAB.

$$P = \begin{bmatrix} 1.4209 & -4.0725 & 0.7023 \\ -4.0725 & 17.5405 & -2.3263 \\ 0.7023 & -2.3263 & 0.7322 \end{bmatrix}.$$

For the above matrix  $V(x) = x^t P x$  will satisfy  $\dot{V} < 0$  according to the construction of  $P$ .

The chaotic nature disappears when  $h = 0.035$  as seen in Fig. 6.1.2.

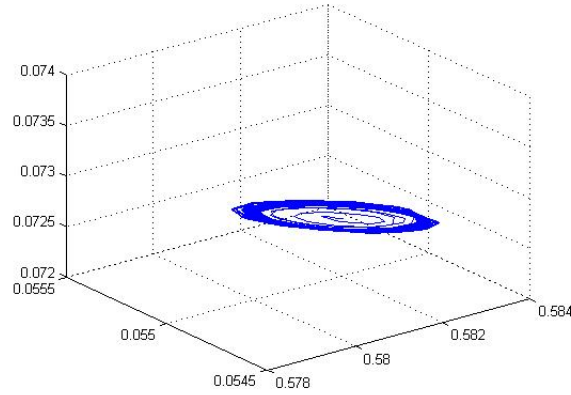


Figure 6.1.2: Permanence when  $h = 0.035$ .

We have seen that for certain harvesting values, we get chaos. This is not necessarily a bad thing. Using the chaotic control algorithm, we can apply the required control to get permanence. In this manner, the species do not die out and the harvesting can still be done.

## 6.2 Example of a one-prey, two-predator system

[35]

Consider an ecosystem where we wish to model the interaction of two predators competing for a single prey. It is assumed that prey species grow logistically and the predator functional response is of ratio-dependent (Michaelis-Menten-Holling, Section 3.3) type. Then the dynamics of the system may be governed by the following system of autonomous differential equations.

$$\begin{aligned}\dot{x} &= rx \left( 1 - x - \frac{a_1 y_1}{1 + b_1 x} - \frac{a_2 y_2}{1 + b_2 x} \right) \\ \dot{y}_1 &= s_1 y_1 \left( -1 + \frac{c_1 x}{1 + b_1 x} - y_1 \right) \\ \dot{y}_2 &= s_2 y_2 \left( -1 + \frac{c_2 x}{1 + b_2 x} - y_2 \right)\end{aligned}\tag{6.3}$$

where  $x(t), y_1(t), y_2(t)$  represent the species concentration of the prey and the two predators respectively.

We assume there are no periodic points on boundary planes.

Also assume that  $a_i, b_i, c_i \geq 0$  for  $i = 1, 2$  and  $r, s_1, s_2 > 0$ .

### 6.2.1 Boundedness of trajectories

Next we shall show the boundedness of solutions which initiate in  $\mathbb{R}_+^3$ . The proof is similar to ones found in [44, 3].

**Theorem 6.2.1.** *All solutions which initiate in  $\mathbb{R}_+^3$  are bounded.*

*Proof.* From our first equation,

$$\dot{x} = rx \left( 1 - x - \frac{a_1 y_1}{1 + b_1 x} - \frac{a_2 y_2}{1 + b_2 x} \right)$$

we have

$$\dot{x} \leq rx(1 - x)$$

Applying the theorem of differential inequality ([12]) we have,

$$x(t) \leq \frac{1}{1 + be^{-rt}} \text{ where } b = \frac{1}{x(0)} - 1$$

$$\text{which implies } \limsup_{t \rightarrow \infty} x(t) \leq 1$$

$\therefore x(t)$  is bounded.

Thus  $y_1(t)$  and  $y_2(t)$  are bounded by the boundedness of  $x(t)$ . □

### 6.2.2 Interior rest point

The interior rest point (i.e. all the coordinates are positive) is obtained by solving the following set of equations.

$$1 - x - \frac{a_1 y_1}{1 + b_1 x} - \frac{a_2 y_2}{1 + b_2 x} = 0 \quad (6.4a)$$

$$-1 + \frac{c_1 x}{1 + b_1 x} - y_1 = 0 \quad (6.4b)$$

$$-1 + \frac{c_2 x}{1 + b_2 x} - y_2 = 0. \quad (6.4c)$$

From (6.4b) we get:

$$\begin{aligned} y_1 &= -1 + \frac{c_1 x}{1 + b_1 x} \\ &= \frac{-1 + (c_1 - b_1)x}{1 + b_1 x}. \end{aligned}$$

For  $y_1 > 0$  we need

$$\begin{aligned} -1 + (c_1 - b_1)x &> 0 \\ \implies (c_1 - b_1)x &> 1 \end{aligned}$$

since  $b_1 \geq 0$  and assuming  $x > 0$ . Using  $x > 0$  we get

$$c_1 > b_1. \quad (6.5)$$

Similarly, from equation (6.4c) we have

$$c_2 > b_2. \quad (6.6)$$

The existence of the interior rest point was proven computationally (using MATLAB) for the parameter values that satisfy conditions (6.5) and (6.6).

### 6.2.3 Equilibrium analysis

The possible biologically viable equilibria are  $E_0 = (0, 0, 0)$ ,  $E_1 = (1, 0, 0)$ ,  $E_2 = (\bar{x}, \bar{y}_1, 0)$ ,  $E_3 = (\tilde{x}, 0, \tilde{y}_2)$  and the interior rest point  $E_4 = (x^*, y_1^*, y_2^*)$ .  $E_4$  is obtained by solving (6.26).

### 6.2.4 Existence of $E_2$ and $E_3$

$E_2 = (\bar{x}, \bar{y}_1, 0)$  is the solution of

$$1 - x - \frac{a_1 y_1}{1 + b_1 x} = 0 \quad (6.7a)$$

$$-1 + \frac{c_1 x}{1 + b_1 x} - y_1 = 0. \quad (6.7b)$$

Solving we get

$$1 - x - \frac{a_1}{1 + b_1x} \left( \frac{-1 + (c_1 - b_1)x}{1 + b_1x} \right) = 0$$

$$x + \frac{a_1(-1 + (c_1 - b_1)x)}{(1 + b_1x)^2} = 1$$

$$(1 + b_1x)^2x - a_1 + a_1(c_1 - b_1)x = (1 + b_1x)^2$$

$$b_1^2x^3 + b_1(2 - b_1)x^2 + (a_1c_1 - a_1b_1 + 1 - 2b_1)x - a_1 - 1 = 0.$$

So we need  $\bar{x}$  to be the positive real root of

$$x^3 + \frac{(2 - b_1)}{b_1}x^2 + \frac{(a_1c_1 - a_1b_1 + 1 - 2b_1)}{b_1^2}x - \frac{(a_1 + 1)}{b_1^2} = 0. \quad (6.8)$$

Using Maple, we get that two solutions to (6.8) are complex.

Using Descartes' Rule of Signs, we have  $n - (p + q) = 2 \implies p + q = 1$  where  $n$  is the degree of the equation,  $p$  is the number of positive real roots,  $q$  is the number of negative real roots, provided we do not have a root at zero, i.e.  $a_1 \neq -1$ .

We want a positive real root so we should have no negative roots. That implies when we plug in  $-x$  in (6.8) we should have no sign changes between the coefficients. Plugging in  $-x$  in (6.8) we get

$$-x^3 + \frac{(2 - b_1)}{b_1}x^2 - \frac{(a_1c_1 - a_1b_1 + 1 - 2b_1)}{b_1^2}x - \frac{(a_1 + 1)}{b_1^2}.$$



So for no sign changes, we need

$$\begin{aligned} 2 - b_1 &\leq 0 \text{ and} \\ a_1 c_1 - a_1 b_1 + 1 - 2b_1 &> 0. \end{aligned} \tag{6.9}$$

To get one positive real root, we need one sign change in (6.8). The possibilities are

$$\begin{aligned} 2 - b_1 &\geq 0 \text{ and} \\ a_1 c_1 - a_1 b_1 + 1 - 2b_1 &> 0 \end{aligned} \tag{6.10}$$

or

$$\begin{aligned} 2 - b_1 &\leq 0 \text{ and} \\ a_1 c_1 - a_1 b_1 + 1 - 2b_1 &< 0. \end{aligned} \tag{6.11}$$

Looking at conditions (6.9), (6.10), (6.11) we get that

$$\begin{aligned} 2 - b_1 = 0 &\implies b_1 = 2 \text{ and} \\ a_1 c_1 - 2a_1 + 1 - 2(2) &> 0 \implies a_1(c_1 - 2) > 3 \end{aligned} \tag{6.12}$$

for  $E_2$  to exist.

Proceeding in exactly the same manner for  $E_3$  we obtain the following conditions for existence

$$\begin{aligned} b_2 &= 2 \text{ and} \\ a_2(c_2 - 2) &> 3. \end{aligned} \tag{6.13}$$

### 6.2.5 Conditions for permanence

We shall use the method of Lyapunov functions [54, 35] (Section 4.2.3) to derive conditions for permanence.

**Theorem 6.2.2.** *Assume the boundary rest points  $E_0 = (0, 0, 0)$ ,  $E_1 = (1, 0, 0)$ ,  $E_2 = (\bar{x}, \bar{y}_1, 0)$ ,  $E_3 = (\tilde{x}, 0, \tilde{y}_2)$  of the system 6.3 exists and we have no periodic orbits in the boundary. Then we need the inequalities (6.15a), (6.15b), (6.15c) and (6.15d) to hold for the system to be permanent.*

*Proof.* Let the Lyapunov function be

$$\sigma(X) = x^p y_1^{p_1} y_2^{p_2}$$

where  $p, p_1, p_2 > 0$  and are constants. Clearly  $\sigma(X)$  is a non-negative  $C^1$  function defined in  $\mathbb{R}_+^3$ .

Consider

$$\begin{aligned} \psi(X) &= \frac{\dot{\sigma}(X)}{\sigma(X)} \\ &= p \frac{\dot{x}}{x} + p_1 \frac{\dot{y}_1}{y_1} + p_2 \frac{\dot{y}_2}{y_2} \\ &= pr \left( 1 - x - \frac{a_1 y_1}{1 + b_1 x} - \frac{a_2 y_2}{1 + b_2 x} \right) \\ &\quad + p_1 s_1 \left( -1 + \frac{c_1 x}{1 + b_1 x} - y_1 \right) \\ &\quad + p_2 s_2 \left( -1 + \frac{c_2 x}{1 + b_2 x} - y_2 \right) \end{aligned}$$

To obtain permanence, we need to show  $\psi(X) > 0 \forall$  equilibria  $X \in \text{bd}\mathbb{R}_+^3$ , i.e. the

following conditions have to be satisfied:

$$\psi(E_0) = pr - p_1s_1 - p_2s_2 > 0 \quad (6.14a)$$

$$\psi(E_1) = p_1s_1 \left( -1 + \frac{c_1}{1+b_1} \right) + p_2s_2 \left( -1 + \frac{c_2}{1+b_2} \right) > 0 \quad (6.14b)$$

$$\psi(E_2) = p_2s_2 \left( -1 + \frac{c_2\bar{x}}{1+b_2\bar{x}} \right) > 0 \quad (6.14c)$$

$$\psi(E_3) = p_1s_1 \left( -1 + \frac{c_1\tilde{x}}{1+b_1\tilde{x}} \right) > 0 \quad (6.14d)$$

We note that by increasing  $p$  to a sufficiently large value,  $\psi(E_0)$  can be made positive.

From (6.14b), (6.14c), (6.14d) we get the following requirements for permanence:

$$-1 + \frac{c_1}{1+b_1} > 0 \quad (6.15a)$$

$$-1 + \frac{c_2}{1+b_2} > 0 \quad (6.15b)$$

$$-1 + \frac{c_2\bar{x}}{1+b_2\bar{x}} > 0 \quad (6.15c)$$

$$-1 + \frac{c_1\tilde{x}}{1+b_1\tilde{x}} > 0. \quad (6.15d)$$

□

### 6.2.6 Introducing harvesting of first predator

Suppose there is harvesting done of predator 1 in the following way:

$$\begin{aligned}\dot{x} &= rx \left( 1 - x - \frac{a_1 y_1}{1 + b_1 x} - \frac{a_2 y_2}{1 + b_2 x} \right) \\ \dot{y}_1 &= s_1 y_1 \left( -1 + \frac{c_1 x}{1 + b_1 x} - y_1 \right) - h y_1 \\ \dot{y}_2 &= s_2 y_2 \left( -1 + \frac{c_2 x}{1 + b_2 x} - y_2 \right)\end{aligned}\tag{6.16}$$

Here  $h > 0$  is the harvesting coefficient. The harvesting is a function of the predator (i.e. constant harvesting effort). Using the analysis done for permanence in Sections 6.2.5 and 6.2.3, we fix the parameters as  $r = s_1 = s_2 = 1$ ,  $a_1 = a_2 = 5$ ,  $b_1 = b_2 = 2$ ,  $c_1 = c_2 = 4$ . So we get the following system

$$\begin{aligned}\dot{x} &= x \left( 1 - x - \frac{5y_1}{1 + 2x} - \frac{5y_2}{1 + 2x} \right) \\ \dot{y}_1 &= y_1 \left( -1 + \frac{4x}{1 + 2x} - y_1 \right) - h y_1 \\ \dot{y}_2 &= y_2 \left( -1 + \frac{4x}{1 + 2x} - y_2 \right).\end{aligned}\tag{6.17}$$

Boundedness of the trajectories does not change as  $y_1(t)$  is still bounded by  $x(t)$  (Refer to Section 6.2.1).

We now wish to investigate conditions on  $h$  for which permanence is obtained.

The only boundary rest point that changes from our original system is  $E_2$ . Let it be denoted by  $E_2^* = (\bar{x}^*, \bar{y}_1^*, 0)$ . It is obtained by solving

$$\begin{aligned}1 - x - \frac{5y_1}{1 + 2x} &= 0 \\ -1 + \frac{4x}{1 + 2x} - y_1 - h &= 0.\end{aligned}\tag{6.18}$$

Solving we get,

$$x^3 + \frac{7-10h}{4}x - \frac{6+5h}{4} = 0.$$

Using Descartes' rule of signs, as in Section 6.2.3, to get  $\bar{x}^* > 0$  we need

$$7 - 10h > 0 \implies h < 0.7 \tag{6.19}$$

To have  $\bar{y}_1^* > 0$ , we need  $1 + \bar{x}^* - 2(\bar{x}^*)^2 > 0$ .

For permanence, we follow the proof of Theorem 6.2.2 (Section 6.2.5),

**Theorem 6.2.3.** *Assume the boundary rest points  $E_0 = (0, 0, 0)$ ,  $E_1 = (1, 0, 0)$ ,  $E_2^* = (\bar{x}^*, \bar{y}_1^*, 0)$ ,  $E_3 = (\tilde{x}, 0, \tilde{y}_2)$  of the system (6.17) exists and we have no periodic orbits in the boundary. Then we need the inequalities (6.21a), (6.21b) and (6.21c) to hold for the system to be permanent.*

*Proof.* Let the Lyapunov function be

$$\sigma(X) = x^p y_1^{p_1} y_2^{p_2}$$

where  $p, p_1, p_2 > 0$  and are constants. Clearly  $\sigma(X)$  is a non-negative  $C^1$  function defined in  $\mathbb{R}_+^3$ .

Consider

$$\begin{aligned}
\psi(X) &= \frac{\dot{\sigma}(X)}{\sigma(X)} \\
&= p \frac{\dot{x}}{x} + p_1 \frac{\dot{y}_1}{y_1} + p_2 \frac{\dot{y}_2}{y_2} \\
&= p \left( 1 - x - \frac{5y_1}{1+2x} - \frac{5y_2}{1+2x} \right) \\
&\quad + p_1 \left( -1 + \frac{4x}{1+2x} - y_1 - h \right) \\
&\quad + p_2 \left( -1 + \frac{4x}{1+2x} - y_2 \right).
\end{aligned}$$

To obtain permanence, we need to show  $\psi(X) > 0 \forall$  equilibria  $X \in \text{bd}\mathbb{R}_+^3$ , i.e. the following conditions have to be satisfied:

$$\psi(E_0) = p - p_1(1+h) - p_2 > 0 \quad (6.20a)$$

$$\psi(E_1) = p_1 \left( \frac{1}{3} - h \right) + p_2 \left( \frac{1}{3} \right) > 0 \quad (6.20b)$$

$$\psi(E_2) = p_2 \left( -1 + \frac{4\bar{x}^*}{1+2\bar{x}} \right) > 0 \quad (6.20c)$$

$$\psi(E_3) = p_1 \left( -1 + \frac{4\tilde{x}}{1+2\tilde{x}} - h \right) > 0. \quad (6.20d)$$

We note that by increasing  $p$  to a sufficiently large value,  $\psi(E_0)$  can be made positive.

From (6.20b), (6.20c), (6.20d) we get the following requirements for permanence:

$$\frac{1}{3} - h > 0 \quad (6.21a)$$

$$-1 + \frac{4\bar{x}^*}{1 + b_2\bar{x}^*} > 0 \quad (6.21b)$$

$$-1 + \frac{4\tilde{x}}{1 + 2\tilde{x}} - h > 0. \quad (6.21c)$$

□

### 6.2.7 Control algorithm with harvesting as control

Now suppose the harvesting coefficient  $h = 0.9$ . This violates the condition for permanence and we also notice that the system is chaotic. We can use the chaos to bring it back to permanence with final control  $U(t) = h = 0.15$  and the interior rest point for the system

$$\begin{aligned} \dot{x} &= x \left( 1 - x - \frac{5y_1}{1 + 2x} - \frac{5y_2}{1 + 2x} \right) \\ \dot{y}_1 &= y_1 \left( -1 + \frac{4x}{1 + 2x} - y_1 \right) - 0.15y_1 \\ \dot{y}_2 &= y_2 \left( -1 + \frac{4x}{1 + 2x} - y_2 \right) \end{aligned} \quad (6.22)$$

is  $\bar{X} = (x = 0.6777, y_1 = 0.0009, y_2 = 0.151)$ . The system is in fact permanent using the boundary rest points which was shown computationally using the MATLAB code in Appendix B.

Applying the algorithm, we get the matrices  $A$  and  $B$

$$A = \frac{\partial F}{\partial X} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} -0.4923 & -1.4386 & -1.4386 \\ 0.0007 & -0.0009 & 0 \\ 0.1088 & 0 & -0.1509 \end{bmatrix}$$

$$B = \frac{\partial F}{\partial U} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} 0 \\ -0.000903 \\ 0 \end{bmatrix}.$$

We again choose the matrices  $Q = I_3$  and  $R=[1]$  which are positive definite.

Applying the *lqr* routine of MATLAB, the gains matrix  $K$  is obtained as

$$K = \begin{bmatrix} -0.0002 & -0.1135 & -0.0041 \end{bmatrix}.$$

So our feedback control given by (5.5) is  $u(x) = -Kx = -0.0002x - 0.1135y_1 - 0.0041y_2$ . To confirm we get the origin as asymptotically stable, the Lyapunov function has also been calculated.

From step 3 of the algorithm, we have

$$\hat{A} = A - BK$$

$$= \begin{bmatrix} -0.4923 & -1.4386 & -1.4386 \\ 0.0007 & -0.0010 & -0.0000 \\ 0.1088 & 0 & -0.1509 \end{bmatrix}$$

We choose  $\hat{Q} = Q = I_3$  and we obtain  $P$  using the *lyap* function in MATLAB.



$$P = \begin{bmatrix} 301.1684 & -293.7054 & 190.9978 \\ -293.7054 & 304.4743 & -202.9344 \\ 190.9978 & -202.9344 & 141.0141 \end{bmatrix}.$$

For the above matrix  $V(x) = x^t P x$  will satisfy  $\dot{V} < 0$  according to the construction of  $P$ .

When harvesting of the first predator is introduced, chaotic orbits are observed as well as the system becomes non-permanent. The control algorithm provides a viable harvesting function that pushes the system into permanence.

## 6.3 Harvesting used as control in a food-chain system

The next system considered is of a simple prey-specialist predator-generalist predator (for ex: plant-insect pest-spider) interaction based on the model found in [34, 8, 67]. In this system, harvesting of the prey is considered as a control. The equations are as follows

$$\begin{aligned}\dot{x} &= a_1x - b_1x^2 - \frac{wxy}{x + D} - hx \\ \dot{y} &= -a_2y + \frac{w_1xy}{x + D_1} - \frac{w_2yz}{y + D_2} \\ \dot{z} &= cz^2 - \frac{w_3z^2}{y + D_3}.\end{aligned}\tag{6.23}$$

In this model, a prey population of size  $x$  serves as the only food for the specialist predator population of size  $y$ . This population, in turn, serves as favorite food for the generalist predator population of size  $z$ . The equations for rate of change of population size for prey and specialist predator are according to the Volterra scheme (predator population dies out exponentially in absence of its prey). The interaction between this predator  $y$  and the generalist predator  $z$  is modeled by the Leslie-Gower scheme (Section 3.4) where the loss in a predator population is proportional to the reciprocal of per capita availability of its most favorite food. The basic characteristic of the Leslie-Gower model is that it leads to a solution which is asymptotically independent of the initial conditions and depends only on the intrinsic attributes of the interacting system, that is, the parameters  $w$ ,  $w_1$ , and so on [33].

The paper did not have harvesting of the prey. When we introduced it to the existing model, we noticed chaos and non-permanence. The  $hx$  term models the harvesting

function being proportional to the population of the prey (constant harvest effort).

The constants are all positive and are described as follows:

$a_1$ : intrinsic growth rate of the prey population  $x$ ;

$b_1$ : strength of intra-specific competition among the prey species;

$w, w_1, w_2, w_3$ : the maximum values which per capita growth can attain;

$D, D_1$ : the extent to which the environment provides protection to the prey  $x$ ;

$a_2$ : intrinsic death rate of the predator  $y$  in the absence of the only food  $x$ ;

$D_2$ : the value of  $y$  at which the per capita removal rate of  $y$  becomes  $w_2/2$ ;

$D_3$ : the residual loss in  $z$  population due to severe scarcity of its favorite food  $y$ ;

$c$ : the rate of self-reproduction of the generalist predator  $z$ . The square term signifies the mating frequency is directly proportional to the number of males and females;

$h$ : harvesting rate of the prey  $x$ .

The parameter values (except for  $h$ ) are taken as in [67] and are given below

$$a_1 = 1.93, b_1 = 0.06, w = 1, D = 10, a_2 = 1, w_1 = 2$$

$$D_1 = 10, w_2 = 0.405, D_2 = 10, c = 0.03, w_3 = 1, D_3 = 20.$$

The above parameter choices are so that the system is bounded and there is possibility of chaotic behavior for different values of  $h$  (shown in the Methodology section of [67]).

### 6.3.1 Equilibrium analysis

The possible biologically viable equilibria are  $E_0 = (0, 0, 0)$ ,  $E_1 = (\frac{a_1 - h}{b_1}, 0, 0)$ ,  $E_2 = (\bar{x}, \bar{y}, 0)$  and the interior rest point  $E_3 = (x^*, y^*, z^*)$ .

### 6.3.1.1 Conditions for existence of $E_1$ .

For  $E_1$  to be biologically relevant, we need

$$a_1 - h > 0 \implies h < a_1 = 1.93. \quad (6.24)$$

### 6.3.1.2 Existence of $E_2$ .

$E_2$  is obtained by solving the subsystem:

$$\begin{aligned} a_1 - b_1x - \frac{wy}{x + D} - h &= 0 \\ -a_2 + \frac{w_1x}{x + D_1} &= 0. \end{aligned}$$

We get  $E_2 = (\bar{x}, \bar{y}, 0) = (10, 20(1.33 - h), 0)$ . Again for  $E_2$  to be biologically viable we need

$$1.33 - h > 0 \implies h < 1.33. \quad (6.25)$$

### 6.3.1.3 Existence of the interior rest point $E_3$ .

$E_3 = (x^*, y^*, z^*)$  is the solution of the following system:

$$a_1 - b_1x - \frac{wy}{x + D} - h = 0 \quad (6.26a)$$

$$-a_2 + \frac{w_1x}{x + D_1} - \frac{w_2z}{y + D_2} = 0 \quad (6.26b)$$

$$cz - \frac{w_3z}{y + D_3} = 0. \quad (6.26c)$$

From (6.26c), we get

$$\begin{aligned}
cz - \frac{w_3 z}{y + D_3} &= 0 \\
c - \frac{w_3}{y + D_3} &= 0 \\
\implies y^* = \frac{w_3}{c} - D_3 &= 13.33 > 0.
\end{aligned}$$

From (6.26a),

$$\begin{aligned}
(a_1 - h - b_1 x)(x + D) &= wy^* \\
0.06x^2 - (1.33 - h)x + (-5.97 + 10h) &= 0.
\end{aligned}$$

For real roots, we need

$$(1.33 - h)^2 - 4(0.06)(-5.97 + 10h) \geq 0.$$

Solving for  $h$  using Maple's *solve* command (up to 4 significant figures), we get

$$h \leq 0.7411 \text{ or } h \geq 4.3189.$$

For the rest point to be biologically valid, we need at least one positive root to the equation  $0.06x^2 - (1.33 - h)x + (-5.97 + 10h)$ .

According to Descartes' Rule of Signs, if  $h \leq 0.7411$ , then we get one sign change of the coefficients. So there is at least one positive root.

Therefore,  $x^*$  exists if

$$h \leq 0.7411. \quad (6.27)$$

From (6.26b),

$$\begin{aligned} \frac{w_2 z^*}{y^* + D_2} &= -a_2 + \frac{w_1 x^*}{x^* + D_1} \\ z^* &= \frac{y^* + D_2}{w_2} \left( -a_2 + \frac{w_1 x^*}{x^* + D_1} \right) \\ z^* &= 57.605 \left( \frac{x^* - 10}{x^* + 10} \right) \end{aligned}$$

$z^*$  exists if  $x^* > 10$ .

### 6.3.2 Conditions for permanence

We shall use the method of Lyapunov functions (Theorem 4.2.4 in Section 4.2.3) to derive conditions for permanence.

**Theorem 6.3.1.** *Assume the boundary rest points  $E_0 = (0, 0, 0)$ ,  $E_1 = (\frac{a_1 - h}{b_1}, 0, 0)$ ,  $E_2 = (10, 20(1.33 - h), 0)$  exist and we have no periodic orbits on the boundary. We need*

$$h < 1.33$$

*for the system (6.23) to be permanent.*

*Proof.* Let the Lyapunov function be

$$\sigma(X) = x^{p_1} y^{p_2} z^{p_3}$$

where  $p_1, p_2, p_3 > 0$  and are constants. Clearly  $\sigma(X)$  is a non-negative  $C^1$  function defined in  $\mathbb{R}_+^3$ .

Consider

$$\begin{aligned}
\psi(X) &= \frac{\dot{\sigma}(X)}{\sigma(X)} \\
&= p_1 \frac{\dot{x}}{x} + p_2 \frac{\dot{y}}{y} + p_3 \frac{\dot{z}}{z} \\
&= p_1 \left( a_1 - b_1 x - \frac{wy}{x+D} - h \right) \\
&\quad + p_2 \left( -a_2 + \frac{w_1 x}{x+D_1} - \frac{w_2 z}{y+D_2} \right) \\
&\quad + p_3 \left( cz - \frac{w_3 z}{y+D_3} \right).
\end{aligned}$$

To show permanence, we need  $\psi(X) > 0 \forall$  equilibria  $X \in \text{bd}\mathbb{R}_+^3$ , i.e. the following conditions have to be satisfied

$$\psi(E_0) = p_1(a_1 - h) - p_2 a_2 > 0 \tag{6.28a}$$

$$\psi(E_1) = p_2 \left( -a_2 + \frac{w_1(a_1 - h)/b_1}{(a_1 - h)/b_1 + D_1} \right) > 0 \tag{6.28b}$$

$$\psi(E_2) = 0. \tag{6.28c}$$

We note that by (6.24) (i.e.  $a_1 - h > 0$ ) and by increasing  $p$  to a sufficiently large value,  $\psi(E_0)$  can be made positive.

From (6.28b) we get the following requirement:

$$\begin{aligned}
-a_2 + \frac{w_1(a_1 - h)/b_1}{(a_1 - h)/b_1 + D_1} &> 0 \\
-a_2 + \frac{w_1(a_1 - h)}{(a_1 - h) + b_1 D_1} &> 0 \\
\frac{2(1.93 - h)}{(1.93 - h) + 0.06 * 10} &> 1.
\end{aligned}$$

Solving we get

$$h < 1.33. \quad (6.29)$$

□

So from the inequalities (6.24), (6.25), (6.27) and (6.29) we get  $h \leq 0.7411$  for the existence of an interior rest point and permanence.

### 6.3.3 Control algorithm using harvesting

Now suppose the harvesting coefficient  $h = 0.93$ . This violates the condition for permanence and we also notice that the system is chaotic by the presence of positive Lyapunov exponent 1.4427. We can use the chaos to bring it back to permanence with final control  $U(t) = h = 0.1$  and the interior rest point for the system:

$$\begin{aligned}
\dot{x} &= 1.93x - 0.06x^2 - \frac{xy}{x + 10} - 0.1x \\
\dot{y} &= -y + \frac{2xy}{x + 10} - \frac{0.405yz}{y + 10} \\
\dot{z} &= 0.03z^2 - \frac{z^2}{y + 20}
\end{aligned} \quad (6.30)$$



is  $\bar{X} = (x = 23.955, y = 13.333, z = 23.679)$ . The system is in fact permanent using the boundary rest points and the analysis in Section 6.3.2.

Applying the algorithm (Section 5.3), we get the matrices  $A$  and  $B$ :

$$A = \frac{\partial F}{\partial X} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} -1.1603 & -0.7055 & 0 \\ 0.2313 & 0.2349 & -0.2314 \\ 0 & 0.5046 & 0 \end{bmatrix}$$

$$B = \frac{\partial F}{\partial U} \Big|_{\bar{X}, \bar{U}} = \begin{bmatrix} -23.9555 \\ 0 \\ 0 \end{bmatrix}.$$

We again choose the matrices  $Q = I_3$  and  $R = [1]$  which are positive definite.

Applying the *lqr* routine of MATLAB, the gains matrix  $K$  is obtained as

$$K = \begin{bmatrix} -0.9630 & -1.0716 & -0.9891 \end{bmatrix}.$$

So our feedback control given by (5.5) is

$$u(x) = -Kx = -0.9630x - 1.0716y - 0.9891z.$$

To confirm we get the origin as asymptotically stable, the Lyapunov function has also been calculated.

From step 3 of the algorithm, we have

$$\begin{aligned}\hat{A} &= A - BK \\ &= \begin{bmatrix} -24.2299 & -26.3759 & -23.6950 \\ 0.2313 & 0.2349 & -0.2314 \\ 0 & 0.5046 & 0 \end{bmatrix}.\end{aligned}$$

We choose  $\hat{Q} = Q = I_3$  and we obtain  $P$  using the *lyap* function in MATLAB.

$$P = \begin{bmatrix} 179.7359 & -85.1218 & -89.0194 \\ -85.1218 & 80.7233 & -0.9909 \\ -89.0194 & -0.9909 & 90.3612 \end{bmatrix}.$$

For the above matrix  $V(x) = x^t P x$  will satisfy  $\dot{V} < 0$  according to the construction of  $P$ .

The paper [67] demonstrated chaotic orbits for certain parameter values. Harvesting was introduced and chaos was also observed. Unfortunately, non-permanence was also observed. With the help of the control algorithm, optimal harvesting was calculated.

In all the three models, instances of chaos and non-permanence were observed for different values of the harvesting coefficient. The control algorithm in Section 5.3 uses the chaotic orbits in the system to obtain a closed loop control (i.e. function of the state of the system) which pushes the system into a permanent state.

# Chapter 7

## Conclusions and discussion

Chaos does occur in many biologically relevant systems ([60, 30, 67] to name a few). The objective of this thesis was to show that chaos can be useful to the species in the long run and be utilized for control. We used permanence to measure whether the species are thriving.

### 7.1 Connections and conclusions

We considered the three-dimensional two prey, one predator Lotka-Volterra system with  $a_{ii} < 0$  for  $i = 1, 2, 3$ . We assumed chaos occurred with the interior rest point as the initial condition. We used the instability of the rest point to derive conditions for permanence. This method, unfortunately, was specific to the Lotka-Volterra case and only used the instability of the rest point which may occur even in non-chaotic orbits. We then showed a connection between chaos and persistence in three-dimensional systems using the Poincaré–Bendixson Theorem.

To better use the chaotic orbits present in the system, we used control theory methods. Based on the control algorithm in [66], we formulated a closed loop control (control which is a function of the state of the system) which uses the chaotic orbits and pushes the system from non-permanence to permanence. The algorithm was used on three types of models, namely, a Lotka-Volterra type two-prey, one-predator model from [30], a ratio-dependent one-prey, two-predator model from [35] and a tritrophic interaction model (a model with three levels: a prey, an intermediate predator and the top predator) [67]. In each model, for certain values of a harvesting parameter, chaos and non-permanence were found. The control algorithm provided the harvesting control required to push the system into permanence and a desired harvesting rate to maintain permanence. So chaos enabled the species to remain at a safe threshold value from extinction with the help of control theory.

## 7.2 Further research

We have used only one algorithm for our control of chaotic orbits. There are other algorithms which use control theory on the chaos present in the system [25, 42, 74, 37]. A comparison of the effectiveness of these algorithms can be done as well.

In this thesis, we investigated autonomous continuous dynamical systems with ordinary differential equations. Permanence of non-autonomous systems [63, 71, 73, 51] and of discrete systems [70] has not been considered. We can measure chaos in such systems and maybe find a suitable control algorithm to obtain similar results as the ones obtained in this thesis.

# Appendices

## Appendix A   MATLAB code for determining Lyapunov Spectrum

This appendix includes the MATLAB code for determining the Lyapunov Spectrum. It is based on the paper by Wolf et al [6].

```
%Code from Wolf paper

%Before passing f make sure f=@system where system is function
%corresponding to your system

function lyapOut = myLyap(f,p,Initial,t,ts)%f is the ode system,
%p is the parameter set, init is the initial conditions,
%t is the time interval for the ode solver, ts is the timestep

%N = number of nonlinear equations,
%NN = Total number of equations

N=length(Initial); %length(Initial) gives us
%the size of original system
NN=N*(N+1);

% initialize arrays

Y=zeros(NN,1);
CUM=zeros(N,1);
```

```

GSC= zeros(N,1);
znorm=zeros(N,1);
y0 = Y;

lyap = zeros(N,1);
S=zeros(N,1);

len = round((t(2)-t(1))/ts);

for i = 1:N
    Y(i,1) = Initial(i);
end

%Initial Conditions for linear system(Orthonormal frame)

for i =1:N
    Y((N+1)*i,1) = 1.0;
end;

tstart = t(1);

for iterLyap=1:len
    [tvals,y] = ode45(@(t,y)(f(t,y,p)), [tstart,tstart+ts], Y);

    Y = y(size(y,1),:)' ;

```

```

for i = 1:N
    for j = 1:N
        y0(N*i+j,1) = Y(N*i+j,1);
    end
end

tstart=tstart+ts;

%Construct a new orthonormal basis by Gram-Schmidt Method
%Normalize first vector
znorm(1,1)=0.0;
for j=1:N
    znorm(1,1)=znorm(1,1) + y0(N*j+1,1)^2;
end;
znorm(1,1)=sqrt(znorm(1,1));
for j=1:N
    y0(N*j+1,1) = y0(N*j+1,1)/znorm(1,1);
end;

%Generate the new orthonormal set of vectors
for j=2:N

    %Generate j-1 GSR coefficients
    for k= 1:j-1
        GSC(k,1) =0.0;
        for l=1:N

```



```

        GSC(k,1) = GSC(k,1) + y0(N*1+j,1)*y0(N*1+k,1);
    end;
end;

%Construct a new vector
for k=1:N
    for l=1:j-1
        y0(N*k+j,1) = y0(N*k+j,1) - GSC(l,1)*y0(N*k+l,1);
    end;
end

%calculate the vector's norm
znorm(j,1) =0.0;
for k=1:N
    znorm(j,1)= znorm(j,1) + y0(N*k+j,1)^2;
end;
znorm(j,1) =sqrt(znorm(j,1));

%normalize the new vector
for k=1:N
    y0(N*k+j,1) = y0(N*k+j,1)/znorm(j,1);
end;
end;

%update running vector magnitudes
for k=1:N

```

```

        CUM(k,1) = CUM(k,1) + log(znorm(k,1))/log(2.0);
    end;

    %normalize exponent and print every 10 iterations
    %if (rem(i,10)== 0)
    for k=1:N
        lyap(1,k) = CUM(k,1)/(tstart-t(1));
    end;

    if iterLyap == 1
        lyapExp = lyap;
    else
        lyapExp = [lyapExp; lyap];
    end

    for i = 1:N
        for j = 1:N
            Y(N*j+i,1) = y0(N*j+i,1);
        end
    end

    lyapOut = lyap(1,1:N);

end

```

## Appendix B   MATLAB code to determine permanence using boundary rest points

This code determines the permanence of the systems considered in Chapter 6 using boundary rest points. The system is said to be permanent if it does not have regular, saturated rest points (Refer to Section 4.2.2). The code first finds the boundary rest points and then checks to see if they are saturated.

```
%Check for permanence
function [r,check] = Perm_Check2(system, p)
sys_harvest=1;%From the harvesting paper by Azar et.al
sys_Eg213=2;%Eg pg 213 of Evolutionary text
sys_Upad=3;%Multiple attractors and crisis route -Upadhyay

if system == sys_harvest
    syms x1 x2 x3;
%parameters
r1 = p(1);
r2 = p(2);
r3 = p(3);

a_11=p(4);
a_12=p(5);
a_13=p(6);
a_21 = p(7);
```

```

a_22=p(8);
a_23=p(9);
a_31=p(10);
a_32=p(11);
H = p(12); %Harvesting function

f1=(r1-a_11*x1-a_12*x2-a_13*x3);
f2=(r2-a_21*x1-a_22*x2-a_23*x3);
f3=(-r3+a_31*x1+a_32*x2 - H/x3);
xp1 = x1*f1== 0;
xp2 = x2*f2== 0;
xp3 = x3*f3== 0;
S = solve([xp1,xp2,xp3]);
V=double([S.x1 S.x2 S.x3]);%gives us the rest points
F= double([subs(f1,S) subs(f2,S) subs(f3,S) ]);
%F gives f_i values at the rest points
end

%Eg Page 213 of Evolutionary Games text book
if system==sys_Eg213
syms x1 x2 x3;
%parameters
a1=p(1);
a2=p(2);
b1=p(3);
b2=p(4);

```

```

c1=p(5);
c2=p(6);
r1=p(7);
s1=p(8);
s2=p(9);
h=p(10); %harvesting coefficient

f1= r1*(1-x1-a1*x2/(1+b1*x1)-a2*x3/(1+b2*x1));
f2= s1*(-1+c1*x1/(1+b1*x1)-x2)-h;
f3= s2*(-1+c2*x1/(1+b2*x1)-x3);
xp1 = x1*f1== 0;
xp2 = x2*f2== 0;
xp3 = x3*f3== 0;
S = solve([xp1,xp2,xp3]);
V=double([S.x1 S.x2 S.x3]);%gives us the rest points
F= double([subs(f1,S) subs(f2,S) subs(f3,S) ]);
%F gives f_i values at the rest points
end

%Multiple attractors and crisis route -Upadhyay
if system ==sys_Upad
syms x1 x2 x3 real;
%parameters
a1=p(1);
b1=p(2);
w=p(3);

```

```

D=p(4);
a2=p(5);
w1=p(6);
D1=p(7);
w2=p(8);
D2=p(9);
c=p(10);
w3=p(11);
D3=p(12);
h=p(13); %harvesting coefficient
f1= a1-b1*x1-(w*x2/(x1+D))-h;
f2= -a2+w1*x1/(x1+D1)-w2*x3/(x2+D2);
f3= c*x3-w3*x3/(x2+D3);
xp1 = x1*f1== 0;
xp2 = x2*f2== 0;
xp3 = x3*f3== 0;
S = solve([xp1,xp2,xp3]);
V=double([S.x1 S.x2 S.x3]);%gives us the rest points
F= double([subs(f1,S) subs(f2,S) subs(f3,S) ]);
%F gives f_i values at the rest points
end

[m,n]=size(V);
for i = 1:m %To get the interior rest point
    if all(V(i,:)>0)
        r=V(i,:);
    end
end

```

```

        break;
    else
        r=[0 0 0];
    end
    if any(V(i,:)<0)
        V1=V([1:i-1,i+1:end],:); %To make sure rest pts are valid biologically
        F1=F([1:i-1,i+1:end],:);
    else
        V1=V;
    end
end
end
flag=0;
[m1,n1]=size(V1);
if all(r>0) %doing the check for permanence if there is an interior rest point
    for i=1:m1
        for j=1:n1
            if V1(i,j)==0
                if F1(i,j) >=0
                    check = 1;
                    flag=1;
                    break;
                else
                    check =0;
                end
            end
        end
    end
    if (flag==1)

```

```
        break;
    end
end
if (flag==1)
    break;
end
end
else
    check=0;
end
```



## Appendix C   MATLAB code for the linearized version of the systems in Chapter 6

This appendix contains the linearized systems of the systems in Chapter 6. This is important to determine Lyapunov exponents via the code in Appendix A.

```
%Lotka volterra system with harvesting by Azar et.al
function xp = Harvest(t,x,p)
xp = zeros(12,1);
%parameters
r1 = p(1);
r2 = p(2);
r3 = p(3);
a_11=p(4);
a_12=p(5);
a_13=p(6);
a_21 = p(7);
a_22=p(8);
a_23=p(9);
a_31=p(10);
a_32=p(11);
H=p(12);

%original system
xp(1,1) = x(1,1)*(r1-a_11*x(1,1)-a_12*x(2,1)-a_13*x(3,1));
xp(2,1) = x(2,1)*(r2-a_21*x(1,1)-a_22*x(2,1)-a_23*x(3,1));
```

```

xp(3,1) = x(3,1)*(-r3+a_31*x(1,1)+a_32*x(2,1))-H;

%linearized copies
for j = 0:2
    xp(4+j,1) = (r1-2*a_11*x(1,1)-a_12*x(2,1)-a_13*x(3,1))*x(4+j,1)-...
        a_12*x(1,1)*x(7+j,1)-a_13*x(1,1)*x(10+j,1);
    xp(7+j,1) = -a_21*x(2,1)*x(4+j,1)+...
        (r2-2*a_22*x(2,1)-a_21*x(1,1)-a_23*x(3,1))*x(7+j,1)-...
        a_23*x(2,1)*x(10+j,1);
    xp(10+j,1) = a_31*x(3,1)*x(4+j,1)+a_32*x(3,1)*x(7+j,1)+...
        (-r3+a_31*x(1,1)+a_32*x(2,1))*x(10+j,1);
end
end

%Eg in page 213 of Evolutionary Games text book
function xp = Eg213(t,x,p)
xp = zeros(12,1);
%parameters
a1=p(1);
a2=p(2);
b1=p(3);
b2=p(4);
c1=p(5);
c2=p(6);
r1=p(7);
s1=p(8);

```

```

s2=p(9);
h=p(10);

%original system
xp(1,1) = r1*x(1,1)*(1-x(1,1)-a1*x(2,1)/(1+b1*x(1,1))-a2*x(3,1)/(1+b2*x(1,1)));
xp(2,1) = s1*x(2,1)*(-1+c1*x(1,1)/(1+b1*x(1,1))-x(2,1))-h*x(2,1);
%With harvesting h
xp(3,1) = s2*x(3,1)*(-1+c2*x(1,1)/(1+b2*x(1,1))-x(3,1));
%linearized copies
for j = 0:2
    xp(4+j,1) = r1*(1-2*x(1,1)-((a1*x(2,1))/((1+b1*x(1,1))^2))-...
        ((a2*x(3,1))/((1+b2*x(1,1))^2)))*x(4+j,1)-...
        (r1*a1*x(1,1)/(1+b1*x(1,1)))*x(7+j,1)-...
        (r1*a2*x(1,1)/(1+b2*x(1,1)))*x(10+j,1);
    xp(7+j,1) = (s1*c1*x(2,1)/(1+b1*x(1,1))^2)*x(4+j,1)+...
        (s1*(-1-2*x(2,1)+c1*x(1,1)/(1+b1*x(1,1)))-h)*x(7+j,1);
    xp(10+j,1) = (s2*c2*x(3,1)/(1+b2*x(1,1))^2)*x(4+j,1)+...
        s2*(-1-2*x(3,1)+c2*x(1,1)/(1+b2*x(1,1)))*x(10+j,1);
end
end

%Multiple attractors and crisis route -Upadhyay
function xp = Upad(t,x,p)
xp = zeros(12,1);
%parameters

```

```

a1=p(1);
b1=p(2);
w=p(3);
D=p(4);
a2=p(5);
w1=p(6);
D1=p(7);
w2=p(8);
D2=p(9);
c=p(10);
w3=p(11);
D3=p(12);
h=p(13); %harvesting coefficient

%original system
xp(1,1) = x(1,1)*(a1-b1*x(1,1)-w*x(2,1)/(x(1,1)+D)-h);

%With harvesting h
xp(2,1) = x(2,1)*(-a2+w1*x(1,1)/(x(1,1)+D1)-w2*x(3,1)/(x(2,1)+D2));
xp(3,1) = x(3,1)*(c*x(3,1)-w3*x(3,1)/(x(2,1)+D3));

%linearized copies
for j = 0:2
    xp(4+j,1) = (a1-h-2*b1*x(1,1)-w*D*x(2,1)/(x(1,1)+D)^2)*x(4+j,1)-...
        (w*x(1,1)/(x(1,1)+D))*x(7+j,1); %With harvesting
    xp(7+j,1) = (w1*D1*x(2,1)/(x(1,1)+D1)^2)*x(4+j,1)+...
        (-a2+w1*x(1,1)/(x(1,1)+D1)-w2*D2*x(3,1)/((x(2,1)+D2)^2))*x(7+j,1)-...

```

```

        (w2*x(2,1)/(x(2,1)+D2))*x(10+j,1);
xp(10+j,1) = (w3*x(3,1)^2/(x(2,1)+D3)^2)*x(7+j,1)+...
        (2*c*x(3,1)-2*w3*x(3,1)/(x(2,1)+D3))*x(10+j,1);
end
end

```

## Appendix D   MATLAB code for the control algorithm

This appendix gives the MATLAB code for the application of the control algorithm in Section 5.3 to the systems in Chapter 6.

```
%Lotka volterra system with harvesting by Azar et.al
%parameters
r1 = 1;
r2 = 1;
r3 = 1;
a_11=1;
a_12=1;
a_13=5;
a_21 = 1.5;
a_22=1;
a_23=1;
a_31=2.5;
a_32=0.5;
H=0.035;
params = [r1,r2,r3,a_11,a_12,a_13,a_21,a_22,a_23,a_31,a_32,H];
r = Perm_Check2(1, params);

syms x1 x2 x3 H
f1=x1*(r1-a_11*x1-a_12*x2-a_13*x3);
```

```

f2=x2*(r2-a_21*x1-a_22*x2-a_23*x3);
f3=x3*(-r3+a_31*x1+a_32*x2) - H;

J=jacobian([f1; f2; f3], [x1 x2 x3 H]);
J1=double(subs(J,[x1,x2,x3,H],[r,0.35]));%Finding the Jacobian at the rest
%point and required control
[m,n]=size(r);
A=J1(:,1:n)
B=J1(:,n+1:end)
Q=ones(3);
R=[1];
K=lqr(A,B,Q,R)
Ahat=A-B*K
P=lyap(Ahat,Q) %For the Lyapunov function V=transpose(x)Px
l=eig(P) %To check if P is positive definite.

%Eg in page 213 of Evolutionary Games text book
%parameters
a1=5;
a2=5;
b1=2;
b2=2;
c1=4;
c2=4;
r1=1;

```

```

s1=1;

s2=1;

h=0.15; %harvesting coefficient

params = [a1,a2,b1,b2,c1,c2,r1,s1,s2,h]';

r = Perm_Check2(4, params);


syms x1 x2 x3 h

f1=x1*r1*(1-x1-a1*x2/(1+b1*x1)-a2*x3/(1+b2*x1));

f2= x2*s1*(-1+c1*x1/(1+b1*x1)-x2)-h*x2;

f3= x3*s2*(-1+c2*x1/(1+b2*x1)-x3);


J=jacobian([f1; f2; f3], [x1 x2 x3 h]);

J1=double(subs(J,[x1,x2,x3,h],[r,0.15]));%Finding the Jacobian at the rest
%point and required control

[m,n]=size(r);

A=J1(:,1:n)

B=J1(:,n+1:end)

Q=ones(3);

R=[1];

K=lqr(A,B,Q,R)

Ahat=A-B*K

P=lyap(Ahat,Q) %For the Lyapunov function V=transpose(x)Px

l=eig(P) %To check if P is positive definite.


%%Multiple attractors and crisis route -Upadhyay

%parameters

```



```

a1=1.93;
b1=0.06;
w=1;
D=10;
a2=1;
w1=2;
D1=10;
w2=0.405;
D2=10;
c=0.03;
w3=1;
D3=20;
h=0.1;
params=[a1,b1,w,D,a2,w1,D1,w2,D2,c,w3,D3,h]';

r = Perm_Check2(7, params);

syms x1 x2 x3 h
f1=x1*( a1-b1*x1-(w*x2/(x1+D))-h);
f2= x2*(-a2+w1*x1/(x1+D1)-(w2*x3/(x2+D2)));
f3= x3*(c*x3-(w3*x3/(x2+D3)));

J=jacobian([f1; f2; f3], [x1 x2 x3 h]);
J1=double(subs(J,[x1,x2,x3,h],[r,0.1]));%Finding the Jacobian at the rest
%point and required control
[m,n]=size(r);

```

```

A=J1(:,1:n)
B=J1(:,n+1:end)
Q=ones(3);
R=[1];
K=lqr(A,B,Q,R)
Ahat=A-B*K
P=lyap(Ahat,Q) %For the Lyapunov function  $V=\text{transpose}(x)Px$ 
l=eig(P) %To check if P is positive definite.

```

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