LECTURE NOTES: MATHEMATICAL EPIDEMIOLOGY

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Contents

1 Introduction to Nonlinear Systems **1**

1.1 Analysis of nonlinear systems 1

1.2 Main tools for analysis of nonlinear systems 1

1.2.1 Equilibrium points 1

1.2.2 Stability 2

1.3 Linearization and Stability 7

1.3.1 Examples on Linearization and Classification of equilibrium points 8

1.4 Liapunov functions 12

1.4.1 Liapunov Theorem for continuous case 13

1.5 Invariant sets 14

1.6 Bifurcations and Manifolds 17

1.7 Types of Bifurcations 21

1.8 Hopf Bifurcation 24

1.9 Population dynamics 26

1.9.1 Population interactions 26

1.9.2 Predator-Prey interactions 27

1.9.3 Competing species 29

1.9.4 Mutualism/Symbiosis 30

2 Mathematical Modelling: Epidemiology **35**

2.1 The SIR epidemic model 35

2.2 Simple extensions of the SIR model 39

2.2.1 Loss of immunity 39

2.2.2 Inclusion of immigration or emigration 40

2.2.3 Immunization 41

3 Calculation of the Reproduction Number 45

3.1 Reproduction numbers 45

3.1.1 The next generation matrix 45

3.2 Applications of the technique 46

3.2.1 Example 1: TB treatment model 47

3.2.2 Example 2: Multi-strain model 48

3.2.3 Example 3: Host-Vector model 48

3.3 Exercises 49

4 Advanced HIV/AIDS Models 51

4.1 HIV/AIDS model with treatment 51

4.1.1 Model formulation 51

4.1.2 Steady state solutions 52

4.1.3 The reproduction numbers R_1 and R_2. 55

4.1.4 Varying population model 56

4.2 Spread of diseases for interlinked discrete geographic locations 58

5 Other Mathematical Modelling Problems 63

5.1 Modelling HIV-TB co-infection 63

5.1.1 The model description 63

5.2 Modelling the role of chemo-prevention in malaria 64

5.2.1 Model formulation 64

5.3 Modelling fisheries 65

5.3.1 Harvesting 65

5.3.2 Maximum sustainable yield (MSY) 66

5.3.3 Fisheries management 67

Chapter 1

Introduction to Nonlinear Systems

1.1 Analysis of nonlinear systems

An n^{th}-order system of continuous differential equations has the following form:

$$\begin{aligned} \dot{x}_1(t) &= f_1(x_1(t), x_2(t), \cdots, x_n(t)), \\ \dot{x}_2(t) &= f_1(x_1(t), x_2(t), \cdots, x_n(t)), \\ . \quad &. \quad \cdots\cdots\cdots\cdots \\ . \quad &. \quad \cdots\cdots\cdots\cdots \\ \dot{x}_n(t) &= f_n(x_1(t), x_2(t), \cdots, x_n(t)), \end{aligned} \tag{1.1.1}$$

which can be expressed in matrix form as

$$\dot{X}(t) = f(X(t), t), \tag{1.1.2}$$

where $X = [x_1, x_2, ..., x_n]^T$ and $f = [f_1, f_2, ..., f_n]^T$. T - meaning transpose.

In general, one does not seek detailed solutions either in numerical or analytical form, but rather one seeks to characterize some aspects of system behaviour. For example one might ask whether there are equilibrium points and whether they are stable. In nonlinear systems, one might look, in addition to equilibrium points, for threshold effects. The approach therefore, includes characterizing in broad terms the critical aspects of the system behaviour.

1.2 Main tools for analysis of nonlinear systems

1.2.1 Equilibrium points

Definition 1.2.1 *A vector $\bar{X}$ is an equilibrium point for a dynamical system if once the state vector is equal to $\bar{X}$ it remains equal to $\bar{X}$ for all future time.*

Example 1.2.2 *If*

$$\dot{X}(t) = f(X(t), t)$$

then an equilibrium point is a state $\bar{X}$ *satisfying*

$$f(\bar{X}, t) = 0$$

for all time t.

An analysis of a nonlinear dynamical system may devote considerable attention to the characterization of the equilibrium points. In the linear systems equilibrium points are basically solutions to linear equations.

The nonlinear case is different in two essential respects:

1. First, since the equilibrium points are solutions, in this case, to nonlinear equations, finding such solutions is somewhat more of an accomplishment than in the linear case.

2. The equilibrium point distribution is potentially more complex in the nonlinear case than in the linear case.

Note: A system may have none, one or any number of equilibrium points in virtually a spatial pattern in state space.

Thus characterization of equilibrium points is not only technically more difficult, it is a much broader question. Ultimately, interest centers not just on the existence of the equilibrium points but also on their stability properties.

1.2.2 Stability

Stability properties characterize how a system behaves if its state is initiated close to, but not precisely at a given equilibrium point.

1. If a system is initiated with the state exactly equal to an equilibrium point, then by definition it will never move.

2. When initiated close by, however, the state may remain close by, or it may move away.

Roughly speaking, an equilibrium point is stable whenever the system state is initiated near that point, the state remains near it, perhaps even tending towards the equilibrium point as time increases.

Suppose $\bar{X}$ is an equilibrium point of a time-invariant system i.e. $\bar{X}$ is an equilibrium point of

$$\dot{X}(t) = f(X(t)).$$

For a precise definition of stability, it is convenient to introduce the notation $S(\bar{X}, R)$ to denote a spherical region in the state space with center at $\bar{X}$ and radius R.

Definition 1.2.3 *An equilibrium point $\bar{X}$ is stable if there exists $R_0 > 0$ for which the following is true. For every $R < R_0$, there exists r, $0 < r < R$, such that if $X(0)$ is inside $S(\bar{X}, r)$, then $X(t)$ is inside $S(\bar{X}, R)$ for all $t > 0$.*

Definition 1.2.4 *An equilibrium point $\bar{X}$ is asymptotically stable if whenever it is stable and in addition there exists $\bar{R}_0 > 0$ such that whenever the state is initiated inside $S(\bar{X}, \bar{R}_0)$, it tends to $\bar{X}$ as time increases.*

Definition 1.2.5 *An equilibrium point $\bar{X}$ is marginally stable if it is stable but not asymptotically stable.*

Definition 1.2.6 *An equilibrium point $\bar{X}$ is unstable if it is not stable. Equivalently, $\bar{X}$ is unstable if for some $R > 0$ and any $r > 0$ there is a point in the spherical region $S(\bar{X}, r)$ such that if initiated there, the system state will eventually move outside of $S(\bar{X}, R)$.*

Below we give examples on stability and classification of equilibrium points.

Example 1.2.7 *Consider the system*

$$\begin{aligned} \dot{x}(t) &= x(t) \\ \dot{y}(t) &= -ky(t) \end{aligned}$$

There is only one fixed point $(0, 0)$. The solution is

$$x(t) = x_0 e^{-t}, \qquad y(t) = y_0 e^{-kt}$$

If $x_0 \neq 0$, we can express y as a function of x as shown below:

$$x(t) = x_0 e^{-t}, \qquad y = bx^k, \tag{1.2.3}$$

where $b = \dfrac{y_0}{x_0^k}$. We can consider some special cases of (1.2.3).

Case 1:

$$x(t) = x_0 e^{-t}, \qquad y(t) = bx$$

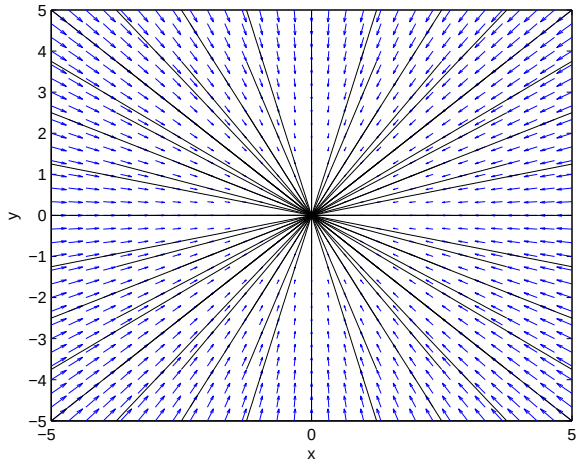

Figure 1.1: *Phase Portraits for* $k = 1$.

$y = bx$ is a family of straight lines with the slope b. As $t \to \infty$, $x(t) \to 0$. Thus $(0, 0)$ is an asymptotically stable proper node.

Case 2:

Consider the case $k = 2$. This gives

$$x(t) \quad = \quad x_0 e^{-t}, \qquad\qquad y(t) = bx^2$$

$y = bx^2$ is a family of parabolas. As $t \to \infty$, $x(t) \to 0$. Thus $(0, 0)$ is an asymptotically stable improper node.

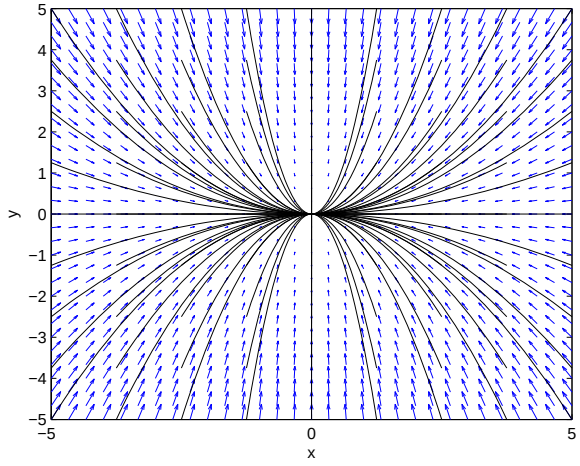

Figure 1.2: *Phase Portraits for* $k = 2$.

Case 3:

For the case $k = -1$ equation (1.2.3) reduces to

$$x(t) = x_0 e^{-t}, \qquad y(t) = y_0 e^{t} \qquad \text{or} \qquad xy = C,$$

$x(t)$ decreases with increasing time t but y increases with increasing t. This yields a saddle node (unstable) at $(0, 0)$.

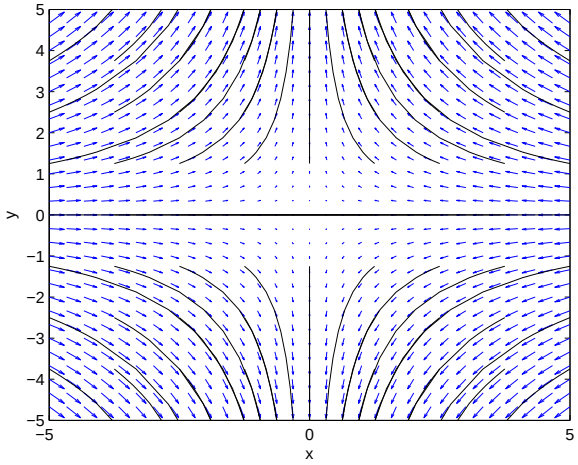

Figure 1.3: *Phase Portraits for* $k = -1$

One can obtain more phase portraits for the values of k but those are of no interest to us.

Example 1.2.8 *Consider the system*

$$\begin{aligned} \dot{x}(t) &= y(t), \\ \dot{y}(t) &= -\omega^2 x(t). \end{aligned}$$

This system has one equilibrium point. However, we proceed by combining the two equations. This gives

$$\ddot{x}(t) = -\omega^2 x(t). \tag{1.2.4}$$

The solution is

$$\begin{aligned} x(t) &= C\cos(\omega t - \alpha), \\ y(t) &= -\omega C \sin(\omega t - \alpha). \end{aligned}$$

This solution yields

$$\frac{x^2}{C^2} + \frac{y^2}{\omega^2 C^2} = 1,$$

which is a family of ellipses with period $\frac{2\pi}{\omega}$.

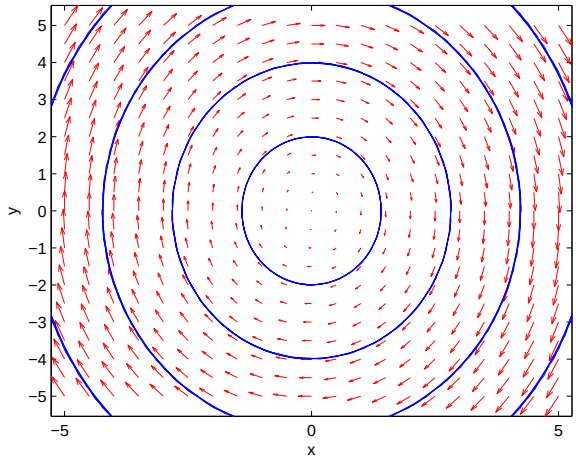

Figure 1.4: *Phase Portraits for simple harmonic motion.*

The equilibrium point $(0, 0)$ is stable but not asymptotically stable. The equation (1.2.4) represents simple harmonic motion in physics. The motion is not subjected to damping.

Example 1.2.9 *For the motion with damping, consider the following example.*

$$\begin{aligned} \dot{x}(t) &= y(t), \\ \dot{y}(t) &= -2x(t) - 2y.(t) \end{aligned}$$

This system has one equilibrium point at $(0, 0)$. *It is important to combine these equations giving*

$$\ddot{x}(t) + 2\dot{x} + 2x = 0$$

The solution is

$$\begin{aligned} x(t) &= Ce^{-t}\cos(t - \alpha), \\ y(t) &= -C\sqrt{2}e^{-t}\sin(t - \alpha + \frac{\pi}{4}). \end{aligned}$$

The amplitude is now time dependent and decreases as $t \to \infty$.

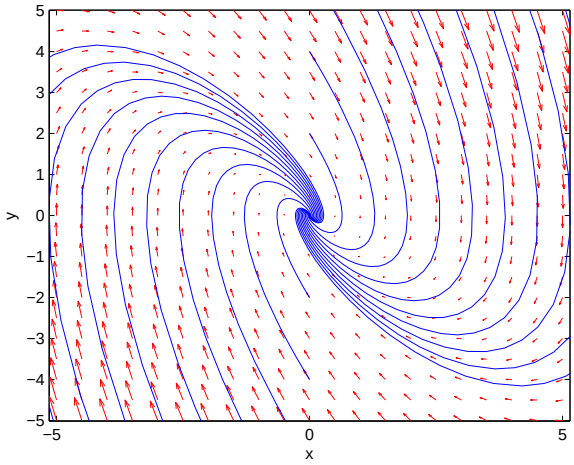

Figure 1.5: *Phase portraits for damped harmonic motion.*

The point $(0, 0)$ is a stable spiral.

1.3 Linearization and Stability

According to the basic definitions, stability properties depend only on the nature of the system near the equilibrium point. Therefore, to conduct an analysis of the stability, it is often theoretically legitimate and mathematically convenient to replace the full nonlinear description by a simpler description that approximates the true system near the equilibrium point. Often a linear approximation is sufficient to reveal the stability properties.

The linearization of a nonlinear system is based on linearization of the nonlinear function f in its description. For the first-order system, defined by a single function $f(x)$ of a single variable, the procedure is to approximate f near $\bar{x}$ by

$$f(\bar{x} + y) = f(\bar{x}) + \frac{df(\bar{x})}{dx} y. \tag{1.3.5}$$

An n-order system is defined by n functions, each of which depends on the n variables. In this case each function is approximated by the relation

$$\begin{aligned} f_i(\bar{x}_1 + y_1, \bar{x}_2 + y_2, \cdots, \bar{x}_n + y_n) \approx\ & f_i(\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n) + \frac{\partial f_i(\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n)}{\partial x_1} y_1 + \\ & \frac{\partial f_i(\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n)}{\partial x_2} y_2 + \frac{\partial f_i(\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n)}{\partial x_3} y_3 + \end{aligned}$$

$$\cdots\cdots\cdots\cdots\cdots + \frac{\partial f_i(\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n)}{\partial x_n} y_n$$

where $i = 1, 2, \cdots n$. In matrix form, this can be written as

$$f(\bar{x} + y) \approx f(\bar{x}) + Fy, \tag{1.3.6}$$

where

$$F = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_n} \\ \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}.$$

The matrix F is called the Jacobian matrix of f. Now consider the matrix equation

$$\dot{x} = f(x(t)). \tag{1.3.7}$$

Setting $x(t) = \bar{x} + y(t)$, we obtain

$$\dot{y} = f(\bar{x} + y(t)) = f(\bar{x}) + Fy(t). \tag{1.3.8}$$

Since $\bar{x}$ is an equilibrium point of f, $f(\bar{x}) = 0$. Therefore

$$\dot{y}(t) = Fy(t). \tag{1.3.9}$$

Thus, the stability properties of the original system can be inferred from the linearized system using the following results.

1. If all eigenvalues of F are strictly in the left half-plane, then $\bar{x}$ is asymptotically stable for the nonlinear system.

2. If at least one eigenvalue of F has a positive real part, then $\bar{x}$ is unstable for the nonlinear system.

3. If the eigenvalues of F are all in the left half-plane, but at least one has a zero real part then $\bar{x}$ may be either stable, asymptotically stable or unstable for the nonlinear system.

1.3.1 Examples on Linearization and Classification of equilibrium points

Example 1.3.1 *Consider the system*

$$\begin{aligned} \dot{x}_1 &= k_1(1 - x_2)x_1, \\ \dot{x}_2 &= -k_2(1 - x_1)x_2, \qquad\qquad x_1,\ x_2 \geq 0,\ k_1,\ k_2 > 0. \end{aligned}$$

This system has two equilibrium points $(0,0)$ and $(1,1)$. We can linearize the system about $(0,0)$ giving

$$\begin{aligned} \dot{x}_1 &= k_1 x_1, \\ \dot{x}_2 &= -k_2 x_2, \end{aligned}$$

or

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} k_1 & 0 \\ 0 & -k_2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = k_1 > 0$ and $\lambda_2 = -k_2 < 0$. Therefore, $(0,0)$ is a saddle point.

Consider the equilibrium point $(1,1)$. We define new local variables so that the point $(1,1)$ is the origin of the new coordinate system. Let

$$y_1 = x_1 - 1 \qquad \text{and} \qquad y_2 = x_2 - 1.$$

The system becomes

$$\begin{aligned} \dot{y}_1 &= k_1 y_2 (y_1 + 1), \\ \dot{y}_2 &= -k_2 y_1 (y_2 + 1). \end{aligned}$$

The associated linear system is

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} 0 & k_1 \\ -k_2 & 0 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = i\sqrt{k_1 k_2}$ and $\lambda_2 = -i\sqrt{k_1 k_2}$. Therefore, $(1,1)$ is either a center or a focus.

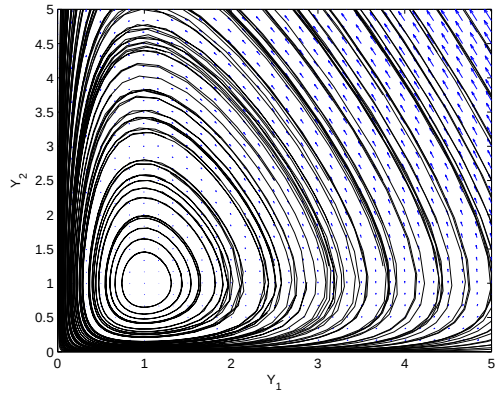

Figure 1.6: *Phase portraits for predator-prey systems.*

The equilibrium point $(1,1)$ is stable but not asymptotically stable.

Example 1.3.2 *Consider the system*

$$\dot{x}_1 = k_1(1-\epsilon x_1 - x_2)x_1, \qquad 0<\epsilon << 1 \tag{1.3.10}$$
$$\dot{x}_2 = -k_2(1-x_1)x_2. \tag{1.3.11}$$

The system has three equilibrium points $(0,0)$, $(1,1-\epsilon)$ and $(\frac{1}{\epsilon},0)$.

Consider the equilibrium point $(0,0)$. We can linearize the given system giving

$$\begin{aligned}\dot{x}_1 &= k_1 x_1,\\ \dot{x}_2 &= -k_2 x_2.\end{aligned}$$

or

$$\begin{pmatrix}\dot{x}_1\\ \dot{x}_2\end{pmatrix} = \begin{pmatrix}k_1 & 0\\ 0 & -k_2\end{pmatrix}\begin{pmatrix}x_1\\ x_2\end{pmatrix}.$$

This is exactly the same as in example 1.3.1. The extra term $-\epsilon k_1 x_1^2$ does not change the nature of the equilibrium point $(0,0)$. Thus, $(0,0)$ remains a saddle point.

Near the fixed point $(\frac{1}{\epsilon},0)$:

Let

$$y_1 = x_1 - \frac{1}{\epsilon} \qquad \text{and} \qquad y_2 = x_2.$$

Then, substituting in the given system, we obtain

$$\begin{aligned}\dot{y}_1 &= -k_1(y_1+\frac{1}{\epsilon})(\epsilon y_1 + y_2),\\ \dot{y}_2 &= -k_2 y_2(1-y_1-\frac{1}{\epsilon}).\end{aligned}$$

The associated linear system is

$$\begin{pmatrix}\dot{y}_1\\ \dot{y}_2\end{pmatrix} = \begin{pmatrix}-k_1 & -\frac{k_1}{\epsilon}\\ 0 & k_2(\frac{1}{\epsilon}-1)\end{pmatrix}\begin{pmatrix}y_1\\ y_2\end{pmatrix}.$$

The eigenvalue equation is

$$\begin{vmatrix}-k_1-\lambda & -\frac{k_1}{\epsilon}\\ 0 & k_2(\frac{1}{\epsilon}-1)-\lambda\end{vmatrix} = 0.$$

with solutions

$$\lambda_1 = -k_1 < 0 \quad \text{and} \quad \lambda_2 = k_2(\frac{1}{\epsilon}-1) > 0.$$

Therefore, the equilibrium point $(\frac{1}{\epsilon}, 0)$ is another saddle point.

Near the fixed point $(1, 1-\epsilon)$: (which was a center when $\epsilon = 0$)

Let

$$y_1 = x_1 - 1 \qquad \text{and} \qquad y_2 = x_2 - 1 + \epsilon.$$

Then,

$$\begin{aligned} \dot{y}_1 &= -k_1(y_1+1)(\epsilon y_1 + y_2), \\ \dot{y}_2 &= -k_2 y_1(y_1 + 1 - \epsilon). \end{aligned}$$

The associated linear system is

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} -k_1\epsilon & -k_1 \\ k_2(1-\epsilon) & 0 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The eigenvalue equation is

$$\begin{vmatrix} -k_1\epsilon - \lambda & -k_1 \\ k_2(1-\epsilon) & -\lambda \end{vmatrix} = 0.$$

with solutions

$$\lambda_1, \lambda_2 = \frac{-k_1\epsilon \pm \sqrt{k_1^2\epsilon^2 - 4k_1k_2(1-\epsilon)}}{2}.$$

If $\epsilon << 1$ then

$$\lambda_1, \lambda_2 \approx \frac{-k_1\epsilon \pm 2i\sqrt{k_1k_2}(1 - \frac{\epsilon}{2})}{2}.$$

We have two complex roots with negative real parts indicating a stable focus at $(1, 1-\epsilon)$.

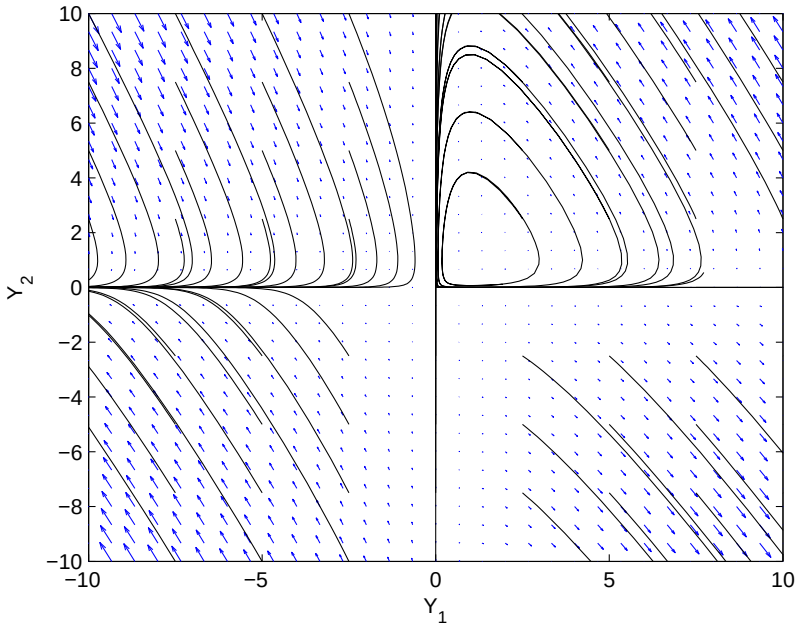

Figure 1.7: *Phase portraits exhibiting bifurcations.*

So the effect of a very small perturbation ϵx_1 is to change the center at $(1, 1)$ to a stable focus (spiral point) at $(1, 1 - \epsilon)$.

Note that if $-1 << \epsilon < 0$ then the eigenvalues would be

$$\lambda_1, \lambda_2 = \frac{1}{2}k_1|\epsilon| \pm i\sqrt{k_1 k_2}(1 + \frac{1}{2}|\epsilon|)$$

and since the real parts are now positive the focus at $(1, 1 + \epsilon)$ is unstable. So we have

- $\epsilon > 0$ stable focus at $(1, 1 - \epsilon)$
- $\epsilon = 0$ not asymptotically stable center at $(1, 1)$
- $\epsilon < 0$ Unstable focus at $(1, 1 + |\epsilon|)$

The system has a bifurcation (splitting into two) point at $\epsilon = 0$.

1.4 Liapunov functions

The method of Liapunov functions enables the analysis to be extended beyond only a small region near the equilibrium point (global analysis). The basic idea of this

technique for verifying stability is to seek an aggregated summarizing function that continually decreases towards a minimum as the system evolves.

Suppose that $\bar{x}$ is an equilibrium point of a given dynamical system. A Liapunov function for the system and the equilibrium point $\bar{x}$ is a real valued function V, which is defined over a region Ω of the state space that contains $\bar{x}$ and satisfies the three requirements:

1. V is continuous
2. $V(x)$ has a unique minimum at $\bar{x}$ with respect to all other points in Ω
3. Along any trajectory of the system contained in Ω, the value of V never increases.

1.4.1 Liapunov Theorem for continuous case

Consider the system

$$\dot{x}(t) = f(x(t)) \tag{1.4.12}$$

together with a given equilibrium point $\bar{x}$. In the time continuous case the requirement that the value of a Liapunov function never increases along a trajectory is expressed in terms of the time derivative.

Suppose $x(t)$ is a trajectory. Then $V(x(t))$ represents the corresponding value of $V(x(t))$ along the trajectory. In order for V not to increase, we require that

$$\dot{V}(x(t)) \leq 0$$

for all t. This derivative can be expressed, using the chain rule for differentiation as

$$\dot{V}(x(t)) = \frac{\partial V}{\partial x_1}\dot{x}_1(t) + \frac{\partial V}{\partial x_2}\dot{x}_2(t) + \cdots + \frac{\partial V}{\partial x_n}\dot{x}_n(t). \tag{1.4.13}$$

Then using the original system, this becomes

$$\begin{aligned} \dot{V}(x(t)) &= \frac{\partial V}{\partial x_1}f_1(t) + \frac{\partial V}{\partial x_2}f_2(t) + \cdots + \frac{\partial V}{\partial x_n}f_n(t), \\ &= \nabla V(x(t))f(x(t)). \end{aligned} \tag{1.4.14}$$

Therefore, the requirement that V is non-increasing along any trajectory of the system translates into the requirement that

$$\dot{V}(x(t)) = \nabla V(x(t))f(x(t)) \leq 0 \tag{1.4.15}$$

for all x is Ω.

Definition 1.4.1 *A function V defined on a region Ω of the state space and containing $\bar{x}$ is a Liapunov function if it satisfies the following three requirements*

1. *V is continuous and has continuous first partial derivatives*
2. *$V(x)$ has a unique minimum at $\bar{x}$ with respect to all other points in Ω*
3. *The function $\dot{V}(x) = \nabla V(x) f(x)$ satisfies $\dot{V}(x) \leq 0$ for all $x(t)$ in Ω.*

Theorem 1.4.2 (Liapunov Theorem) *If there exists a Liapunov function $V(x)$, then the equilibrium point $\bar{x}$ is stable. If, furthermore, the function $\dot{V}(x)$ is strictly negative for every point then the stability is asymptotic.*

Example 1.4.3 *Consider the system*

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

Show that the equilibrium point $(0, 0)$ is stable.

Solution

Define

$$V(x_1, x_2) = x_1^2 + x_2^2.$$

This function is certainly continuous with continuous first partial derivatives. $V(x_1, x_2$ is clearly minimum at $(0, 0)$. The chosen Liapunov $V(x_1, x_2)$ satisfies the first two requirements of a Liapunov function. We want to check the final requirement.

$$\begin{aligned} \dot{V} &= \frac{\partial V}{\partial x_1}\dot{x}_1 + \frac{\partial V}{\partial x_2}\dot{x}_2 \\ &= 2x_1x_2 + 2x_2(-x_1 - x_2) \\ &= 2x_1x_2 - 2x_1x_2 - 2x_2^2 \\ &= -2x_2^2 < 0. \end{aligned}$$

Therefore, the equilibrium point $(0, 0)$ is stable, but not asymptotically stable since $\dot{V}$ is strictly negative at every non-zero point.

1.5 Invariant sets

The Liapunov function concept and stability theorems can be generalized in several directions to treat special circumstances. One generalization based on the idea of an invariant set is particularly useful.

1. Where a Liapunov function is found and $\dot{V}(x)$ is strictly less than zero for some values of x but not for all x. In this case the Liapunov theorem only assures stability. By employing the invariant set concept, however, one can often establish asymptotic stability with the same Liapunov function.

2. For systems that do not have equilibrium points, but in which the state vector does tend to follow a fixed pattern as time increases.

Definition 1.5.1 *A set G is an invariant set for a dynamic system if whenever a point x on a system trajectory is in G, the trajectory remains in G. An equilibrium point is the simplest example of an invariant set. Once the system reaches such a point, it never leaves. Also, if a system has several equilibrium points, the collection G of these points is an invariant set.*

Example 1.5.2

$$\begin{aligned} \dot{x}_1 &= x_2 + x_1(1 - x_1^2 - x_2^2), \\ \dot{x}_2 &= -x_1 + x_2(1 - x_1^2 - x_2^2). \end{aligned}$$

The only equilibrium point of the system is $(0, 0)$. The linearized system is

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

The eigenvalue equation is

$$\begin{aligned} & \begin{vmatrix} 1-\lambda & 1 \\ -1 & 1-\lambda \end{vmatrix} = 0. \\ \equiv\ & (1-\lambda)^2 + 1 = 0 \\ \equiv\ & \lambda^2 - 2\lambda + 2 = 0, \end{aligned}$$

with solutions

$$\lambda_1, \lambda_2 = \frac{2 \pm \sqrt{4-8}}{2} = 1 \pm i.$$

Therefore, the origin is an unstable spiral. The question is "where does the trajectory tend as $t \to \infty$?"

Note that

$$\begin{aligned} x_1\dot{x}_1 + x_2\dot{x}_2 &= x_1x_2 + x_1^2 - x_1^4 - x_1^2x_2^2 - x_1x_2 + x_2^2 - x_1^2x_2^2 - x_2^4 \\ &= x_1^2(1 - x_1^2 - x_2^2) + x_2^2(1 - x_1^2 - x_2^2) \\ &= (x_1^2 + x_2^2)(1 - x_1^2 - x_2^2). \end{aligned}$$

We can write this as

$$(x_1, x_2)\begin{pmatrix}\dot{x}_1\\ \dot{x}_2\end{pmatrix} = (x_1^2 + x_2^2)(1 - x_1^2 - x_2^2),$$

or

$$< x_1, x_2 > \cdot < \dot{x}_1, \dot{x}_2 >= (x_1^2 + x_2^2)(1 - x_1^2 - x_2^2).$$

where $< x_1, x_2 >$ and $< \dot{x}_1, \dot{x}_2 >$ are respectively the state space vector and velocity vector.

Hence, the velocity vector and the state space vector are orthogonal on the unit circle $1 - x_1^2 - x_2^2 = 0$. The unit circle is an invariant set for the system. To obtain the useful generalized Liapunov results, the concept of invariant sets is combined with another key idea form the Liapunov stability theorem.

Theorem 1.5.3 (Invariant Set Theorem) *Let $V(x)$ be a scalar function with continuous first partial derivatives. Let Ω_s denote the region where $V(x) < s$. Assume that Ω_s is bounded and that $\dot{V}(x) \leq 0$ within Ω_s. Let S be the set of points within Ω_s where $\dot{V}(x) = 0$, and let G be the largest invariant set within S. Then every trajectory in Ω_s tends to G as time increases.*

Example 1.5.4 *For the system*

$$\begin{aligned}\dot{x}_1 &= x_2 + x_1(1 - x_1^2 - x_2^2),\\ \dot{x}_2 &= -x_1 + x_2(1 - x_1^2 - x_2^2).\end{aligned}$$

Define the function

$$V(x_1, x_2) = (1 - x_1^2 - x_2^2)^2.$$

Then

$$\begin{aligned}\dot{V}(x_1, x_2) &= \frac{\partial V}{\partial x_1}\dot{x}_1 + \frac{\partial V}{\partial x_2}\dot{x}_2\\ &= 2(-2x_1)(1 - x_1^2 - x_2^2)\dot{x}_1 + 2(-2x_2)(1 - x_1^2 - x_2^2)\dot{x}_2\\ &= -4(1 - x_1^2 - x_2^2)(x_1\dot{x}_1 + x_2\dot{x}_2)\\ &= -4(x_1^2 + x_2^2)(1 - x_1^2 - x_2^2)^2\\ &\leq 0.\end{aligned}$$

This result is zero if and only if $x_1^2 + x_2^2 = 1$ on the unit circle. The set S consists of the origin and the unit circle. S is not an invariant set because it contains the origin. The invariant set G is the unit circle.

1.6 Bifurcations and Manifolds

A characteristic of nonlinear oscillating systems is the sudden change in behaviour which occurs as a parameter passes through a critical value called a bifurcation point (as we saw in example 1.3.10). A system may contain several bifurcation points and display extremely complex behaviour. In this section, we consider some elementary characteristics of bifurcations as they arise in the fold or cusp catastrophes, the hopf bifurcation and structural stability.

Example 1.6.1 *Consider the system*

$$\begin{aligned} \dot{x}_1 &= x_2, \\ \dot{x}_2 &= -mx_1. \end{aligned}$$

The system has an equilibrium point at $(0, 0)$. In matrix form, the system can be written as

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -m & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

The eigenvalues of the system are obtained from

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

If $m > 0$ then $\lambda = \pm i\sqrt{m}$, that is $(0, 0)$ is a centre.

If $m < 0$, let $m = -k$, where $k > 0$ then $\lambda_1 = \sqrt{k}$, $\lambda_1 = -\sqrt{k}$. Thus, $(0, 0)$ is a saddle point. The classification of $(0, 0)$ represents radically different types of the system behaviour. The change in the system behaviour occurs as λ passes through $\lambda = 0$. A bifurcation occurs at $\lambda = 0$ called the bifurcation point.

Example 1.6.2 *To demonstrate that a system can display extremely complex behaviour, consider the damped system*

$$\begin{aligned} \dot{x}_1 &= x_2, \\ \dot{x}_2 &= -kx_2 - \omega^2 x_1, \end{aligned}$$

where $\omega > 0$ and $-\infty < k < \infty$. The system has an equilibrium point at $(0, 0)$. It is more convinient to convert the system to a second order differential equation, that is

$$\ddot{x}_1 + k\dot{x}_1 + \omega^2 x_1 = 0.$$

The characteristic equation is

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

The roots are

$$\lambda = \frac{-k \pm \sqrt{k^2 - 4\omega^2}}{2} = \frac{-k \pm \sqrt{(k-2\omega)(k+2\omega)}}{2}.$$

We have the following cases

1. If $k < -2\omega$, then $(0,0)$ is an unstable node.
2. If $-2\omega < k < 0$, then $(0,0)$ is an unstable spiral.
3. If $0 < k < 2\omega$, then $(0,0)$ is a stable spiral.
4. If $k > 2\omega$, then $(0,0)$ is a stable node.

These can be written in tabular form as

Unstable node	Unstable Spiral	Stable Spiral	Stable node
$-\infty < k < -2\omega$	$-2\omega < k < 0$	$0 < k < 2\omega$	$2\omega < k < \infty$

Note that the transition from stable spiral to stable node is not a bifurcation since both states are asymptotically stable. Even though the stable spiral is different from a stable node we do not call the value $k = 2\omega$ a bifurcation point.

However, the transition from unstable spiral to stable spiral as k increases from -2ω through $k = 0$ is a bifurcation point.

Example 1.6.3 *Find the bifurcation points of the system*

$$\begin{aligned} \dot{x}_1 &= -kx_1 + x_2, \\ \dot{x}_2 &= -kx_1 - 3x_2. \end{aligned}$$

In matrix form, this can be written as

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} -k & 1 \\ -k & -3 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

This system has an equilibrium point at $(0,0)$. The characteristic equation is

$$\begin{vmatrix} -k-\lambda & 1 \\ -k & -3-\lambda \end{vmatrix} = \lambda^2 + (3+k)\lambda + 4k = 0.$$

The roots are

$$\begin{aligned} \lambda_1 &= \frac{-(3+k) + \sqrt{(k-1)(k-9)}}{2}, \\ &\text{or} \\ \lambda_2 &= \frac{-(3+k) - \sqrt{(k-1)(k-9)}}{2}. \end{aligned}$$

There are three important points, namely $k = 0$, $k = 1$ and $k = 9$. Classification of the equilibrium points is as follows:

$k - 1 < 0$ $k - 9 < 0$ $k < 0$	$k - 1 < 0$ $k - 9 < 0$ $k > 0$	$k - 1 > 0$ $k - 9 < 0$ $k > 0$	$k - 1 > 0$ $k - 9 > 0$ $k > 0$
Roots are real with opposite signs. $(0, 0)$ is a saddle point.	Roots are real with same signs (positive) $(0, 0)$ is an unstable node.	Complex roots with negative real part. $(0, 0)$ is a stable spiral.	Roots are real with same signs (negative) $(0, 0)$ is a stable node.

There is a change of stability at $k = 0$ from saddle point to a stable node as k increases through $k = 0$.

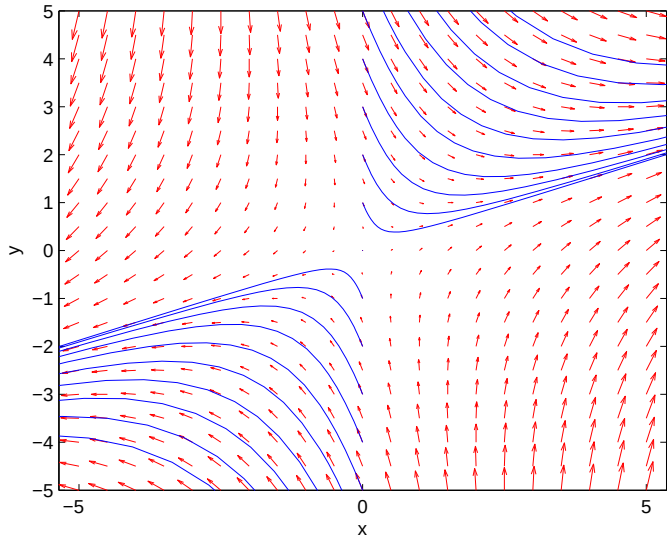

Figure 1.8: Phase portraits of $\dot{x}_1 = -kx_1 + x_2$, $\dot{x}_2 = -kx_1 - 3x_2$: for $k < 0$.

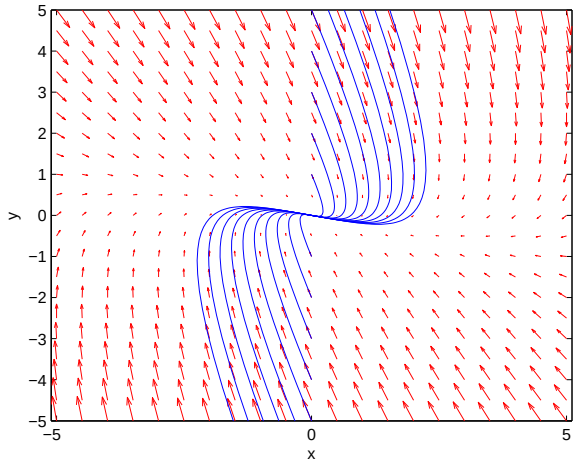

Figure 1.9: Phase portraits of $\dot{x}_1 = -kx_1 + x_2$, $\dot{x}_2 = -kx_1 - 3x_2$: for $0 < k < 1$.

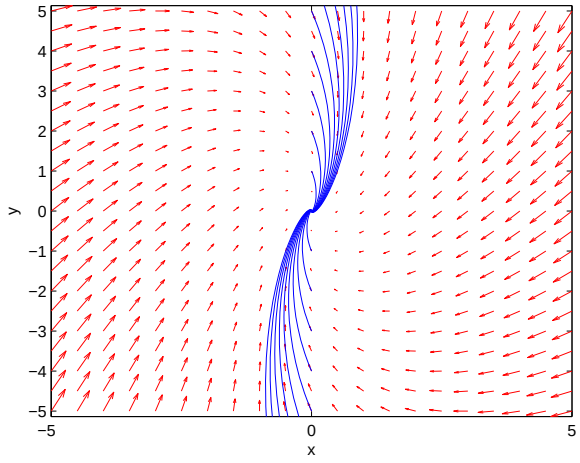

Figure 1.10: Phase portraits of $\dot{x}_1 = -kx_1 + x_2$, $\dot{x}_2 = -kx_1 - 3x_2$: for $1 < k < 9$.

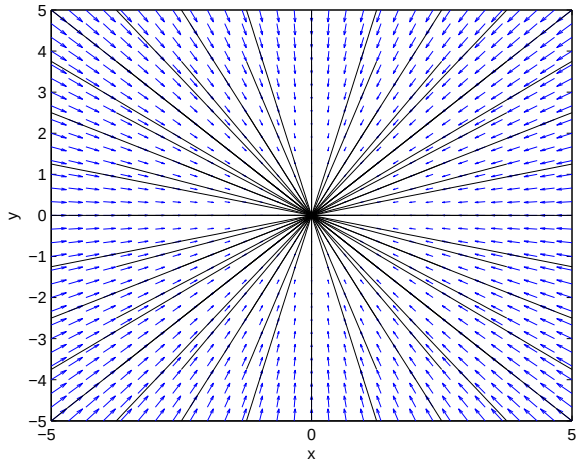

Figure 1.11: Phase portraits of $\dot{x}_1 = -kx_1 + x_2$, $\dot{x}_2 = -kx_1 - 3x_2$: for $k > 9$.

There is a change of stability at $k = 0$ from saddle point to a stable node as k increases through $k = 0$.

1.7 Types of Bifurcations

Consider

$$\dot{x} = f(x, \mu), \quad x \in \mathcal{R}^n, \mu \in \mathcal{R}^m \tag{1.7.16}$$

Equilibrium points occur where

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

for any given μ. Suppose that (μ_0, x_0) is a solution of the equation. Then $\mu = \mu_0$ is a bifurcation point if the structure of the phase diagram changes as μ passes through μ_0.

Example 1.7.1 *Consider the system*

$$\begin{aligned} \dot{x}_1 &= x_2, \\ \dot{x}_2 &= x_1^2 - x_2 - \mu. \end{aligned}$$

The equilibrium points occur where

$$x_2 = 0, \quad x_1^2 - x_2 - \mu = 0 \text{ or } x_1^2 = \mu.$$

For $\mu > 0$: $(\sqrt{\mu}, 0)$ and $(-\sqrt{\mu}, 0)$ are the equilibrium points. For $\mu < 0$ there are no equilibrium points.

Consider the equilibrium point $(\sqrt{\mu}, 0)$, define

$$y_1 = x_1 - \sqrt{\mu}, \quad y_2 = x_2,$$

then

$$\begin{aligned} \dot{y}_1 &= y_2, \\ \dot{y}_2 &= (y_1 + \sqrt{\mu})^2 - y_2 - \mu = y_1^2 + 2\sqrt{\mu} y_1 - y_2. \end{aligned}$$

The associated linear system is

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ 2\sqrt{\mu} & -1 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The characteristic equation is

$$\begin{vmatrix} -\lambda & 1 \\ 2\sqrt{\mu} & -1-\lambda \end{vmatrix} = \lambda(1+\lambda) - 2\sqrt{\mu} = \lambda^2 + \lambda - 2\sqrt{\mu} = 0.$$

The eigenvalues are

$$\lambda_{1,2} = \frac{-1 \pm \sqrt{1 + 8\sqrt{\mu}}}{2}.$$

Therefore $(\sqrt{\mu}, 0)$ is a saddle point.

Consider the equilibrium point $(-\sqrt{\mu}, 0)$: The eigenvalues are

$$\lambda_{1,2} = \frac{-1 \pm \sqrt{1 - 8\sqrt{\mu}}}{2}.$$

Therefore, $(-\sqrt{\mu}, 0)$ is a stable node which becomes a stable spiral for $\sqrt{\mu} > \frac{1}{8}$. This is called the saddle node bifurcation.

Example 1.7.2 *Consider the system (Transcritical bifurcation)*

$$\begin{aligned} \dot{x}_1 &= x_2, \\ \dot{x}_2 &= \mu x_1 - x_1^2 - x_2. \end{aligned}$$

The system has two equilibrium points at $(0, 0)$ and $(\mu, 0)$.

Consider $(0, 0)$:

The linearized system is

$$\begin{pmatrix} \dot{x}_1, \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ \mu & -1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

The characteristic equation is

$$\begin{vmatrix} -\lambda & 1 \\ 2\mu & -1-\lambda \end{vmatrix} = \lambda(1+\lambda) - \mu = \lambda^2 + \lambda - \mu = 0.$$

with roots

$$\lambda_{1,2} = \frac{-1 \pm \sqrt{1+4\mu}}{2}.$$

1. For $\mu < 0$, the origin is stable; a node if $\frac{1}{4} < \mu < 0$ and a spiral if $\mu < -\frac{1}{4}$.
2. For $\mu > 0$, the origin is a saddle point.

Consider $(\mu, 0)$: Define

$$y_1 = x_1 - \mu, \quad y_2 = x_2.$$

The system becomes

$$\begin{aligned} \dot{y}_1 &= y_2, \\ \dot{y}_2 &= \mu(y_1+\mu) - (y_1+\mu) - y_2 = -\mu y_1 - y_1^2 - y_2. \end{aligned}$$

The associated linear system is

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -\mu & -1 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The characteristic equation is

$$\begin{vmatrix} -\lambda & 1 \\ -\mu & -1-\lambda \end{vmatrix} = \lambda(1+\lambda) + \mu = \lambda^2 + \lambda + \mu = 0.$$

The eigenvalues are

$$\lambda_{1,2} = \frac{-1 \pm \sqrt{1-4\mu}}{2}.$$

1. For $\mu < 0$, $(\mu, 0)$ is a saddle point.
2. For $\mu > 0$, the equilibrium point $(\mu, 0)$ is a stable node for $0 < \mu < \frac{1}{4}$ and a spiral if $\mu > \frac{1}{4}$.

This is an example of a transcritical bifurcation where, at the intersection of the two bifurcation curves, stable equilibrium point switches from one curve to the other at the bifurcation point. As μ increases through zero, the saddle point collides with the node at the origin and then remains there whilst the stable node moves away from the origin.

1.8 Hopf Bifurcation

Some bifurcation generate limit cycles or other periodic solutions. Consider the system

$$\begin{aligned} \dot{x}_1 &= \mu x_1 + x_2 - x_1(x_1^2 + x_2^2), \\ \dot{x}_2 &= -x_1 + \mu x_2 - x_2(x_1^2 + x_2^2). \end{aligned}$$

Solution

The system has one equilibrium point at $(0, 0)$. The linearized system is

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} \mu & 1 \\ -1 & \mu \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}.$$

The characteristic equation is

$$\begin{vmatrix} \mu - \lambda & 1 \\ -1 & \mu - \lambda \end{vmatrix} = (\mu - \lambda)^2 + 1 = \lambda^2 - 2\mu\lambda + \mu^2 + 1 = 0.$$

The eigenvalues are

$$\lambda_{1,2} = \frac{2\mu \pm \sqrt{4\mu^2 - 4(\mu^2 + 1)}}{2} = \mu \pm i.$$

(i) If $\mu < 0$ then the origin is a stable spiral.

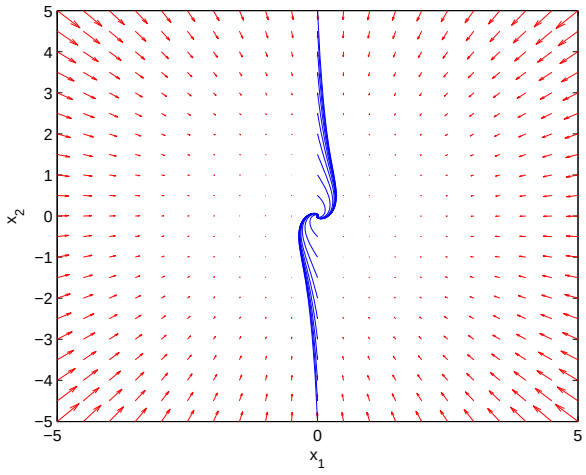

Figure 1.12: *Catastrophic behavior: case* $\mu = -1 < 0$

(ii) If $\mu = 0$ then the origin is a centre. It is not asymptotically stable.

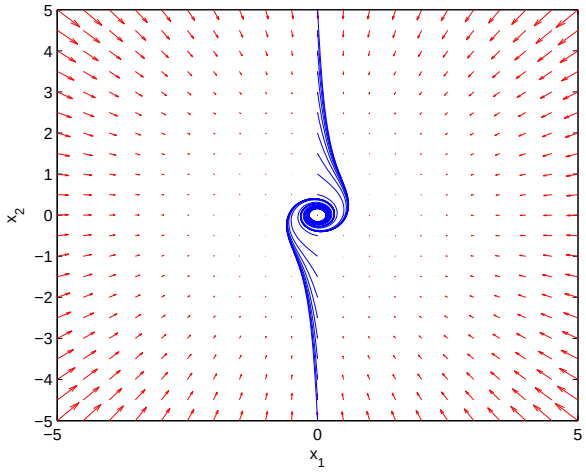

Figure 1.13: *Catastrophic behavior: case* $\mu = 0$.

(iii) If $\mu > 0$, then the origin is an unstable spiral which is surrounded by a stable limit cycle. This was demonstrated using the invariant set theorem. The case $\mu > 0$ is an example of a Hopf bifurcation because it generates a limit cycle.

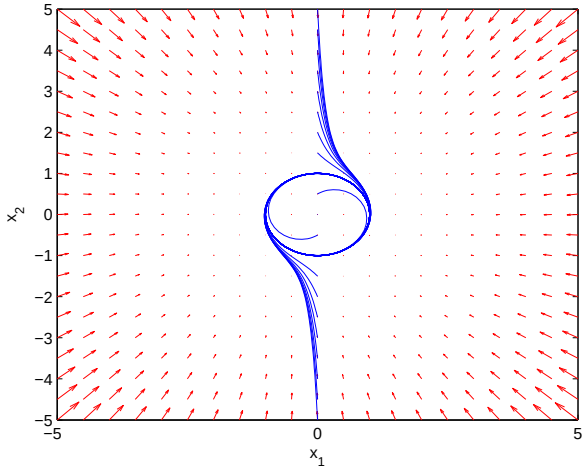

Figure 1.14: *Catastrophic behavior: case* $\mu = 1 > 0$.

Exercise

Show that the equation

$$\ddot{x} + (x^2 + \dot{x}^2 - \mu)\dot{x} + x = 0$$

exhibits a hopf bifurcation as μ increases through zero.

1.9 Population dynamics

In the study of population ecology, we use mathematical models in order to understand the interaction between species and their environment. Dynamic processes such as predator-prey, competition and symbiotic interactions, renewable resource management, ecological control of pest etc can be understood by studying mathematical models.We begin by a consideration of interaction between species living in an ecosystem.Their interaction affects the dynamics of each species.There are three main types of interactions:

1. predator-prey interaction,

2. competition interactions,

3. mutualism or symbiotic interaction.

1.9.1 Population interactions

In 1926, Volterra proposed a mathematical model that tried to explain the oscillatory levels of some fish species in the Adriatic. If we assume that n species live in an ecosystem with density x_i for species $i = 1, 2, \ldots$, then the ecological equation is given by

$$x_i = x_i f_i(x). \tag{1.9.17}$$

If f_i is linear then we have the Lotka-Voltera equation

$$x_i = x_i \left(r_i + \sum_{j=1}^{m} a_{ij} x_j \right) \qquad i = 1, 2, ..n. \tag{1.9.18}$$

where r_i is the per capita growth rate and a_{ij} are the interaction parameters for species i and j, for example a_{12} measures the effect of species 2 on species 1.

1.9.2 Predator-Prey interactions

Let $N(t)$ be the number (or density) of the prey and let $P(t)$ be the number (or density) of the predators. The Volterra model is defined by the following system of equations:

$$\frac{dN}{dt} = rN - cNP, \tag{1.9.19}$$

$$\frac{dP}{dt} = bNP - mP, \tag{1.9.20}$$

where r, c, b, m are positive constants.

The model is set under the following assumption:

1. in the absence of the predator N grows unboundedly (in equation (1.9.19) set $P = 0$).
2. the effect of predation is to reduce the prey population N by a rate proportional to the prey and predator population.
3. If there is no prey the predator population decays exponentially.
4. the predator grows due to the presence of the prey.

Analysis of the model

We introduce a change of variables for the sake of parameter reduction and rescaling (*It is easier to work with fewer parameters*). Let

$$x_1 \equiv \frac{b}{m}N, \qquad x_2 \equiv \frac{c}{r}P$$

Equations (1.9.19) and (1.9.20) can now be written as

$$\frac{dx_1}{dt} = r(1 - x_2)x_1, \tag{1.9.21}$$

$$\frac{dx_2}{dt} = m(x_1 - 1)x_2. \tag{1.9.22}$$

Equations (1.9.21) and (1.9.22) determine whether the variables x_1 and x_2 increase or decrease at each point of the (x_1, x_2) phase plane. The ratio

$$\frac{dx_2}{dx_1} = \frac{m(x_1 - 1)x_2}{r(1 - x_2)x_1}, \tag{1.9.23}$$

determines the slope of the vector field at every point of the phase plane. By setting equation (1.9.23) to zero we will have the predator zero growth isoclines (nucclines), $x_1 = 1$ and $x_2 = 0$. This is the locus of all points where predator numbers stay constant. The prey zero-growth isocline are $x_2 = 1$ and $x_1 = 0$, the prey numbers do not change. The figure below shows the direction fields of the vector. The vectors in

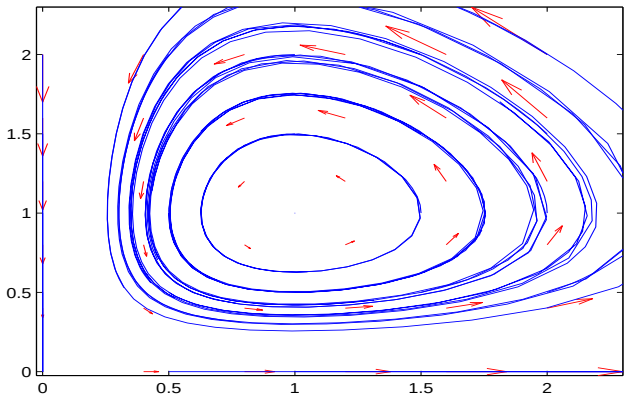

Figure 1.15: Predator-prey direction fields

Figure 1.15 rotate as we move through the plane. If the predator and prey populations are all less than one, the predator numbers decrease and the prey numbers increase. If the prey population is high and the predator population is low ie $x_1 > 1$ and $x_2 < 1$, both population increase. As the predator population increases i.e $x_1 > 1$ and $x_2 > 1$ the prey population begins to decrease. When the predator population is high and the prey population is low i.e $x_1 < 1$ and $x_2 > 1$, both the predators and the prey population will decrease.

We can put some further analysis as regards the equilibrium points. These equilibria occur at the intersection of the predator and prey zero-growth isoclines. We thus have two equilibria, one at $E_0 = (0, 0)$, called the trivial equilibrium point) and the other at $E_1 = (1, 1)$ called the nontrivial equilibrium point. Linearization about the point E_0 gives the following system

$$\begin{pmatrix} \dot{x_1} \\ \dot{x_2} \end{pmatrix} = \begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$$

which is of the form $\dot{X} = AX$.
Stability of the steady state is determined by the eigenvalues of A. In this case the eigenvalues of A are $\lambda_1 = r$ and $\lambda_2 = -m$. This means the prey increases exponentially fast near the origin while the predators decrease. The equilibrium at the origin will thus have one stable direction along x_2 and one unstable direction

along x_1. E_0 is referred to as a saddle point.

Linearizing about the nontrivial equilibrium point, we define new variables

$$y_1 \equiv x_1 - 1, \qquad y_2 \equiv x_2 - 1.$$

The resulting system will be,

$$\frac{dy_1}{dt} = -ry_2(1+y_1), \tag{1.9.24}$$

$$\frac{dy_2}{dt} = my_1(1+y_2). \tag{1.9.25}$$

Neglecting the nonlinear terms we have

$$\begin{pmatrix} \dot{y_1} \\ \dot{y_2} \end{pmatrix} = \begin{pmatrix} 0 & -r \\ m & 0 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}$$

which is again of the form $\dot{Y} = BY$.
The eigenvalues of B are $\lambda_{1,2} = \pm i\sqrt{rm}$. We conclude that the linearized system is neutrally stable, and thus a center. This is the situation represented by figure 1.15.

1.9.3 Competing species

Competition is active demand by two or more organism for the same resource. Competing species need not be similar e.g. agricultural pests compete with man for food. Competition is depends mostly on density, given limited resources, greater population size causes greater intensity of competition and greater scarcity leading to adverse effects on population growth rates and sizes.
If species are competing for the same resources, we to assume that the growth rates are positive and interaction terms are negative. For two species, on each positive axis, there is one fixed point F_i corresponding to equilibrium of one species in the absence of the other species. There are generally three possible outcomes

1. - dominance: all trajectories in the IntR^2_+ converge to one of the fixed points F_i on the axis.

2. - coexistence: a fixed point $F_{12} \in \text{Int}\mathbf{R^2_+}$ exists and is globally stable, i.e it attracts all orbits in the IntR^2_+.

3. - bistability: F_{12} is a saddle point and almost all trajectories in the IntR^2_+ converge to F_1 or F_2 depending on the initial conditions.

Consider a simple two species Volterra competition model. Let N_1 and N_2 be two species that diminish each other's per capita growth rate by direct interference. The model is given by

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{1.9.26}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right), \tag{1.9.27}$$

where r, c, b, m are positive constants, with r_1, r_2 being the intrinsic growth rates, K_1, K_2, the carrying capacities and b_{12}, b_{21} the interaction coefficients of N_1, N_2 respectively.

We can non-dimensionalize the system by letting

$$x_1 \equiv \frac{N_1}{K_1}, \quad x_2 \equiv \frac{N_2}{K_2}, \quad \tau = r_1 t \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}.$$

so that system (1.9.26-1.9.27) becomes

$$\frac{dx_1}{d\tau} = x_1\left(1 - x_1 - a_{12}x_2\right) = f_1(x_1, x_2), \tag{1.9.28}$$

$$\frac{dx_2}{d\tau} = \rho x_2\left(1 - x_2 - a_{21}x_1\right) = f_2(x_1, x_2). \tag{1.9.29}$$

This system has four equilibria given by

$$(0,0), \quad (1,0), \quad (0,1) \quad \text{and} \quad \left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right).$$

1.9.4 Mutualism/Symbiosis

Mutualism is an interaction in which species help one another. These are situations in which the interaction of the two species is mutually beneficial e.g the plant pollinator system, seed dispersal (many plants rely on animals to carry their seeds to favorable sites), digestion (animals depend on bacteria, yeast etc for digestion, ruminants depend on bacteria for the digestion of cellulose) and protection (ants protect the Acacia from predators but they find refuge in the trees). The interaction may be facultative (two species can survive separately, the interaction is helpful but not essential) or obligatory (each species will become extinct without the other).

We assume that two species N_1 and N_2 interact and each one of them grows logistically in the absence of the other. Consider the model,

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}\right), \tag{1.9.30}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_2}\right), \tag{1.9.31}$$

where r_1, r_2 are the intrinsic growth rates, K_1, K_2, the carrying capacities and b_{12}, b_{21} the interaction coefficients of N_1, N_2 respectively.

Exercises

1. Examine the stability of the fixed point at the origin of

$$(i) \qquad \begin{aligned} \dot{x}_1 &= -x_1^3 + x_2^4 \\ \dot{x}_2 &= x_2(2x_1^2 - x_2^2 - x_1 x_2^2) \end{aligned}$$

$$(ii) \qquad \begin{aligned} \dot{x}_1 &= x_2 \\ \dot{x}_2 &= -x_1 - x_2^3 \end{aligned}$$

2. Prove that the function

$$V(x_1, x_2) = x_1^2 + x_1^2 x_2^2 + x_2^4 \qquad (x_1, x_2) \in \mathcal{R}^2$$

is a strong Liapunov function for the system

$$\begin{aligned} \dot{x}_1 &= 1 - 3x_1 + 3x_1^2 + 2x_2^2 - x_1^3 - 2x_1 x_2^2, \\ \dot{x}_2 &= x_2 - 2x_1 x_2 + x_1^2 x_2 - x_2^3. \end{aligned}$$

3. Discuss the stability of the system

$$\begin{aligned} \dot{x}(t) &= y(t), \\ \dot{y}(t) &= 2x(t) + 2y(t). \end{aligned}$$

4. Consider system (1.9.28)-(1.9.29):

   (a) Determine the stability of the equilibrium points, clearly stating the stability conditions.

   (b) Draw the phase portraits for the following cases:

   i. $a_{12} < 1, \quad a_{21} < 1.$
   ii. $a_{12} > 1, \quad a_{21} > 1.$
   iii. $a_{12} < 1, \quad a_{21} > 1.$
   iv. $a_{12} > 1, \quad a_{21} < 1.$

5. Consider the system (1.9.30)-(1.9.31):

   (a) Non dimensionalize the system by letting

$$x_1 \equiv \frac{N_1}{K_1}, \quad x_2 \equiv \frac{N_2}{K_2}, \quad \tau = r_1 t \quad \rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2},$$

   and determine the four equilibrium points.

(b) Carry out the stability analysis of each of the equilibrium points.

(c) Draw the phase portraits for each of the following cases:

i. $1 - a_{12}a_{21} < 0$.

ii. $a_{12} > 1, \quad a_{21} < 1$.

6. Suppose there exist self elimination in the prey (density restriction), the predator prey model will be given by

$$\begin{aligned} \frac{dx_1}{dt} &= (a - ex_1 - bx_2)x_1, \\ \frac{dx_2}{dt} &= (dx_1 - c)x_2. \end{aligned}$$

Investigate the stability of the above system and draw phase diagrams to illustrate your analysis.
What happens if $e \gg 0$?

7. Consider the following equations

$$\frac{dN_1}{dt} = N_1(a - bN_1 - cN_2), \qquad \frac{dN_2}{dt} = N_2(e - f\frac{N_2}{N_1}).$$

For this system verify the following.

(a) If N_1 is very large relative to N_2, the second population grows exponentially.

(b) The isoclines are straight lines, the prey isocline has a negative slope and the predator isocline has a positive slope.

(c) At equilibrium ${N^*}_1 = \frac{af}{bf + ce}; \quad {N^*}_2 = \frac{ae}{bf + ce}$.

(d) roots of the community matrix are complex with negative real parts ensuring a convergence to the equilibrium through a spiral trajectory, i.e stable spiral.

8. Consider the predator prey system

$$\frac{dN_1}{dt} = rN_1 - c_1N_2(N_1 - H), \qquad \frac{dN_2}{dt} = N_2[c_2(N_1 - H) - d].$$

(a) Verify that, when the prey population falls to level H it becomes immune to predators and grows exponentially whereas the predator population declines exponentially. This process is called refugium. How can this be insured?

(b) Sketch the isoclines.

(c) Obtain the community matrix and verify that the system converges.

(d) Interpret the case $H = 0$.

9. Give a full analysis of the model of interacting species given by

$$\begin{aligned} \frac{dx}{dt} &= x(\lambda - ax + by), \\ \frac{dy}{dt} &= y(\mu + cx - dy). \end{aligned}$$

Draw nulclines and give the stability analysis.

10. Given that two interacting populations x and y are governed by the equations

$$\begin{aligned} x' &= 0.15(1 - 0.005x - 0.01y)x, \\ y' &= 0.03(1 - 0.006x - 0.005y)y. \end{aligned}$$

(a) What king of interaction is defined by this system.

(b) If x and y are both small, which species exhibits a faster growth rate.

(c) (This requires Matlab program) Staring with the various cases $(x, y) = (10, 10), \ (150, 25), \ (300, 10), \ (50, 200), \ (10, 300)$, examine the behavior of the system.

(d) Is the mathematical model consistent with the principle of competitive exclusion.

Program 1

$g = \text{inline}('[y(1)*(1-y(1)-0.5*y(2)); 2*y(2)*(1-y(2)-0.4*y(1))]','t','y');$
$\text{vectfield}(g, 0 : .2 : 2, 0 : .2 : 2);$
hold on
% the initial conditions for $y(1)$ *and* $y(2)$ *are set as follows.*
for $y10 = 0 : .1 : 2$*;*
for $y20 = 0 : .1 : 2$*;*
% to call the Runge-Kutta method of order 4 and 5 we type
$[\text{ts}, \text{ys}] = \text{ode45}(g, [0, 10], [y10, y20]);$
$plot(ys(:, 1), ys(:, 2))$
end
end
hold off

11. Consider the model given by

$$\begin{aligned} x' &= 0.x(1 - \frac{x}{10} - \frac{0.5xy}{x+1}, \\ y' &= 0.1y\left(1 - \frac{y}{2x}\right). \end{aligned}$$

(a) Show that the constant functions $x(t) = 10$ and $y(t) = 0$ are solutions of the above system. Explain the behavior of this solution.

(b) Find the other equilibrium solutions.

(c) Use the programme above to graph the solution of the model for the initial conditions $x(0) = 5$ and $y(0) = 5$. The graph should be as given below

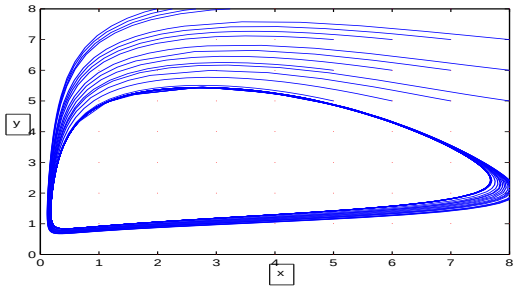

Figure 1.16: limit cycle for initial conditions far away from the non trivial equilibrium point

(d) Graph the solution of the model for the initial conditions $x(0) = 1$ and $y(0) = 4$, these are very near to the non trivial solution. The graph should be as given below

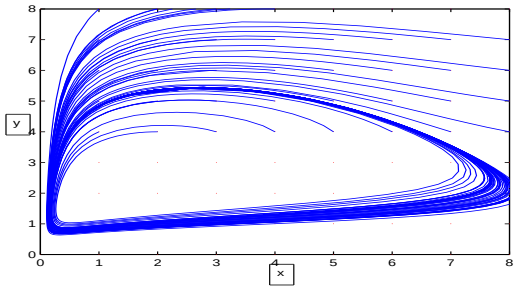

Figure 1.17: limit cycle for initial conditions near the non trivial equilibrium point

(e) Suppose that the prey species is actually an agricultural pest and the predator of the pests does not harm the crops. If farmers propose to eliminate the pest by bringing a large number of predators, would the strategy work? If not why?

Chapter 2

Mathematical Modelling: Epidemiology

2.1 The SIR epidemic model

Let us consider a large population of n individuals and a disease in which infection spreads by contact between individuals. Let us consider a simple model whereby individuals who are once infected either die or are isolated or recover with immunity. Thus, at any one time the population is comprised of x_1 susceptible individuals, x_2 infected and circulating individuals, and x_3 individuals who either have been removed (by death or isolation) or are immune. We have $x_1 + x_2 + x_3 = n$, for all time.

We assume that the population is subject to some form of homogeneous mixing, and that the rate of contact between susceptibles and infectives is proportional to the product $x_1 x_2$.

The rate of generation of new infectives is therefore $\beta x_1 x_2$, where β is an infection-rate constant. Infectives are assumed to be removed or become immune at the rate proportional to their number with an associated removal rate γ. The governing differential equations are therefore

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2, \\ \dot{x}_2 &= \beta x_1 x_2 - \gamma x_2, \\ \dot{x}_3 &= \gamma x_2. \end{aligned}$$

It is easy to verify that this is a constant population model. Since x_3 does not appear in the first two equations, the model can be reduced to two equations given below;

$$\dot{x}_1 = -\beta x_1 x_2, \tag{2.1.1}$$

$$\dot{x}_2 = \beta x_2 (x_1 - \frac{\gamma}{\beta}) = \beta x_2 (x_1 - \rho). \tag{2.1.2}$$

Obviously, any point $(x_1, x_2) = (c, 0)$ is a fixed point. That is, we have a line of fixed points. Also the x_2-axis is a separatrix because

$$\frac{dx_2}{dx_1} = \frac{\beta x_1 - \gamma}{-\beta x_1}.$$

Let us examine the nature of one of the fixed points $(c, 0)$. Define

$$y_1 = x_1 - c, \quad y_2 = x_2.$$

Then

$$\begin{aligned} \dot{y}_1 &= -\beta(y_1 + c)y_2, \\ \dot{y}_2 &= \beta y_2(y_1 + c - \rho). \end{aligned}$$

When $c = 0$, there is a non-simple fixed point at $(0, 0)$. Again when $c = \rho$, we have another non-simple fixed point at $(\rho, 0)$. Keeping away from these two special fixed points, the linearized equations at $(c, 0)$ are

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} 0 & -\beta c \\ 0 & \beta(c - \rho) \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = 0$, $\lambda_2 = \beta(c - \rho)$. The solution in the neighborhood of $y_1 = 0, y_2 = 0$ is

$$\begin{aligned} y_1 &= C_1 + C_2 e^{\lambda_2 t}, \\ y_2 &= -\frac{1}{\beta c}\dot{y}_1 = -\frac{\lambda_2}{\beta c} C_2 e^{\lambda_2 t}. \end{aligned}$$

Special orbits:

$C_2 = 0$, $y_1 = c$, $y_2 = 0$. This is not an orbit.

Consider a case: $C_1 = 0$,

$$\begin{aligned} y_2 &= C_2 e^{\lambda_2 t} = -\frac{\lambda_2}{\beta c} C_2 e^{\lambda_2 t} = -\frac{\lambda_2}{\beta c} y_1 \\ &= -\left(\frac{c - \rho}{c}\right) y_1. \end{aligned}$$

This is a family of straight lines with slope $-\frac{(c-\rho)}{c}$. The maximum value of x_2 occurs where $\dot{x}_2 = 0$. That is when $x_1 = \rho$. If $c > \rho$ then the straight lines have negative slope and if $c < \rho$ then the straight lines have a positive slope (figure 2.1). The solution above is an approximate solution which has given us information on the nature of trajectories. We can solve (2.1.1)-(2.1.2) exactly as follows:

$$\frac{\dot{x}_2}{\dot{x}_1} = \frac{\beta x_1 - \gamma}{-\beta x_1}.$$

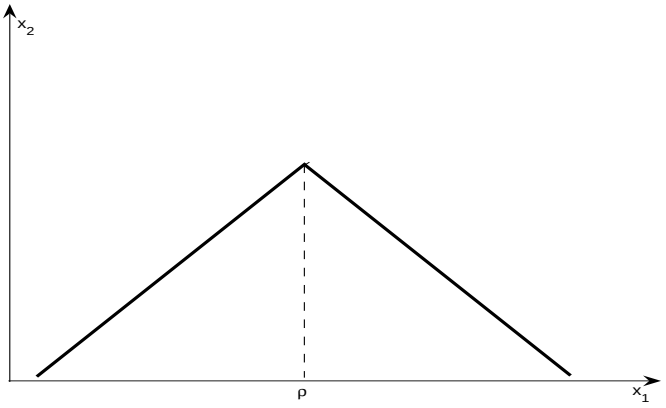

Figure 2.1: *Special orbits for the SIR epidemic model*

Upon rearranging, we obtain

$$dx_2 = (-1 + \frac{\rho}{x_1})dx_1, \qquad \rho = \frac{\gamma}{\beta}.$$

Integrating this gives

$$x_2 = -x_1 + \rho \ln x_1 + Const.$$

At $t = 0$, $x_1(0) = n = x_0$, $x_2(0) = a$.

$$x_2 = -x_1 + \rho \ln \left(\frac{x_1}{x_0}\right) + n + a$$

x_2 is a family of trajectories. Several interesting qualitative conclusions can be made from this.

1. The threshold effect: The maximum value of x_2 occurs at the point $x_1 = \rho$. Suppose that a number of infectives $x_2(0)$ is introduced in a population x_0 of susceptibles. If $x_0 > \rho$, the level of infectives will increase until the number of susceptibles is reduced below ρ and will decrease thereafter. If $x_0 < \rho$, the level of infectives will decrease monotonically to zero (no epidemic). Thus, ρ represents a threshold value of susceptibles for the phenomena of an epidemic to occur.

2. The Escape Effect: Since $x_2(0) = -\infty$, it follows that x_2 must vanish at some positive value of x_1. This means that the trajectories terminate on the x_1-axis at a positive value. Therefore, the epidemic terminates for lack of infectives rather than lack of susceptibles, and some individuals escape the disease entirely.

3. Symmetry Effect: For the case $x_1(0) > \rho$ but $x_1(0) - \rho$ is small, the epidemic curves are nearly symmetric with respect to the point $x_1 = \rho$. This means that during the course of the epidemic the number of susceptibles is ultimately reduced to a level about as far below the threshold value ρ as it was initially above this value-(Threshold theorem).

Theorem 2.1.1 (The Threshold Theorem) *Let $x_1(0) = \rho + \epsilon$, $\epsilon << \rho$ and suppose that $x_2(0)$ is very small, then ultimately $x_1(0) - x_1(\infty) = 2\epsilon$.*

Proof

$$\begin{aligned} \frac{dx_2}{dx_1} &= \frac{\beta x_1 x_2 - \gamma x_2}{-\beta x_1 x_2} = -1 + \frac{\rho}{x_1}, \\ x_2 &= C - x_1 + \rho \ln\left(\frac{x_1}{x_0}\right). \end{aligned}$$

At $t = 0$, $x_2(0) = C - x_1(0)$, thus $C = x_2(0) + x_1(0)$.

$$x_2 = x_2(0) + x_1(0) - x_1 + \rho \ln\left(\frac{x_1}{x_1(0)}\right).$$

At a very long time $x_1(t) \to x_1(\infty), \quad x_2(t) \to 0$.

Then

$$0 = x_2(0) + x_1(0) - x_1(\infty) + \rho \ln\left(\frac{x_1(\infty)}{x_1(0)}\right).$$

We can neglect $x_2(0)$ since it is small

$$\begin{aligned} 0 &= x_1(0) - x_1(\infty) + \rho \ln\left(1 - \frac{x_{(0)} - x_1(\infty)}{x_1(0)}\right) \\ &= x_1(0) - x_1(\infty) + \rho \left[\frac{x_{(0)} - x_1(\infty)}{x_1(0)} + \frac{1}{2}\left(\frac{x_{(0)} - x_1(\infty)}{x_1(0)}\right)^2\right] \\ &= (x_1(0) - x_1(\infty)) \left[1 - \frac{\rho}{x_1(0)} - \frac{\rho}{2x_1^2(0)}(x_1(0) - x_1(\infty))\right] \end{aligned}$$

Thus

$$\begin{aligned} x_1(0) - x_1(\infty) &= 2x_1(0)\left(\frac{x_1(0)}{\rho} - 1\right) \\ &= 2(\rho + \epsilon)\left(\frac{\rho + \epsilon}{\rho} - 1\right) \\ &= 2(\rho + \epsilon)\left(\frac{\epsilon}{\rho}\right) \\ &\approx 2\epsilon. \end{aligned}$$

2.2 Simple extensions of the SIR model

2.2.1 Loss of immunity

Suppose that the problem is as before, except that the susceptibles are being added to by (births-deaths) at rate μ and that the removed population looses immunity at a rate μ_2. For simplicity, let's take $\mu_2 = \mu$, so that the total population remains constant. The system becomes

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 + \mu, \\ \dot{x}_2 &= \beta x_1 x_2 - \gamma x_2, \\ \dot{x}_3 &= \gamma x_2 - \mu, \end{aligned}$$

with $x_1 + x_2 + x_3 = N$.

Normally, a plot of x_3 against x_2 is of special interest because medical records are kept on those who are infected and those who have died or recovered with immunity. Let us eliminate x_1 to obtain

$$\begin{aligned} \dot{x}_2 &= \beta x_2 \left(N - x_2 - x_3 - \frac{\gamma}{\beta} \right), \\ \dot{x}_3 &= \gamma x_2 - \mu, \end{aligned}$$

with

$$x_2 + x_3 = N - x_1 \leq N.$$

There is only one fixed point E given by $(x_2, x_3) = (\frac{\mu}{\gamma}, N - \frac{\mu}{\gamma} - \frac{\gamma}{\beta})$ which lies in the feasible region provided $\dfrac{\mu}{\gamma} < N$. The isoclines are given by

$$\frac{dx_3}{dx_2} = \frac{\gamma x_2 - \mu}{x_2[\beta(N - x_2 - x_3) - \gamma]} = \begin{cases} 0, & \text{when } x_2 = \frac{\mu}{\gamma} \\ \infty, & \text{when } x_2 = 0. \end{cases}$$

Also $\dfrac{dx_3}{dx_2} = \infty$ along the line $x_2 + x_3 = N - \dfrac{\gamma}{\beta}$.

Let us examine the nature of the fixed point E. Introduce local coordinates at E

$$y_2 = x_2 - \frac{\mu}{\gamma}, \quad y_3 = x_3 - \left(N - \frac{\mu}{\gamma} - \frac{\gamma}{\beta} \right).$$

The system becomes

$$\begin{aligned} \dot{y}_2 &= \left(y_2 + \frac{\mu}{\gamma} \right)(-\beta y_2 - \beta y_3), \\ \dot{y}_3 &= \gamma \left(y_2 + \frac{\mu}{\gamma} \right) - \mu = \gamma y_2. \end{aligned}$$

The linearized system is

$$\begin{pmatrix} \dot{y}_2 \\ \dot{y}_3 \end{pmatrix} = \begin{pmatrix} -\frac{\mu\beta}{\gamma} & -\frac{\mu\beta}{\gamma} \\ \gamma & 0 \end{pmatrix} \begin{pmatrix} y_2 \\ y_3 \end{pmatrix}.$$

The eigenvalues are

(i) If $\gamma > \frac{1}{2}\sqrt{\mu\beta}$, then $\lambda_{1,2} = \dfrac{-\mu\beta \pm i\mu\beta\sqrt{\frac{4\gamma^2}{\mu\beta} - 1}}{2\gamma}$. In this case E is a stable focus.

(ii) If $\gamma < \frac{1}{2}\sqrt{\mu\beta}$, then $\lambda_{1,2} = \dfrac{-\mu\beta \pm \mu\beta\sqrt{1 - \frac{4\gamma^2}{\mu\beta}}}{2\gamma}$. In this case both roots are real and negative, Hence E is a stable node.

In either case, the infection never clears up but the number of cases x_3 reaches a ceiling value of $N - \dfrac{\mu}{\gamma} - \dfrac{\gamma}{\beta}$.

2.2.2 Inclusion of immigration or emigration

If immigrants arrive at a rate μ, the system becomes

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 + \mu, \\ \dot{x}_2 &= \beta x_2(x_1 - \rho), \quad \rho = \frac{\gamma}{\beta}, \\ \dot{x}_3 &= \gamma x_2 \end{aligned}$$

Take the first two equations: $\dot{x}_2 = 0$ when $x_1 = \rho$ and then the first equation is $\dot{x}_1 = -\beta\rho x_2 + \mu$. Therefore, $\dot{x}_1 = 0$ when $x_2 = \dfrac{\mu}{\rho\beta} = \dfrac{\mu}{\gamma}$.

Let

$$y_1 = x_1 - \rho, \qquad y_2 = x_2 - \frac{\mu}{\gamma}$$

So that the system becomes

$$\begin{aligned} \dot{y}_1 &= -\beta(y_1 + \rho)\left(y_2 + \frac{\mu}{\gamma}\right) \\ \dot{y}_2 &= \beta\left(y_2 + \frac{\mu}{\gamma}\right) y_1 \end{aligned}$$

The linearized system is

$$\begin{pmatrix} \dot{y}_1 \\ \dot{y}_2 \end{pmatrix} = \begin{pmatrix} -\frac{\mu}{\rho} & -\gamma \\ \frac{\mu}{\rho} & 0 \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \end{pmatrix}.$$

The eigenvalues are

$$\lambda_{1,2} = \frac{-\mu \pm \mu\sqrt{1 - \frac{4\rho^2}{\mu}}}{2\rho}$$

Thus,

1. $E(\rho, \frac{\mu}{\gamma})$ is a stable focus if $\frac{4\rho^2}{\mu} > 1$, that is if $\mu < 4\rho^2$.
2. $E(\rho, \frac{\mu}{\gamma})$ is a stable node if $\frac{4\rho^2}{\mu} < 1$, that is if $\mu > 4\rho^2$.

Immigration or emigration can not make the situation worse. The infection never clears.

2.2.3 Immunization

Suppose susceptibles are immunized at a rate μ starting at $t = 0$. Then

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 - \mu, \\ \dot{x}_2 &= \beta x_2 (x_1 - \rho,) \\ \dot{x}_3 &= \gamma x_2, \end{aligned}$$

where $x_1 + x_2 + x_3 = N - \mu t$.

The equilibrium point is at $(\rho, -\frac{\mu}{\gamma})$. The eigenvalues are

$$\lambda_{1,2} = \frac{-\mu \pm \mu\sqrt{1 + \frac{4\rho^2}{\mu}}}{2\rho}.$$

The roots are real and of opposite sign. Therefore, $E(\rho, -\frac{\mu}{\gamma})$ is a saddle point. An orbit starting at (n, a) will have $x_2 \to 0$ as $t \to \infty$. The infection clears up. If a is too large then $x_1 \to 0$ as $t \to \infty$.

Exercises

1. A simple deterministic model for the spread of an epidemic is

$$\begin{cases} \dot{x}_1 = -\beta x_1 x_2 \\ \dot{x}_2 = \beta x_1 x_2 - \gamma x_2, \quad x_1 \geq 0, \ \ x_2 \geq 0, \ \ (\beta, \gamma > 0), \end{cases}$$

where

- $x_1 = s(t)$, the number of susceptibles at time t,
- $x_2 = I(t)$, the number of infectives at time t.

Draw a diagram showing the orbits in the x_1x_2 plane and explain the significance of the fixed point $(\rho, 0)$, where $\rho = \dfrac{\gamma}{\beta}$. Show that if an orbit starts at $(\rho + \epsilon, \delta)$ with $\epsilon, \delta << \rho$, then it ends at $(\rho - \epsilon, 0)$.

2. The following model is proposed for the immunization of a population consisting of x_1 susceptibles, x_2 infectives and x_3 removals:

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 - \mu x_3, \\ \dot{x}_2 &= \beta x_1 x_2 - \gamma x_2, \\ \dot{x}_3 &= \gamma x_2 + \mu x_3, \end{aligned}$$

where $N = x_1 + x_2 + x_3$. Take $\beta = 1$, $\mu = 2$, $N = 1000$ and $\gamma = 400$ and find in the x_2x_3 plane:

(a) The feasible region.

(b) The nature of the fixed point $(0, 0)$ and the equations giving the orbits in the neighbourhood of $(0, 0)$. Give a sketch of these orbits.

(c) The isoclines

$$\frac{dx_3}{dx_2} = \infty \quad \text{and} \quad \frac{dx_3}{dx_2} = 0.$$

Further, answer the following questions:

(d) Describe the variation of $\dfrac{dx_3}{dx_2}$ along the line $x_2 + x_3 = N$ from the point $(N, 0)$ to the point $(0, N)$.

(e) Sketch the phase portraits in the feasible region.

3. A recurrent epidemic in the constant population is modelled by the equations

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 + \mu, \\ \dot{x}_2 &= \beta x_1 x_2 - \gamma x_2, \\ \dot{x}_3 &= \gamma x_2 - \mu, \qquad (\beta,\ \gamma,\ \mu > 0), \end{aligned}$$

where, at time t, $x_1(t)$ is the number of susceptibles, $x_2(t)$ is the numbers of infectives and $x_3(t)$ is the number of confirmed cases of the disease. Initial values are $x_1(0) = n$, $x_2(0) = a$ and $x_3(0) = 0$. The plot of x_3 against x_2 is of special interest. Show that

(a) provided $\dfrac{\mu}{\gamma} + \dfrac{\gamma}{\beta} < N$; where $N = n + a$, a fixed point E (the endemic point) exists in the feasible region of the x_2x_3 plane;

(b) Provided $\frac{\mu}{\gamma} < a$, the orbit approaches E along a spiral path;

(c) Provided $\gamma > \frac{1}{2}(\mu\beta)^{\frac{1}{2}}$, the number of cases fluctuates and near to E the period of fluctuation is

$$\left(\frac{4\pi\gamma}{\mu\beta}\right)\left(\frac{4\gamma^2}{\mu\beta} - 1\right)^{\frac{1}{2}}.$$

(d) Discuss briefly the situation of $\frac{\mu}{\gamma} + \frac{\gamma}{\beta} > N$. Is it possible in this case for the epidemic to clear up in a finite time?

4. A preliminary model to describe heartbeats is

$$\begin{aligned} \epsilon\dot{x} &= x - x^3 - b \quad (0 < \epsilon << 1), \\ \dot{b} &= x - x_0 \quad (x_0 > 3^{-\frac{1}{2}}), \end{aligned}$$

where x represents the length of the muscle fibre and b is an electro-chemical control variable.

Examine the stability of the fixed point $x = x_0$, $b = x_0 - x_0'$. Sketch the global phase portrait and explain briefly the terms fast movement and slow movement.

5. A epidemiological model has, after time t,

$$\begin{aligned} \dot{x}_1 &= -\beta x_1 x_2 - \mu, \\ \dot{x}_2 &= \beta x_2(x_1 - \rho), \quad (\rho = \frac{\gamma}{\beta}) \\ \dot{x}_3 &= \gamma x_2, \end{aligned}$$

where

- $x_1(t)$ is the number of susceptibles,
- $x_2(t)$ is the numbers of infectives,
- $x_3(t)$ is the number of removals and
- μ is constant rate of immunization (starting at $t = 0$).

(a) Show that a first integral is

$$x_1 + x_2 + x_3 = N - \mu t,$$

where N is the total population when $t = 0$.

(b) Working in the x_1x_2 plane, show that the fixed point exists at $(\rho, -\frac{\mu}{\gamma})$. Establish that this is a saddle point.

(c) Draw a diagram showing the feasible region after time t. Show how an orbit starting at $x_1 = n$, $x_2 = a$ at time $t = 0$ is influenced by the presence of the saddle point found in part (b) (assume that μ is small, so that the saddle point is only outside the feasible region). What can you deduce is the effect of immunization on the epidemic if a is small?

Chapter 3

Calculation of the Reproduction Number

3.1 Reproduction numbers

In all the models presented in Chapter 2, the reproduction number could be obtained by inspection. This was possible because there was only one infective class. If the number of infective classes is two or more, then the technique due to Diekmann (1990) is more appropriate. The technique has been studied by a number of researchers, among them (van den Driessche and Watmough (2002), Hyman *et al.*(2004). In the next subsection, we summarize the technique known as the next generation matrix technique and some examples from van den Driessche and Watmough (2002).

3.1.1 The next generation matrix

Define X_s to be the set of all disease free states, that is

$$X_s = \{x \geq 0 \mid x_i = 0,\ i = 1, 2, ...m\}.$$

In order to compute $\Re_0$, it is important to distinguish new infections from all other changes in the population.

Let $\mathcal{F}_i(x)$ be the rate of appearance of new infections in compartments i,

$\mathcal{V}_i^+$ be the rate of transfer of individuals into compartment i by all other means.

$\mathcal{V}_i^-$ be the rate of transfer of individuals out of compartment i.

It is assumed that each function ($\mathcal{F}_i(x)$, $\mathcal{V}_i^+$ and $\mathcal{V}_i^-$) is continuously differentiable at least twice with respect to each variable.

The transmission model consists of the non-negative initial conditions together with

the following system of equations

$$\dot{x}_i = f_i(x) = \mathcal{F}_i(x) - \mathcal{V}_i(x), \quad i = 1, 2, ..., n \tag{3.1.1}$$

where $\mathcal{V}_i = \mathcal{V}_i^- - \mathcal{V}_i^+$ and the functions satisfying the following conditions:

C1: If $x \geq 0$, then $\mathcal{F}_i, \mathcal{V}_i^-, \mathcal{V}_i^+ \geq 0$ for $i = 1, 2, ..., n$.
Note: If the compartment is empty, then there can be no transfer of individuals out of the compartment by death, infection nor any other means.

C2: If $x_i = 0$, then $\mathcal{V}_i^- = 0$ (Nobody leaves the compartment). In particular if $x \in X_s$, then $\mathcal{V}_i^- = 0$ for $i = 1, 2, ..., m$.

C3: $\mathcal{F}_i = 0$, $i > m$. (m is the number of infective classes)

C4: If $x \in X_s$, then $\mathcal{F}_i = 0$, and $\mathcal{V}_i = 0$ for all $i = 1, 2, ..., m$.

C5: If $\mathcal{F}(x)$ is set to zero, then all the eigenvalues of $Df(x_0)$ have negative real parts.

Lemma 3.1.1 *If x_0 is a disease-free equilibrium (DFE) of (3.1.1) and $f_i(x)$ satisfies $C1 - C5$ then the derivatives $D\mathcal{F}(x_0)$ and $D\mathcal{V}(x_0)$ are partitioned as*

$$D\mathcal{F}(x_0) = \begin{pmatrix} F & 0 \\ 0 & 0 \end{pmatrix}, \quad \mathcal{V}(x_0) = \begin{pmatrix} V & 0 \\ J_3 & J_4 \end{pmatrix}. \tag{3.1.2}$$

where F and V are the $m \times m$ matrices defined by

$$F = \left[\frac{\partial \mathcal{F}(x_0)}{\partial x_j}\right] \quad \textit{and} \quad V = \left[\frac{\partial \mathcal{V}(x_0)}{\partial x_j}\right] \tag{3.1.3}$$

with $1 \leq i \leq m$. F is non-negative and V is a is non-singular M-matrix.

Following Diekmann et al. (1990) we call FV^{-1} the next generation matrix for the model and we shall set R_0 as equal to the spectral radius $\rho(FV^{-1})$ i.e,

$$\Re_0 = \rho(FV^{-1}), \tag{3.1.4}$$

where $\rho(A)$ denotes the spectral radius of the matrix A.

3.2 Applications of the technique

We consider three examples obtained from van den Driessche and Watmough (2002).

3.2.1 Example 1: TB treatment model

Consider the model

$$\begin{aligned}
\frac{dS}{dt} &= bN - dS - \beta_1 \tfrac{SI}{N}, \\
\frac{dE}{dt} &= \beta_1 \tfrac{SI}{N} + \beta_2 \tfrac{TI}{N} - (d+\nu+r_1)E + pr_2 I, \\
\frac{dI}{dt} &= \nu E - (d+r_2)I - qr_2 I, \\
\frac{dT}{dt} &= r_1 E + qr_r I - dT - \beta_2 \tfrac{TI}{N}.
\end{aligned} \tag{3.2.5}$$

Re-arranging the equations so that we start with infective classes, we obtain

$$\begin{aligned}
\frac{dE}{dt} &= \beta_1 \tfrac{SI}{N} + \beta_2 \tfrac{TI}{N} - (d+\nu+r_1)E + pr_2 I, \\
\frac{dI}{dt} &= \nu E - (d+r_2)I - qr_2 I, \\
\frac{dS}{dt} &= bN - dS - \beta_1 \tfrac{SI}{N}, \\
\frac{dT}{dt} &= r_1 E + qr_r I - dT - \beta_2 \beta_2 \tfrac{TI}{N}.
\end{aligned} \tag{3.2.6}$$

In this case $m = 2$ (Two infected compartments). From (3.2.6), we obtain

$$\mathcal{F} = \begin{pmatrix} \beta_1 \frac{SI}{N} + \beta_2 \frac{TI}{N} \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad \mathcal{V} = \mathcal{V}_i^- - \mathcal{V}_i^+ = \begin{pmatrix} (d+\nu+r_1)E - pr_2 I \\ (d+r_2)I + qr_2 I - \nu E \\ dS + \beta_1 \frac{SI}{N} - bN \\ dT - r_1 E - qr_2 I + \beta_2 \frac{TI}{N} \end{pmatrix}.$$

The disease free equilibrium point of the system (3.2.6) has coordinates

$$(E^*, I^*, S^*, T^*) = (0, 0, 1, 0).$$

The derivatives of $\mathcal{F}$ and $\mathcal{V}$ at $(0, 0, 1, 0)$ are given by

$$F = \begin{pmatrix} 0 & \beta_1 \\ 0 & 0 \end{pmatrix} \text{ and } V = \begin{pmatrix} d+\nu+r_1 & -pr_2 \\ -\nu & d+r_2 \end{pmatrix}$$

respectively. The inverse of V is given by

$$V^{-1} = \frac{1}{(d+\nu+r_1)(d+r_2) - \nu pr_2} \begin{pmatrix} d+r_2 & pr_2 \\ \nu & d+\nu+r_1 \end{pmatrix}$$

and a calculation of FV^{-1} gives the reproduction number of the model as

$$\Re_0 = \frac{\nu\beta_1}{(d+\nu+r_1)(d+r_2)-\nu p r_2}.$$

3.2.2 Example 2: Multi-strain model

We consider the model

$$\begin{aligned}
\frac{dI_1}{dt} &= \beta_1 S I_1 - (b+\gamma_1)I_1 + \nu I_1 I_2, \\
\frac{dI_2}{dt} &= \beta_2 I_2 S - (d+r_2)I_2 - \nu I_1 I_2, \\
\frac{dS}{dt} &= b - bS + \nu_1 I_1 + r_2 I_2 - (\beta_1 I_1 + \beta_2 I_2)S,
\end{aligned} \tag{3.2.7}$$

The disease-free equilibrium is $(0,0,1)$ and the derivatives of $\mathcal{F}$ and $\mathcal{V}$

$$F = \begin{pmatrix} 0 & \beta_1 \\ 0 & \beta_2 \end{pmatrix} \text{ and } V = \begin{pmatrix} b+r_1 & 0 \\ 0 & b+r_2 \end{pmatrix}$$

giving

$$R_i = \frac{\beta_i}{b+r_i} \quad i = 1, 2.$$

So that the reproduction of the model is given by

$$\Re_0 = \max_{i=\{1,2\}} R_i. \tag{3.2.8}$$

3.2.3 Example 3: Host-Vector model

We consider the model governed by the system of differential equations (proposed by Feng and Velasco-Hernandez (1997) for Dengue fever)

$$\begin{aligned}
\frac{dI}{dt} &= \beta_s S V - (b+r)I, \\
\frac{dV}{dt} &= \beta_m M I - cV, \\
\frac{dS}{dt} &= b - bS + \gamma I - \beta_s S V, \\
\frac{dM}{dt} &= c - cM - \beta_m M I.
\end{aligned} \tag{3.2.9}$$

The DFE is $x_0 = (0, 0, 1, 1)$ and the derivatives of $\mathcal{F}$ and $\mathcal{V}$ at the disease free equilibrium point are

$$F = \begin{pmatrix} 0 & \beta_s \\ \beta_m & 0 \end{pmatrix} \text{ and } V = \begin{pmatrix} b+\gamma & 0 \\ 0 & c \end{pmatrix}.$$

So that the reproduction number of the model is given by

$$\Re_0 = \sqrt{\frac{\beta_s \beta_m}{c(b+\gamma)}}. \tag{3.2.10}$$

The interpretation of terms under the square-root is as follows: Infected vector produces on average $\frac{\beta_s}{b+\gamma}$ new hosts, while infected host produces $\frac{\beta_m}{c}$ new vectors. The square root means that the disease is passed on through a vector i.e two generations are required for an infected vector or host to 'reproduce' itself.

3.3 Exercises

1. Given a model dividing the population into three classes susceptibles (S), infected (I) and vaccinated (V); (Kgosimore, Koga and Lungu) with equations

$$\begin{aligned} \frac{dS}{dt} &= \mu N - \frac{\beta SI}{N} - (\mu + \phi)S + \theta V, \\ \frac{dI}{dt} &= \beta \frac{(S + \sigma V)}{N} - (\mu + c)I, \\ \frac{dV}{dt} &= \phi S - \sigma\beta \frac{VI}{N} - (\mu + \phi)V, \end{aligned} \tag{3.3.11}$$

   Calculate $\Re_0$.

2. Consider the model given by

$$\begin{aligned}
\frac{dX_0}{dt} &= \mu N - \bar{\lambda}X_0 - (\mu+\phi)X_0,\\
\frac{dX_1}{dt} &= \phi X_0 - (1-\gamma)\bar{\lambda}X_1 - \mu X_1,\\
\frac{dX_2}{dt} &= \bar{\lambda}X_0 - (\mu+\alpha+\nu_1)X_2,\\
\frac{dX_3}{dt} &= (1-\gamma)\bar{\lambda}X_1 - (\mu+\sigma+\nu_2)X_3,\\
\frac{dX_4}{dt} &= \alpha X_2 + \sigma X_3 - (\mu+\nu_3)X_4,\\
\frac{dX_5}{dt} &= \nu_1 X_2 + \nu_2 X_2 + \nu_3 X_4 - (\mu+\delta)X_5,
\end{aligned} \tag{3.3.12}$$

where $\bar{\lambda} = \dfrac{c\beta_0 X_2 + c\beta_1 X_3 + \beta_2 X_4}{N}$ and X_0- susceptible class, X_1- vaccinated susceptible class, X_2- normal infected class, X_3- vaccinate infected class, X_4- treated infected class, X_5- full blown AIDS class. Draw the model diagram and calculate reproduction number for the model (Kgosimore and Lungu (2006)).

3. For the SIR model

$$\begin{aligned}
\frac{dS}{dt} &= \Pi - \beta SI - \mu S,\\
\frac{dI}{dt} &= \beta SI - (\mu+\gamma)I,\\
\frac{dR}{dt} &= \gamma I - \nu R,
\end{aligned} \tag{3.3.13}$$

Show that the basic reproduction number of the model is $\Re_0 = \dfrac{\beta S^*}{\mu+\gamma}$.

4. For the SIS model

$$\begin{aligned}
\frac{dS}{dt} &= \Pi - \beta SI - \mu S + \alpha I,\\
\frac{dI}{dt} &= \beta SI - (\mu+\gamma+\alpha)I,
\end{aligned} \tag{3.3.14}$$

Show that the basic reproduction number of the model is $\Re_0 = \dfrac{\beta S^*}{\mu+\gamma+\alpha}$.

Chapter 4

Advanced HIV/AIDS Models

4.1 HIV/AIDS model with treatment

4.1.1 Model formulation

It is known (WHO 2006), that there are three stages of HIV before full blown AIDS develops. Hence, staging of HIV introduces reality into the model. Accordingly, we study a population divided into the following classes: Susceptible individuals X, infected individuals in the primary (high viral load stage) HIV stage Y, infected individuals in the incubation stage of HIV I_1, the pre-AIDS (a period of high viral load or the pre AIDS stage) stage of HIV I_2, and treated individuals with full blown AIDS A.

We shall consider two scenarios namely (i) the case when treated AIDS individuals remain in the AIDS stage. This is true in the case where individuals reduce their viral load but their $CD4$ count is still significantly lower than that of the individuals in classes I_1 and I_2. (ii) In the second scenario, treated AIDS individuals are assumed to achieve a very low viral load and a significantly high $CD4$ count and can therefore be considered to have made a transition to the incubation HIV stage. In both scenarios, we ignore disease related death in order to allow us to understand the disease dynamics. The error of this assumption is investigated numerically.

New susceptible individuals enter the sexually active population at a rate bN. Susceptible individuals become HIV-infected at rate λX. The force of infection given by

$$\lambda = \frac{c_1\beta_1 Y + c_2\beta_2 I_1 + c_3\beta_3 I_2 + c_4\beta_4 A}{N}, \tag{4.1.1}$$

where β_1 denotes the per partnership transmission probability of individuals in the Y class, β_2 denotes the per partnership transmission probability of individuals in the I_1 class, β_3 denotes the per partnership transmission probability of individuals

individuals in the I_2 class, β_4 denotes the per partnership transmission probability of individuals in the A class and c_i where $i = 1, 2, 3, 4$ is the average number of new sexual partners acquired per unit time. Infected individuals in the primary stage progress to the incubation stage at the rate σ. Infected individuals in the incubation stage progress to the pre-AIDS stage at the rate ν_1. Infected individuals in the pre-AIDS stage progress to full blown AIDS at the rate θ. The model is then described by a system of ordinary differential equations

Model 1

$$\begin{aligned} \dot{X} &= bN - \lambda X - \mu X, \\ \dot{Y} &= \lambda X - (\mu + \sigma)Y, \\ \dot{I}_1 &= \sigma Y - (\mu + \nu_1)I_1, \\ \dot{I}_2 &= \nu_1 I_1 - (\mu + \theta)I_2, \\ \dot{A} &= \theta I_2 - \hat{\mu} A, \end{aligned} \tag{4.1.2}$$

where we shall assume $\hat{\mu} \approx \mu$ and

$$N = X + Y + I_1 + I_2 + A.$$

Adding equations of system (4.1.2), we obtain $\dot{N} = (b - \mu)N$. We shall assume that $b = \mu$, so that the model becomes a constant population model.

Define local variables

$$y_1 = \frac{X}{N}, \quad y_2 = \frac{Y}{N}, \quad y_3 = \frac{I_1}{N}, \quad y_4 = \frac{I_2}{N}, \quad y_5 = \frac{A}{N},$$

then system (4.1.2) can be written as

$$\begin{aligned} \dot{y}_1 &= b - by_1 - \bar{\lambda} y_1, \\ \dot{y}_2 &= \bar{\lambda} y_1 - (b + \sigma)y_2, \\ \dot{y}_3 &= \sigma y_2 - (b + \nu_1)y_3, \\ \dot{y}_4 &= \nu_1 y_2 - (b + \theta)y_4, \\ \dot{y}_5 &= \theta y_4 - by_5. \end{aligned} \tag{4.1.3}$$

where

$$y_1 + y_2 + y_3 + y_4 + y_5 = 1 \quad \text{and} \quad \bar{\lambda} = c_1\beta_1 y_2 + c_2\beta_2 y_3 + c_3\beta_3 y_4 + c_4\beta_4 y_5.$$

4.1.2 Steady state solutions

We solve the system

$$b - by_1^* - \bar{\lambda}^* y_1^* = 0, \tag{4.1.4}$$

$$\bar{\lambda}^* y_1^* - (b+\sigma)y_2^* = 0, \tag{4.1.5}$$
$$\sigma y_2^* - (b+\nu_1)y_3^*, \tag{4.1.6}$$
$$\nu_1 y_3^* - (b+\theta)y_4^* = 0, \tag{4.1.7}$$
$$\theta y_4^* - b y_5^* = 0. \tag{4.1.8}$$

Equations (4.1.4) to (4.1.8) yield

$$\begin{aligned}
y_1^* &= \frac{1}{R_1}, \\
y_2^* &= \left(\frac{\mu}{\mu+\sigma}\right)\left(\frac{R_1-1}{R_1}\right), \\
y_3^* &= \left(\frac{\mu}{\mu+\sigma}\right)\left(\frac{\sigma}{\mu+\theta}\right)\left(\frac{R_1-1}{R_1}\right), \\
y_4^* &= \left(\frac{\mu}{\mu+\theta}\right)\left(\frac{\sigma}{\mu+\sigma}\right)\left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{R_1-1}{R_1}\right), \\
y_5^* &= \left(\frac{\theta}{\mu+\theta}\right)\left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\mu}{\mu+\sigma}\right)\left(\frac{\sigma}{\mu+\sigma}\right)\left(\frac{R_1-1}{R_1}\right),
\end{aligned}$$

where

$$R_1 = \frac{\mu}{\mu+\sigma}R_{op} + \frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot},$$

where

$$R_{op} = \frac{c_1\beta_1}{\mu}, \quad R_{om}\frac{c_2\beta_2}{\mu+\nu_1}, \quad R_{oa}\frac{c_3\beta_3}{\mu+\theta}, \quad R_{ot}\frac{c_4\beta_4}{\mu}.$$

Theorem 4.1.1 *The endemic equilibrium point exits for* $R_1 > 1$.

In the model above, we assumed that treated HIV individuals remained in the AIDS class, which dynamically is equivalent to a no treatment model. In the next model, we consider a scenario in which the viral load of treated AIDS individuals reduces significantly and their $CD4$ count improves to a level of individuals in the intermediate stage. Such individuals may be considered to have made a transition to the incubation stage. The model may now be described by the following system:

Model 2

$$\begin{aligned}
\dot{X} &= bN - \lambda X - \mu X, \\
\dot{Y} &= \lambda X - (\mu+\sigma)Y, \\
\dot{I}_1 &= \sigma Y - (\mu+\nu_1)I_1 + \nu_2 A, \\
\dot{I}_2 &= \nu_1 I_1 - (\mu+\theta)I_2, \\
\dot{A} &= \theta I_2 - (\mu+\nu_2)A,
\end{aligned} \tag{4.1.9}$$

where

$$\lambda = \frac{c_1\beta_1 Y + c_2\beta_2 I_1 + c_3\beta_3 I_2 + c_4\beta_4 A}{N},$$

and

$$N = X + Y + I_1 + I_2 + A.$$

Define dimensionless variables

$$x = \frac{X}{N}, \quad y = \frac{Y}{N}, \quad i = \frac{I_1}{N}, \quad a_1 = \frac{I_2}{N}, \quad a_2 = \frac{A}{N},$$

the system becomes

$$\begin{aligned} \dot{x} &= b - \hat{\lambda}x - \mu x, \\ \dot{y} &= \hat{\lambda}x - (\mu + \sigma)y, \\ \dot{i} &= \sigma y - (\mu + \nu_1)i + \nu_2 a_2, \\ \dot{a}_1 &= \nu_1 i - (\mu + \theta)a_1, \\ \dot{a}_2 &= \theta a_1 - (\mu + \nu_2)a_2, \end{aligned} \tag{4.1.10}$$

where

$$\lambda = c_1\beta_1 y + c_2\beta_2 i + c_3\beta_3 a_1 + c_4\beta_4 a_2$$

and

$$x + y + i + a_1 + a_2 = 1.$$

The disease free equilibrium is given by

$$(x^*, y^*, i^*, a_1^*, a_2^*) = (1, 0, 0, 0, 0)$$

and the endemic equilibrium is given by $(x^*, y^*, i^*, a_1^*, a_2^*)$ where the components are given by

$$x^* = \frac{1}{R_2},$$

$$y^* = \left(\frac{\mu}{R_2}\right)(R_2 - 1),$$

$$i^* = \frac{\sigma\mu\,(\mu + \nu_2)\,(\mu + \theta)}{((\mu + \nu_1)\,(\mu + \nu_2)\,(\mu + \theta) - \nu_1\nu_2\theta)}\,(R_2 - 1), \tag{4.1.11}$$

$$a_1^* = \frac{\sigma\nu_1\mu\,(\mu + \nu_2)}{((\mu + \nu_1)\,(\mu + \nu_2)\,(\mu + \theta) - \nu_1\nu_2\theta)}\,(R_2 - 1), \tag{4.1.12}$$

$$a_2^* = \frac{\sigma\nu_1\mu\theta}{((\mu + \nu_1)\,(\mu + \nu_2)\,(\mu + \theta) - \nu_1\nu_2\theta)}\,(R_2 - 1), \tag{4.1.13}$$

where

$$\begin{aligned} R_2 &= \frac{\mu}{\mu+\sigma}R_{op} + \left(\frac{\sigma}{\mu+\sigma}\right)R_{om} + \left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\sigma}{\mu+\sigma}\right)R_{oa} \\ &+ \left(\tfrac{\theta}{\mu+\theta}\right)\left(\tfrac{\nu_1}{\mu+\nu_1}\right)\left(\tfrac{\sigma}{\mu+\sigma}\right)R_{ot}\left(1-\left(\tfrac{\nu_1}{\mu+\nu_1}\right)\left(\tfrac{\nu_2}{\mu+\nu_2}\right)\left(\tfrac{\theta}{\mu+\theta}\right)\right)^{-1}. \end{aligned}$$

Theorem 4.1.2 *The endemic equilibrium point exists for $R_2 > 1$.*

4.1.3 The reproduction numbers R_1 and R_2.

In this section, we compare the reproduction numbers from our two models. By expanding

$$(1-\epsilon)^{-1} = 1 + \epsilon + O(\epsilon)^2,$$

where

$$\epsilon = \left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\nu_2}{\mu+\nu_2}\right)\left(\frac{\theta}{\mu+\theta}\right),$$

we can rewrite the reproduction number R_2 as follows:

$$\begin{aligned} R_2 &= \frac{\mu}{\mu+\sigma}R_{op} + \left\{\left(\frac{\sigma}{\mu+\sigma}\right)R_{om} + \left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\sigma}{\mu+\sigma}\right)R_{oa} \right. \\ &+ \left.\left(\frac{\theta}{\mu+\theta}\right)\left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\sigma}{\mu+\sigma}\right)R_{ot}\right\}(1-\epsilon)^{-1}, \\ &= \frac{\mu}{\mu+\sigma}R_{op} + \frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot} \\ &+ \left[\frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot}\right]\epsilon + O(\epsilon^2) \\ &= R_1 + \left[\frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot}\right]\epsilon + O(\epsilon^2), \\ &> R_1. \end{aligned}$$

In the two models considered above, we have considered the effect of decreased infectivity and increased duration of infectiousness. We have demonstrated through a comparison of the reproduction numbers R_1 and R_2 that the effect of decreased infectivity and increased duration of infectiousness may be to increase the pool of transmitters of infection. This confirms the result by Baggaley R. F et al. (2005), who also concluded that ARV administration may result in increase in life expectancy of individuals over time and over this time this may cause an increase in a pool of transmitters of the disease. Our result has been obtained in the absence of education

on prevention. The situation may of course improve with effective education on prevention.

Exercise

Use the Routh-Hurwitz conditions to study the stability of the two models in this chapter.
Hint: For the coefficients of a polynomial equation

$$\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} \cdot \cdots \cdot a_{n-1}\lambda + a_n = 0,$$

the conditions for $n = 4$ are

$$a_4 > 0, \;\; a_2 > 0, \;\; a_1 > 0, \;\; a_3(a_1a_2 - a_4) > a_1^2 a_4.$$

4.1.4 Varying population model

In the previous sections, we analyzed constant population models in order to gain understanding of the dynamics of the disease. Exclusion of disease related death in the case of AIDS is a very unreasonable assumption but it allows us to investigate the worst scenario as the accumulation of AIDS individuals is at its maximum. In this chapter, we consider the effect of deaths due to HIV. Let δ be the death rate due to AIDS. Then, the system (4.1.10) becomes

$$\begin{aligned} \dot{X} &= bN - \lambda X - \mu X, \\ \dot{Y} &= \lambda X - (\mu + \sigma)Y, \\ \dot{I}_1 &= \sigma Y - (\mu + \nu_1)I_1 + \nu_2 A, \\ \dot{I}_2 &= \nu_1 I_1 - (\mu + \theta)I_2, \\ \dot{A} &= \theta I_2 - (\mu + \nu_2 + \delta)A, \end{aligned} \tag{4.1.14}$$

where

$$\lambda = \frac{c_1\beta_1 Y + c_2\beta_2 I_1 + c_3\beta_3 I_2 + c_4\beta_4 A}{N}$$

and

$$N = X + Y + I_1 + I_2 + A.$$

Adding the equations in (4.1.14) we obtain

$$\dot{N} = (b - \mu)N - \delta A.$$

It is not easy to find the endemic equilibrium point as in the previous sections. However, to understand the effect of disease related deaths, we only need to find the reproduction number from which the effect of disease related deaths can be inferred.

The reproduction number for this model can be found using the disease free equilibrium point. This is given by

$$\begin{aligned}
R_3 &= \frac{\mu}{\mu+\sigma}R_{op} + \left\{\left(\frac{\sigma}{\mu+\sigma}\right)R_{om} + \left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\sigma}{\mu+\sigma}\right)R_{oa}\right. \\
&+ \left.\left(\frac{\theta}{\mu+\theta}\right)\left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\sigma}{\mu+\sigma}\right)R_{ot}\right\}(1-\hat{\epsilon})^{-1} \\
&= \frac{\mu}{\mu+\sigma}R_{op} + \frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot} \\
&+ \left[\frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot}\right]\hat{\epsilon} + O(\hat{\epsilon}^2) \\
&= R_1 + \left[\frac{\sigma}{\mu+\sigma}R_{om} + \frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{oa} + \frac{\theta}{\mu+\theta}\frac{\nu_1}{\mu+\nu_1}\frac{\sigma}{\mu+\sigma}R_{ot}\right]\epsilon + O(\hat{\epsilon}^2) \\
&< R_2.
\end{aligned}$$

where

$$\hat{\epsilon} = \left(\frac{\nu_1}{\mu+\nu_1}\right)\left(\frac{\nu_2}{\mu+\nu_2+\delta}\right)\left(\frac{\theta}{\mu+\theta}\right) < \epsilon.$$

Clearly, if the total population is decreasing, that is, when $b \leq \mu$, then the effect of disease related deaths is to lower the reproduction number. We investigate numerically what happens when the population is increasing.

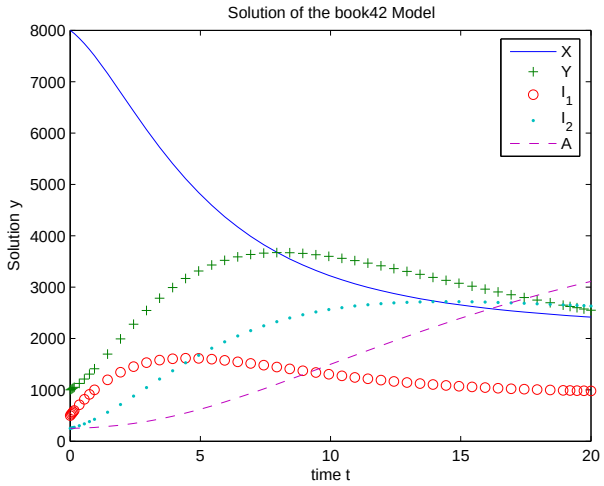

Figure 4.1: Graphs showing sub-population levels for a decreasing population for the following parameter values: $b = \mu = 0.02,\ \beta_1 = 0.001,\ \beta_2 = 0.5,\ \beta_3 = 0.01,\ \beta_4 = 0.01,\ \nu_1 = 0.03,\ \nu_2 = 0.02,\ c_1 = 1,\ c_2 = 2,\ c_3 = 1.25,\ c_4 = 1.25,\ \theta = 0.1,\ \sigma = 0.1$

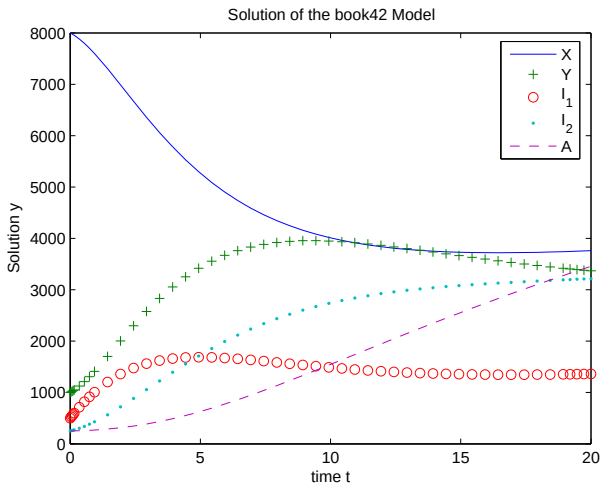

Figure 4.2: Graphs showing sub-population levels for an increasing population for the following parameter values: $b = 0.03,\ \mu = 0.02,\ \beta_1 = 0.001,\ \beta_2 = 0.5,\ \beta_3 = 0.01,\ \beta_4 = 0.01,\ \nu_1 = 0.03,\ \nu_2 = 0.02,\ \nu_3 = 0.005,\ c_1 = 1,\ c_2 = 2,\ c_3 = 1.25,\ c_4 = 1.25,\ \theta = 0.1,\ \sigma = 0.1$

When $b \leq \mu$, the population size of susceptible individuals can decrease to below the population size of AIDS individuals. However, when $b > \mu$, the population size of susceptible individuals remains greater, in the short term, even though there is an accumulation of AIDS individuals in the total population.

4.2 Spread of diseases for interlinked discrete geographic locations

There are many factors that affect the spread of infectious diseases. Some of these are

1. Cultural beliefs
2. Living styles
3. Sexual practices
4. Climatic and Environmental factors.

For some infectious diseases such as (i) Foot and Mouth diseases (in Southern Africa) (ii) SARS (in South East Asia/Western Countries), e.t.c, travel and movement of

animals are important factors that must be included in eradication strategies. For Foot and Mouth and SARS, quarantine is a very important option as an eradication strategy. For HIV/AIDS, cultural beliefs and sexual practices are very important factors in disease propagation. In the case of HIV, travel is also important, but because the incubation period is very long, eradication strategies that work for SARS might not be appropriate. Infectious diseases such as foot and mouth disease and SARS are spread over a very short time scale. Diseases such HIV/AIDS, TB are spread over a long period of time scale. Information on time scales help us to know which effects to include in our model. Consider the spread of SARS for two neighbouring distinct settlements with road/train travel between them. While on the bus/train some of the susceptibles on the journey (αS_2) may be infected by infectives (I_2) at the rate $\gamma\alpha$ to produce

$$\frac{\gamma\alpha S_2 I_2}{S_2 + I_2}$$

infectives for settlement 1. Similarly, for those travelling to settlement 2, some of the susceptibles (αS_1) may be infected by infectives I_1 at the rate $\alpha\gamma$ to produce

$$\frac{\gamma\alpha S_1 I_1}{S_1 + I_1}$$

infectives for settlement 2. Because of the time scales involved here, we can ignore cross infection i.e.

$$\frac{\gamma\alpha S_i I_j}{S_i + I_j} \text{ where } i \neq j.$$

The model in this case can be written as

Settlement 1

$$\begin{aligned} \dot{S}_1 &= a - \frac{\beta S_1 I_1}{S_1 + I_1} - bS_1 + dI_1 - \alpha S_1 + \alpha S_2 - \frac{\alpha\gamma S_2 I_2}{S_2 + I_2}, \\ \dot{I}_1 &= \frac{\beta S_1 I_1}{S_1 + I_1} - (c + d + \alpha)I_1 + \alpha I_2 + \frac{\alpha\gamma S_2 I_2}{S_2 + I_2}. \end{aligned} \tag{4.2.15}$$

Settlement 2

$$\begin{aligned} \dot{S}_2 &= a - \frac{\beta S_2 I_2}{S_2 + I_2} - bS_2 + dI_2 - \alpha S_2 + \alpha S_1 - \frac{\alpha\gamma S_1 I_1}{S_1 + I_1}, \\ \dot{I}_1 &= \frac{\beta S_2 I_2}{S_2 + I_2} - (c + d + \alpha)I_2 + \alpha I_1 + \frac{\alpha\gamma S_1 I_1}{S_1 + I_1}. \end{aligned} \tag{4.2.16}$$

For HIV/AIDS the time scale for infection of susceptibles is much longer. Indeed most likely nobody will be infected during travel. Now we cannot ignore the terms

of the type

$$\frac{S_i I_j}{S_i + I_j} \text{ where } i \neq j.$$

Now, if we want to reduce the number of terms, we can take into account the quality of education in the two settlements, cultural beliefs e.t.c.

Consider the model (4.2.15-4.2.16):

We can study several sub-cases to understand the broader picture.

Case 1: Neglect movement of individuals i.e. $\alpha = 0$.

Then, the two settlements are not communicating, each one is an absorbing state. This gives the Brauer-Castillo-Chavez model in each settlement given by

$$\begin{aligned} \dot{S} &= a - \frac{\beta SI}{S+I} - bS + dI, \\ \dot{I} &= \frac{\beta SI}{S+I} - (c+d)I. \end{aligned} \tag{4.2.17}$$

Here, there is one infective class

$$\mathcal{F} = \frac{\beta SI}{S+I}, \quad \mathcal{V} = (c+d)I. \tag{4.2.18}$$

Note that the DFE is given by $\left(\frac{a}{b}, 0\right)$ and

$$F = \frac{\partial \mathcal{F}}{\partial I} = \beta, \quad V = \frac{\partial \mathcal{V}}{\partial I} = c + d, \quad FV^{-1} = \Re_0 = \frac{\beta}{c+d}.$$

The endemic equilibrium point is given by

$$(S^*, I^*) = \left(\frac{a}{b + c(\Re_0 - 1)}, \frac{a(\Re_0 - 1)}{b + c(\Re_0 - 1)}. \right) \tag{4.2.19}$$

The disease-free equilibrium exists and is globally asymptotically stable for $\Re_0 < 1$. The endemic equilibrium point S^*, I^* exists for $\Re_0 > 1$ and is globally asymptotically stable where it exists.

Case 2: Only susceptible individuals travel:

In this case, infected individuals are prohibited from travelling. The model becomes

$$\begin{aligned}
\dot{S}_1 &= a - \frac{\beta S_1 I_1}{S_1 + I_1} - bS_1 + dI_1 - \alpha S_1 + \alpha S_2, \\
\dot{I}_1 &= \frac{\beta S_1 I_1}{S_1 + I_1} - (c+d)I_1, \\
\dot{S}_2 &= a - \frac{\beta S_2 I_2}{S_2 + I_2} - bS_2 + dI_2 - \alpha S_2 + \alpha S_1, \\
\dot{I}_2 &= \frac{\beta S_2 I_2}{S_2 + I_2} - (c+d)I_2.
\end{aligned} \tag{4.2.20}$$

The disease-free equilibrium in both settlements is given by

$$(S_1^*, I_1^*, S_2^*, I_2^*) = \left(\frac{a}{b}, 0, \frac{a}{b}, 0\right).$$

The disease-free in one settlement but endemic in the other settlement is either

$$(S_1^*, I_1^*, S_2^*, I_2^*) = \left(\frac{a}{b}, 0, \frac{a}{b}, \frac{bd}{a(\beta + d)}\right),$$

or

$$(S_1^*, I_1^*, S_2^*, I_2^*) = \left(\frac{a}{b}, \frac{a\beta}{b+d}, \frac{a}{b}, 0\right).$$

The model reproduction number $\Re_0$:

In this case $m = 2$

$$\mathcal{F} = \begin{pmatrix} \dfrac{\beta S_1 I_1}{S_1 + I_1} \\ \dfrac{\beta S_2 I_2}{S_2 + I_2} \end{pmatrix}, \quad \mathcal{V} = \begin{pmatrix} (c+d)I_1 \\ (c+d)I_2 \end{pmatrix}$$

$$F = \begin{pmatrix} \beta & 0 \\ 0 & \beta \end{pmatrix} \text{ and } V = \begin{pmatrix} c+d & 0 \\ 0 & c+d \end{pmatrix},$$

so that

$$FV^{-1} = \begin{pmatrix} \frac{\beta}{c+d} & 0 \\ 0 & \frac{\beta}{c+d} \end{pmatrix} \text{ and } \Re_0 = \frac{\beta}{c+d}.$$

The model behaves like a disease-free model. Clearly we can see that quarantine is very effective.

Exercises

1. Investigate the stability of the model (4.2.15) - (4.2.16) when there is free movement.

2. Consider a model described by a system of ordinary differential equations

$$\begin{aligned}
\dot{X}_1 &= \pi - BX_1 - \mu X_1, \\
\dot{X}_2 &= BX_1 - (\rho + \mu)X_2, \\
\dot{X}_3 &= \rho X_2 - (\sigma + \mu)X_3, \\
\dot{X}_4 &= \sigma X_3 - \mu X_4
\end{aligned}$$

   where $B = \frac{\beta X_1 + \gamma X_3}{N}$, π is constant recruitment for the susceptible population X_1, β and γ are transmission probabilities for normal infectives X_2 and carriers X_3 respectively, μ is the natural death rate, ρ is the rate at which normal infectives become carriers and σ is the rate at which carriers are removed.

   (a) Find the equilibrium points.

   (b) Determine the model reproduction number R.

   (c) Investigate the stability of the equilibrium points.

3. An HIV/AIDS model with carriers in the presence of random screening is given by

$$\begin{aligned}
\dot{X}_1 &= \pi - BX_1 - \mu X_1, \\
\dot{X}_2 &= BX_1 - (\rho_1 + \rho_2 + \mu)X_2, \\
\dot{X}_3 &= \rho_1 X_2 - (\sigma_1 + \mu + \epsilon)X_3, \\
\dot{X}_4 &= \epsilon X_3 - (\sigma_2 + \mu)X_4 \\
\dot{X}_5 &= \rho_2 X_2 + \sigma_1 X_3 + \sigma_2 X_4 - \mu X_5
\end{aligned}$$

   where $B = \dfrac{\beta X_2 + \gamma X_3}{N}$, $N = X_1 + X_2 + X_3 + X_4 + X_5$, and the parameters $\beta,\ \gamma,\ \rho_1,\ \rho_2,\ \gamma_1,\ \gamma_2,\ \mu,\ \epsilon$ are positive constants.

   (a) Define the parameters in the model.

   (b) Find the equilibrium points.

   (c) Determine the model reproduction number R.

   (d) Investigate the stability of the equilibrium points.

Chapter 5

Other Mathematical Modelling Problems

5.1 Modelling HIV-TB co-infection

The estimated incidence of Tuberculosis (TB) is growing worldwide. The HIV pandemic has increased the TB case load by five or more times in Sub-Saharan Africa. TB is an example of a disease with an exposed non-infectious class. Infected individuals are called active TB cases. Worldwide more than 2 billion individuals are known to harbor the TB bacteria. For this reason, it is important to develop the TB models with the hope of providing insight into the dynamics of the disease.

5.1.1 The model description

We assume that individuals enter the susceptible class (S) at the rate bN and leave all classes at the rate μ. Susceptible individuals are infected at a per capita rate λ. This force of infection depends on the probability of infection β. Once infected, individuals are not immediately infectious, they enter the exposed class E. A fraction of individuals develop noninfectious sputum-smear-negative $SS-$ TB and join the class L. The rest develop infectious sputum-smear-positive $SS+$ and join the class I. The parameters in the $SELIR$ disease transmission model have the following meaning.

1. an average infective individual produces β new infections per unit of time when all contacts are with susceptibles but otherwise this rate is reduced by the ratio S/N, where $N = S + E + L + I$.

2. individuals in the exposed class E progress to the noninfectious sputum-smear-negative $SS-$ class at the per capita rate $(1 - \alpha)\kappa$.

3. individuals in the exposed class E progress to the sputum-smear-positive $SS+$ class at the per capita rate $\alpha\kappa$.

4. the removal rates from the L and I classes are γ_1 and γ_2 respectively.

The model equations are

$$\begin{aligned}
\dot{S} &= bN - \mu S - \beta S\frac{I}{N}, && (5.1.1)\\
\dot{E} &= \beta S\frac{I}{N} - (\kappa+\mu)E, && (5.1.2)\\
\dot{L} &= (1-\alpha)\kappa E - (\gamma_1+\mu)L, && (5.1.3)\\
\dot{I} &= \alpha\kappa E - (\gamma_2+\mu)I, && (5.1.4)\\
\dot{R} &= \gamma_1 L + \gamma_2 I - \mu R. && (5.1.5)
\end{aligned}$$

5.2 Modelling the role of chemo-prevention in malaria

5.2.1 Model formulation

The model consists of six ordinary differential equations which specify the rate of change of four categories of individuals in the human population and two categories of the vector population over time. The human population consists of a class susceptible individuals (S), a class of individuals under chemoprevention (V), a class infected individuals (I) and a class of individuals who recover with temporary immunity (R), while the vector population consists of a class of susceptible mosquitoes (S_v) and a class of infected mosquitoes (I_v). Suppose the human population N_H (where $N_H = S + V + I + R$) and the vector population N_v (where $N_v = S_v + I_v$) have constant mortality rates μ and ν respectively. The mortality rate of the vector population is a sum of the natural and induced (for example by the use of pesticides) mortality rates. A proportion ϵ of the population is under chemotherapy (i.e given malaria prevention drugs) while $(1-\epsilon)$ are not. Furthermore, therapy only reduces the probability of infection when exposed to pathogens, i.e it offers a degree of protection denoted ψ with $(1-\psi)$ measuring the protection failure of the therapy, so that $\psi = 0$ means the therapy is completely ineffective in preventing infection, while $\psi = 1$ means the therapy is very effective i.e no individual under therapy will be infected. We let β_1, β_2 and β_3 be the effective contacts between susceptible individuals and vectors, individuals under chemoprevention and vectors and susceptible vectors and infected individuals respectively. The effective contact rate between the human and vector populations may be defined as the average number of contacts per given time that will lead to the infection of one population if the other population is infectious. It is taken to be the product of the number of bites per vector per host per unit time, the

proportion of bites that lead to an infection and the ratio of the vector numbers to the host numbers. Even though the human population under chemoprevention can still be infected and become infections, it will be reasonable to assume that $\beta_1 > \beta_2$. The chemoprevention immunity wanes at a rate θ and thus the average time of prevention is $\frac{1}{\theta}$. We assume a recovery rate γ for infected individuals who loose immunity at a rate σ. The dynamics of the disease is modelled by the following system of differential equations. All parameters in the model are positive.

$$\begin{aligned}
\dot{S}(t) &= \mu(1-\epsilon)N_H - \mu S(t) - \beta_1 S(t)\frac{I_v(t)}{N_v} + \theta V(t) + \sigma R, \\
\dot{V}(t) &= \mu\epsilon N_H - (1-\psi)\beta_2 V(t)\frac{I_v(t)}{N_v} - (\mu+\theta)V(t), \\
\dot{I}(t) &= \beta_1 S(t)\frac{I_v(t)}{N_v} + (1-\psi)\beta_2 V(t)\frac{I_v(t)}{N_v} - (\gamma+\mu)I(t), \\
\dot{R}(t) &= \gamma I(t) - (\mu+\sigma)R(t), \\
\dot{S}_v(t) &= \nu N_v - \nu S_v - \beta_3 S_v(t)\frac{I(t)}{N_H}, \\
\dot{I}_v(t) &= \beta_3 S_v(t)\frac{I(t)}{N_H} - \nu I_v(t).
\end{aligned} \tag{5.2.6}$$

5.3 Modelling fisheries

5.3.1 Harvesting

The theory of harvesting is important in natural resource management and bioeconomics. Most species have a growth rate which more or less maintains a constant population equal to the carrying capacity of the environment K (this of course depend on the population). In this case the growth and death rates are nearly equal. The harvesting of species affects their mortality rates and if the harvesting is not too much the population will adjust to a new equilibrium $N^* < K$. It has been evident that there is need to develop ecologically acceptable strategies for harvesting any renewable resources such as fish, plants, animals etc. It is interesting to note that even if the excess harvest does not threaten extinction, it can cause damage to the resource in the long run. Massive fruit collection from the forest has an adverse effect on regeneration. The problem then is to determine a strategy which ensures steady harvest year after year without a progressive decline in the abundance of the resource. The aim of this section is to determine the acceptable harvesting strategies.

5.3.2 Maximum sustainable yield (MSY)

The problem here is how to maximize the sustainable yield (SY) by determining the population growth dynamics so as to obtain a harvesting rate which keeps the population at its maximum growth. We consider a logistic population growth model in which the mortality rate is enhanced by harvesting, by a term that is proportional to the existing population N. We consider a logistic growth model

$$F(N) = rN\left(1 - \frac{N}{K}\right), \tag{5.3.7}$$

where r is the intrinsic growth rate and K the carrying capacity of the environment. Considering the effort E of harvesting, we assume that the harvest is proportional to the stock level as well as the effort ie $h = qEN$ where q is the constant of proportionality called the catchability constant. The effort is measured in man days. If grass is cut with strokes of a sickle, the harvest depends on the number of strokes E on the grass density. If the effort is constant then the harvest as a function of the stock is a straight line passing through the origin. The greater the effort the steeper the slope. The intersection of the line or the growth curve gives the sustainable yield. The net growth rate after harvest is given by

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

At equilibrium ie $\frac{dN}{dt} = 0$ We have

$$N\left[r(1 - \frac{N}{K} - qE)\right] = 0$$

We thus have $N_1^* = 0$ and

$$N_2^* = (r - qE)\frac{k}{r} = k(1 - \frac{qE}{r}) \tag{5.3.8}$$

Note that $N_2^* > 0$ if $\frac{qE}{r} < 1$ i.e $qE < r$ and this ensures population growth in the presents of harvesting. On the other hand if $qE > r$ the only steady state that exists is N_1^* i.e if the harvesting effort is greater than r then the species die out.

Since $h = qEN$, from (5.3.8) we get

$$h = qEK\left(1 - \frac{qE}{r}\right).$$

The sustainable yield is a quadratic function of E and is maximized when $\frac{dh}{dE} = 0$ i.e $E^* = \frac{r}{2q}$. At this effort we will get the MSY given by

$$h^* = \frac{rK}{4}$$

5.3.3 Fisheries management

Most dams in Africa have put restrictions on fishing. They are now allowing seasonal fishing as opposed to continuous fishing to allowing for breeding. Fisheries can either be open access or sole fisheries.

Open access fisheries

Definition 5.3.1 *An open-access fishery is an unrestricted fishery in which fisherman fish at will.*

We give a model below for such a fishery;

$$\begin{aligned} \frac{dN}{dt} &= rN\left(1-\frac{N}{K}\right)-qEN, \\ \frac{dE}{dt} &= \kappa(pqN-c)E, \end{aligned}$$

where N is the stock level, E is the fishing effort level, r is the intrinsic growth of the stock, K is the carrying capacity of the stock, q is the catchability constant, p is the price of fish, c is the (opportunity) cost per unit effort and κ a constant of proportionality. We have looked at the first equation but the second equation states that the rate of change of the fishing effort is proportional to the profit where $pqEN$ is the revenue and cE the costs. Despite the economic interpretation of the model, it is still a Volterra model with fisherman as the predator.

Exercise

Carry out the stability analysis of the model and give logical interpretations.

Sole-owner fishery (Optimal Harvesting)

Definition 5.3.2 *A sole-owner fishery is one owned and regulated by an individual.*

We shall assume that the sole owner is a profit maximizer, the question here is; how is he expected to harvest his fish? One common approach is to use the 'present value' to make decisions for future gains. This is like considering an interest rate of 10% per year, on income of 100 units will be equivalent to 110 units the following year. In general if the interest is $100n\%$, then the present value of the income P_t will be $P_t(1+n)^{-t}$, t years from today and

$$P_t(1+n)^{-t} = P_t e^{-\delta t}$$

where $\delta = \ln(1+n)$. If the income flow over a period $(0,T)$ given by P_t, then the total total present value of this income flow is

$$\mathcal{P} = \int_0^T P_t e^{-\delta t} = \int_0^T e^{-\delta t}(pqN - c)Edt$$

This is the objective function to be maximized in the present value approach. The variable to cost is E. The maximization is subject to the condition

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - qEN = F(N) - qEN.$$

The owner wishes to control the fishing effort $E(t)$ so as to maximize the discounted net economic rent (profit) over a period T of ownership. The profit is discounted at a rate δ because a dollar today is worth more than a dollar tomorrow if only the owner can invest today's dollar. The maximum fishing effort is usually determined by the number of boats, the labor, and any purchase of new fishing equipment or reduced boat sizes. Any change in the fishing effort has an immediate effect on the state variable and stock level $N(t)$. This then is an *optimal control theory* problem.

Let us then begin by considering a sole-owner fishery with no cots and discounting.

Example 5.3.3 *Consider a problem to find*

$$\max_{0 \le E \le E_{max}} \quad \int_0^T pqE(t)N(t)dt$$

subject to

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - qEN = f(N) - qEN, \qquad (0) = K.$$

This is a typical optimal control problem which contains

1. the state variable $N(t)$.
2. a set of admissible controls $\mathcal{E}$.
3. the control variable $E(t) \in \mathcal{E}$.
4. the objective functional, payoff $J(N(t), E(t))$.

We need one more tool to tackle our example.

Pontryagin's Maximum Principle

We wish to find

$$\max_{E \in \mathcal{E}} \quad J(N(t), E(t))$$

where

$$J(N(t), E(t)) = \int_{t_0}^{t_1} F[N(t), E(t), t]dt + G[t_0, N(t_0), t_1, N(t_1)]$$

subject to

$$\frac{dN_i}{dt} = f_i(N(t), E(t), t)$$

for $i = 1, 2, \cdots n$ state variables with initial and terminal conditions $x_i(t_0) = x_{i0}$ and $x_i(t_1) = x_{i1}$ respectively. We will also assume that each of the control variables is piecewise continuous and the functions F, G and f_i are well behaved. If $E(t)$ is an optimal control and if $N(t)$ is the corresponding response then;

1. we can define adjoint variables $\lambda(t) = [\lambda_0, \lambda_1(t), \cdots, \lambda_n(t)]$ with λ_0 a constant and $\lambda(t) \neq 0$.

2. we can define a Hamiltonian:

$$H(N, E, \lambda, t) = \lambda_0 F + \sum_{i=1}^{n} \lambda_i(t) f_i(N, E, t)$$

and a maximized Hamiltonian is defined

$$M[N(t), \lambda(t), t] = \sup_{E \in \mathcal{E}} H[N(t), E(t), \lambda(t), t]$$

3. the control variable $E(t) \in \mathcal{E} H[N(t), E(t), \lambda(t), t]$.

Pontryagin's Maximum Principle states that:
If $E(t)$ is an optimal control and if $N(t)$ is the corresponding response, then:

1. there exists

$$\lambda(t) = [\lambda_0, \lambda_1(t), \cdots, \lambda_n(t)]$$

with

$$\lambda(t) \neq 0, \qquad t_0 \leq t \leq t_1$$

such that the canonical equations

$$\frac{dN_i}{dt} = \frac{\partial H}{\partial \lambda_i}, \tag{5.3.9}$$

$$\frac{d\lambda_i}{dt} = -\frac{\partial H}{\partial N_i}, \tag{5.3.10}$$

are satisfied for each $i = 1, 2, \cdots, n$.

2. $E(t)$ satisfies

$$H[N(t), E(t), \lambda(t), t] = M[N(t), \lambda(t), t]. \tag{5.3.11}$$

3. the transversality condition

$$\lambda_0 dG + \left[M(t_1)dt_1 - \sum_{i-1}^{n} \lambda_i(t_1)dx_{i1} \right] - \left[M(t_0)dt_0 - \sum_{i-1}^{n} \lambda_i(t_0)dx_{i0} \right] = 0$$

is satisfied.

Equations (5.3.9) and (5.3.10) form a system of ordinary differential equations for the state variables and the adjoint variables. Equation (5.3.11) additional conditions for the control variables. The transversality condition supplies the missing initial and terminal conditions.

We can now go back to the example (5.3.3). The initial condition suggests that the fishery is in its pristine condition at the beginning. The procedure is as follows:
We form the Hamiltonian

$$H = pqEN + \lambda[f(N) - qEN]$$

or

$$H = q(p - \lambda)EN + \lambda f(N)$$

The corresponding canonical equations are simply

$$\frac{dN}{dt} = G(N) - qEN \tag{5.3.12}$$

$$\frac{d\lambda}{dt} = -\frac{dH}{dN} = -q(p - \lambda)E - \lambda f'(N) \tag{5.3.13}$$

The Hamiltonian is linear in the control variable E. To maximize the Hamiltonian we must close.

$$E(t) = \begin{cases} E_{maximum} + \lambda(t) < p \\ 0 + \lambda(t) > p. \end{cases}$$

if $\lambda = p$ then $G^1(N) = 0$ we must then keep the stock at a level that maximizes the sustainable yield

$$N(t) = N^*_{MSY}$$

The control variable

$$E^*(t) = \frac{f(N^*_{MSY})}{qN^*_{MSY}} \tag{5.3.14}$$

We conclude that we must harvest at the maximum possible rate,leave the stock alone or apply singular control (5.3.14) depending on the magnitude of $\lambda(t)$.

The transversality condition is supposed to provide use with missing initial and terminal conditions. We will take $dt_0 = dt_1 = 0$ the initial and terminal times. We also

do not have the initial and terminal payoffs ie $df = 0$. The state variable is fixed at $t_0 = 0$ $(dN, = 0)$. The state variable is unconstrained at $t_1 = T$ so that dN_1 is arbitrary. This reduces the transversality condition to $\lambda(T) = 0$. This is actually the terminal value on the adjoint variable and not on the initial condition. We thus have a boundary value problem (BVP).

Example 5.3.4 *Find*

$$\max_{0 \leq E \leq E_{max}} \int_0^T e^{-\delta t}[pqN(t) - c]E(t)dt$$

subject to

$$\frac{dN}{dt} = f(N) - qEN, \qquad N(0) = K.$$

The Hamiltonian, which is linear in the control variable is given by

$$\begin{aligned} H &= e^{-\delta t}[pqN - c]E + \lambda[f(N) - qEN] \\ &= [e^{-\delta t}(pqN - c)E - \lambda qN]E + f(N). \end{aligned}$$

The coefficient of E,

$$\psi = e^{-\delta t}(pqN - c)E - \lambda qN$$

is a switching function, i.e it may change sign.

We are interested in the interval where the switching function is identically zero. On such intervals we have singular controls that dominate the problem. There will also be a rapid approach to singular state at the beginning of the problem and some profit taking at the end of the problem. Setting ψ to zero, we have

$$\lambda = e^{-\delta t}\left(p - \frac{c}{qN}\right).$$

Differentiating with respect to t gives

$$\frac{d\lambda}{dt} = -\delta e^{-\delta t}\left(p - \frac{c}{qN}\right) + e^{-\delta t}\frac{c}{qN^2}\frac{dN}{dt} \tag{5.3.15}$$

$$= -\delta e^{-\delta t}\left(p - \frac{c}{qN}\right) + e^{-\delta t}\frac{c}{qN^2}(f(N) - qEN). \tag{5.3.16}$$

For the canonical equation for the time derivative of λ is given by

$$\frac{d\lambda}{dt} = -\delta e^{-\delta t}pqE + \lambda qE - \lambda f'(N). \tag{5.3.17}$$

Equating (5.3.16) and (5.3.17) gives

$$f'(N) = \delta - \frac{cf(N)}{N(pqN - c)}. \tag{5.3.18}$$

Exercise Derive result (5.3.18).

Equation (5.3.18) is an implicit equation for the unknown N. So, any unknown N^*, which satisfies the above equation is a singular solution of our original control problem. We can rewrite the equation as

$$f'(N) = \delta - \frac{\frac{c}{qN^2}f(N)}{p - \frac{c}{qN^2}}. \tag{5.3.19}$$

If we multiply by the denominator on the right hand side of (5.3.19) and doing some nit of manipulation, we obtain

$$\left[(p - \frac{c}{qN})f'(N) + \frac{c}{qN^2}f(N)\right] = \delta\left(p - \frac{c}{qN}\right),$$

or simply

$$\frac{dS}{dN} = \delta\left(p - \frac{c}{qN}\right), \tag{5.3.20}$$

where $S = (p - \frac{c}{qN})f(N)$.

S can be taken as the sustainable rent (profit).

Definition 5.3.5 *The sustainable rent is the difference between the revenue and the costs for a given level of effort.*

Considering (5.3.20), the case $\delta = 0$, gives $\frac{dS}{dN} = 0$. This corresponds to choosing the stock level that maximizes the sustainable rent. We can find the stock level by considering

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

and at equilibrium we have

$$N^* = K\left(1 - q\frac{E^*}{r}\right)$$

The equilibrium stock is a function of the effort level. Note that

$$qE^*N^* = qKE^*\left(1 - \frac{qE^*}{r}\right).$$

The sustainable rent S can be written as

$$S = \left(\frac{pqN - c}{qN}\right) f(N)$$

but at equilibrium $N'(t) = 0$, giving $f(N) = qEN$, giving

$$S = pqE^*N^* - cE^*.$$

To maximize the rent we need to maximize the difference between revenue and the cost functions. We can do this by choosing the effort level so that the slope of the revenue curve is identical to the slope of the cost function. Costs lead to reduced fishing and greater amounts of environmental conservation.

The case where $\delta = \infty$, we require that

$$pqN^* = c$$

and the sustainable rent is zero. If there are costs, increases in discount rate need not lead to the extinction of the stock. The sole-owner fishery looks more and more like an open access fishery, all economic rent is squandered.

Exercises

1. Consider the model (5.1.1) - (5.1.5).

   (a) Show that the mean number of secondary infections (belonging to the exposed class) produced by one infective individual in a population of susceptibles is $Q_0 = \frac{\beta}{\gamma}$

   (b) Assuming that κ and μ are time-independent, show that R_0 is given by $Q_0 f$ where $f = \kappa/(\kappa + \mu)$. What is the epidemiological interpretation of $Q_0 f$?

   (c) Choose suitable values of b and set $\gamma = 1yr^{-1}$, $\beta = 10yr^{-1}$. Simulate the epidemic starting at $t = 0, S = 250888$ for constant values of f.

   (d) Find the equilibrium points and find conditions under which the model is stable.

   (e) Use Watmough's technique to find the model reproduction number and discuss the existence and stability of the endemic equilibrium point.

   (f) Suppose the suscetible individuals are vaccinated but the vaccine wanes with time, write down the modified model and repeat the analysis.

2. If we include treatment of infected individuals as well as treatment failure, the model equations are:

$$\begin{aligned}
\dot{S} &= bN - \mu S - \beta S\tfrac{I}{N}, \\
\dot{E} &= \beta S\tfrac{I}{N} - (\kappa + \mu)E + \sigma pI, \\
\dot{I} &= \alpha\kappa E - (\sigma + \mu)I, \\
\dot{T} &= \sigma(1-p)I - (\gamma + \mu)T, \\
\dot{R} &= \gamma T - \mu R,
\end{aligned}$$

where σ is the rate of treatment failure, $0 < p < 1$, T is the class of treated individuals, and γ is the rate of removal.

   (a) Find the equilibrium points and find conditions under which the model is stable.

   (b) Use Watmough's technique to find the model reproduction number and discuss the existence and stability of the endemic equilibrium point.

3. Consider model (5.2.6) and answer the following questions.

   (a) Introducing the following fractions

$$s = \frac{S(t)}{N_H},\ v = \frac{V(t)}{N_H},\ i = \frac{I(t)}{N_H},\ r = \frac{R(t)}{N_H},\ s_v = \frac{S_v(t)}{N_v} \text{ and } i_v = \frac{I_v(t)}{N_v}$$

   and using the relations $r = 1 - v - i - s$ and $s_v = 1 - i_v$ show that the system reduces to

$$\begin{aligned}
\dot{s} &= \pi - (\mu + \sigma)s - \beta_1 s i_v + (\theta - \sigma)v - \sigma i, && (5.3.21)\\
\dot{v} &= \mu\epsilon - (1-\psi)\beta_2 v i_v - (\mu + \theta)v, && (5.3.22)\\
\dot{i} &= \beta_1 s i_v + (1-\psi)\beta_2 v i_v - (\gamma + \mu)i, && (5.3.23)\\
\dot{i}_v &= \beta_3 i(1 - i_v) - \nu i_v. && (5.3.24)
\end{aligned}$$

   where $\pi = \mu(1-\epsilon) + \sigma$.

   (b) Determine the disease free equilibrium point of the system (5.3.21) - (5.3.24).

   (c) Show that reproductive number is given by

$$R = \sqrt{\frac{\beta_3(\beta_1(1-\phi) + (1-\psi)\beta_2\phi)}{\nu(\gamma + \mu)}}.$$

   (d) Show that this reproduction number can be written as

$$R = \sqrt{R_v \cdot R_h}$$

where $R_v = \frac{\beta_3}{\nu}$, and

$$R_h = (1-\phi)R_1 + \phi(1-\psi)R_2,$$

with $R_1 = \frac{\beta_1}{\mu+\gamma}$ and $R_2 = \frac{\beta_2}{\mu+\gamma}$.

(e) From the value of R, show that the critical chemoprevention coverage is given by

$$\epsilon_* = \frac{\mu+\theta}{\mu}\left(\frac{1-R_0}{(1-\psi)R_m - R_0}\right)$$

where $R_m = R_v R_2$.

(f) Show that the disease free equilibrium point is asymptotically stable for $R < 1$ and unstable for $R > 1$.

(g) Show that in the case where where $\psi = 1$, there is a unique stable endemic equilibrium given by,

$$E_1 = \left(\frac{1+(1-\phi)\eta R_v}{\eta R_v + R_0}, \phi, \frac{\eta(R_0-1)}{R_0+\eta R_v}, \frac{\eta(R_0-1)}{R_1+\eta R_0}\right).$$

(h) Show that if $0 < \psi < 1$, multiple endemic equilibria exist.